

SPATIAL ENVIRONMENTAL CORRELATES OF INTERTIDAL RECRUITMENT: A TEST USING BARNACLES IN NORTHERN CHILE

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Abstract. Nearshore circulation processes and local geomorphological patterns are thought to be important correlates of spatial variation in larval recruitment of benthic organisms. However, few studies have attempted to quantitatively separate their relative influences upon recruitment dynamics. Here we use 12 study sites spanning 250 km of the northern Chile upwelling ecosystem and the intertidal barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* to examine the extent to which spatial variation in larval recruitment is related to environmental variability and how these relationships depend on spatial autocorrelation. We find that upwelling intensity and wind velocity are negatively related to larval recruitment while surface slicks showed a positive correlation. However, the *pure* effect of each environmental variable was lower than its *combined* effects. Taking spatial autocorrelation into account, we find that the spatially structured variation of upwelling dynamics, distance to upwelling fronts, wind velocity, and slick occurrence explained most of the variation in barnacle recruitment. Spatial variation in recruitment rates of barnacles showed a characteristic length scale of 60–70 km, similar to the scale estimated for the spatially structured variables (upwelling, wind velocity, and surface slicks). We find that conditions for the occurrence of surface slicks (as surrogates of internal waves activity) seem to operate across several sites, suggesting a meso- instead local-scale influence over spatial variation in barnacle recruitment. Our results suggest that spatial variation in barnacle recruitment is modulated by the combined influence of several spatially structured nearshore processes operating at scales of 60–70 km and that spatial autocorrelation must be taken into account in the study of the recruitment–environment relationship. However, the influence of local and small-scale factors on recruitment dynamics of benthic invertebrates should be interpreted cautiously.

Key words: *benthic recruitment; geomorphology; Jehlius cirratus; nearshore circulation; Notochthamalus scabrosus; spatial autocorrelation.*

INTRODUCTION

Spatial variation in the availability of propagules is recognized as a leading ecological factor influencing population and community dynamics (Roughgarden et al. 1988, Bolker et al. 2003, Navarrete et al. 2005). Spatial scales at which propagules disperse across terrestrial and marine habitats have shown an astonishing diversity among species (Clark et al. 1999, Nathan and Muller-Landau 2000, Kinlan and Gaines 2003, Shanks et al. 2003), which are largely modulated by

differences in the way in which propagule characteristics, such as lifetime, size, shape, and behavior, interact with the physical forces operating during the dispersal phase (Bjørnstad et al. 1999, Nekola and White 1999, Shanks et al. 2003, Soininen et al. 2007). This form of physical–biological interaction is ubiquitous for marine organisms with complex life cycles, whose dispersal abilities must confront the spatiotemporal variability of coastal circulation processes in order to successfully settle in the benthic habitat (Roughgarden et al. 1988, Gaines and Bertness 1992, Cowen et al. 2006). Since variability in larval recruitment in coastal ecosystems may determine the regional persistence of adult populations and, by affecting species interactions, influence the metacommunity structure (Guichard et al. 2004, Navarrete et al. 2005), the understanding of the spatial scales at which physical processes are coupled with larval recruitment has crucial importance to implementing marine ecosystem management and conservation approaches (Botsford 2001).

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A recurrent theme of studies about physical–biological interactions in the coastal ocean is that upwelling dynamics have a pervasive and primary role over spatial variability in larval recruitment of benthic invertebrates (Roughgarden et al. 1988, Caley et al. 1996, Connolly and Roughgarden 1998, Botsford 2001). However, several studies have shown that larval recruitment is not only strongly correlated with coastal upwelling (Farrell et al. 1991, Connolly et al. 2001, Broitman et al. 2005, Lagos et al. 2005, Navarrete et al. 2005), but there is also evidence that a set of environmental and larval behavior mechanisms may explain how changes in the upwelling–recruitment relationship translate to variations in larval supply and in the way that these larvae, in turn, survive and successfully recruit to the adult population (Shanks 1995, Pineda 2000). Besides the evidence of behavioral responses some invertebrate larvae displayed in order to avoid cross-shore transport during coastal upwelling–downwelling dynamics (e.g., Poulin et al. 2002, Shanks and Brink 2005), of particular interest is the evidence related to interactions of geomorphology with nearshore circulation process (Gaines and Bertness 1992, Wing et al. 1998, Archambault and Bourget 1999, Mace and Morgan 2006, McQuaid and Phillips 2006, Palma et al. 2006), the role of internal waves (Shanks 1983, Shanks and Wright 1987), and the interaction of local heterogeneity with small-scale flows (Guichard and Bourget 1998). These environmental correlates of larval recruitment operate across a hierarchy of spatial and temporal scales from large-scale ocean circulation to small-scale flow in benthic habitats, thus are not alternative hypotheses in a strict sense, but can be thought to be responsible for some component, perhaps large or at least similar, of spatial variation in larval recruitment of benthic invertebrates.

At the largest scales, the complex interaction of atmospheric circulation with coastal geomorphology may modify nearshore circulation patterns in coastal upwelling ecosystems (Smith 1995). Several studies have shown that wind-driven ocean flow that is coherent over regional scales is modified by its interaction with local topographic features, generating an alongshore mosaic of physical transport conditions (Barth et al. 2000, Castilla et al. 2002, Largier 2003, Roughan et al. 2005). These spatially structured circulation patterns are topographically controlled and have been shown to influence the patterns of larval recruitment across a neighborhood of sites along a coastline (Connolly et al. 2001, Broitman et al. 2005, Lagos et al. 2005, Navarrete et al. 2005). For instance, studies performed across the Oregon–California upwelling ecosystem suggest that contrasting larval recruitment patterns for several intertidal invertebrates may result from the large-scale spatial variation in the intensity of cross-shore transport induced by coastal upwelling which, in turn, may determine differences in community structure and regulation between both regions (Connolly and Rough-

garden 1998, Connolly et al. 2001, Menge et al. 2004). Biogeographic (100s to 1000s of kilometers) variation in the strength of the benthic–pelagic coupling has also been observed in other east-boundary upwelling ecosystems such as the coasts of central Chile, South Africa, and New Zealand (Harris et al. 1998, Menge et al. 2004, Navarrete et al. 2005). At comparatively smaller spatial scales, abrupt changes in larval recruitment patterns have been reported between areas separated by major geomorphological features that determine sharp transitions between contrasting oceanographic regimes. Some examples include comparisons of open coastline sites with sites located on sheltered locations such as embayments or channels or between the windward and lee sides of headlands (Gaines and Bertness 1992, Wing et al. 1998, Archambault and Bourget 1999, Mace and Morgan 2006, McQuaid and Phillips 2006, Palma et al. 2006).

From local to regional scales (1–100s of kilometers), several studies have suggested that geomorphological factors may influence the recurrence of coastal fronts or the presence of nearshore retention zones that may modify patterns of aggregation and transport of benthic invertebrate larvae and, in turn, benthic recruitment (Ebert and Russell 1988, Ebert et al. 1994, Wing et al. 1995, 1998, Graham and Largier 1997, Archambault and Bourget 1999, Castilla et al. 2002, Palma et al. 2006). Very nearshore coastal circulation features can also generate spatial variation in larval recruitment. For instance, at scales between 1 and 10s of kilometers, localized internal wave activity (Pineda 1994), the convergence zones of internal waves as surface slicks, and Langmuir flow-driven surface foamlines and slicks have been reported as factors influencing the larval accumulation, transport, and recruitment of benthic species (Shanks 1983, Kingsford and Choat 1986, Shanks and Wright 1987, Wolanski and Hamner 1988, Kingsford 1990, Shanks 1995, McCulloch and Shanks 2003, Shanks et al. 2003). At scales of 1–1000 m, local topography can interact with flow, affecting settlement and recruitment of benthic species within local habitats (Pineda 1994, Guichard and Bourget 1998). Within this hierarchy of physical transport process, it is postulated that mesoscale coastal circulation (10–100s of kilometers) should overwhelmingly influence spatial variation in larval distribution and thus, in settlement and recruitment patterns (Connolly and Roughgarden 1998, Pineda 2000). Then, the influence of processes on the inner shelf region (i.e., 1–10 km from shore) would be disproportionately larger than circulation processes operating at the very nearshore (<1 km from shore; Pineda 2000, Botsford 2001; but see Poulin et al. 2002, Shanks and Brink 2003). Nonetheless, no previous studies have sought to determine simultaneously the relative influence of small, local, and regional scale environmental process on larval recruitment of benthic invertebrates.

The scales at which these environmental processes operate suggest that alongshore patchiness in larval recruitment may result from the combined influence of (1) small-scale factors inducing local differentiation across the benthic habitats and (2) the shared and simultaneous influence of environmental process operating at meso- or larger scales, which introduce correlation or similarities among localities. Spatial autocorrelation (i.e., nearby populations share more similarity than would be expected by chance; Legendre 1993) is present in upwelling dynamics and has important implications for the study of spatial variation in recruitment of benthic populations (Lagos et al. 2005, 2007). For instance, spatial variation in marine and terrestrial populations and community dynamics has been described as correlated over characteristic spatial scales and modulated by the underlying spatial structure of environmental forcing or community processes (e.g., Borcard et al. 1992, Legendre 1993, Belgrano et al. 1995a, b, Bjørnstad et al. 1999, Lichstein et al. 2002, van Resburg et al. 2002, Astorga et al. 2003). In the case of the benthic-ocean coupling, coastal upwelling has been described as a mesoscale process (Hoffman and Powell 1998, Lagos et al. 2005). Thus, one should expect an environmentally driven correlation in larval recruitment patterns among sites located at distances shorter than the characteristic spatial scale of the larval delivery process and a spatially correlated pattern of recruitment among sites. Recently, it has been found that along the coast of central Chile the mesoscale influence of upwelling dynamics (correlated over 30–40 km) modulates the spatial correlation in barnacle recruitment and other benthic invertebrates across a neighborhood of sites within a spatial extent of 30 km (Lagos et al. 2005, 2007; see also Aiken et al. 2007). Thus, sites located within this neighborhood do not represent independent samples of the spatial variation in recruitment. Not incorporating this spatial autocorrelation in the analysis the recruitment-upwelling relationship over space (i.e., regarding each site as independent replicates) violates the independence assumption of standard statistical procedures, yielding spurious cause-effect relationships assessments (Legendre 1993). For instance, in the Oregon-California upwelling ecosystem, the study of intertidal larval recruitment has been focused on its relationship with the latitudinal gradient in upwelling intensity (Connolly and Roughgarden 1998, Connolly et al. 2001). That latitudinal gradient represents an example of spatially structured environmental variation (Legendre 1993). However, the spatial structure of the latitudinal gradient in upwelling has not been included explicitly in the analyses and has been interpreted as the *pure* influence of upwelling forcing over benthic recruitment (e.g., Connolly and Roughgarden 1998, Connolly et al. 2002). Legendre (1993) introduced the analysis of environmental process operating simultaneously across several sites, such as coastal upwelling circulation. However, few large-scale studies aimed to examine the

recruitment-upwelling relationship over space (or with other spatially structured environmental correlates) have taken into account the confounding effects induced by the presence of spatial autocorrelation in the variables (see Lagos et al. 2005, 2007, Navarrete et al. 2005).

Understanding spatial variation in recruitment patterns and their scale-specific association with environmental forcing has major implications for the conservation and management of marine ecosystems and requires rigorous experimental design. In order to examine the spatially structured relation between recruitment and environmental forcing, we studied patterns of spatial variation in the larval recruitment of *Jehlius cirratus* and *Notochthamalus scabrosus*, the two dominant intertidal barnacle species on the northern Chile upwelling ecosystem (Camus and Lagos 1996) and distributed our study sites to encompass two contiguous sections of coastline of contrasting oceanographic and geomorphological settings: the Antofagasta Bay characterized as an “upwelling shadow” area (Castilla et al. 2002, see also Piñones et al. 2007) and the almost linear open coast influenced by coastal upwelling (Marín et al. 2001). Our main working hypothesis was that mesoscale (10–100 km) spatial variation in barnacle recruitment would be largely modulated by the spatially structured environmental factors operating at the mesoscale, and to a lesser extent by local- (1–10 km) and small-scale (within-site, 1–100 m) process. Taking into account spatial autocorrelation, we examined the relation between spatial variation in barnacle recruitment and a comprehensive subset of environmental correlates derived from the literature, including local topographic variables and inner shelf and very nearshore circulation features. In this way, we present the first attempt to disentangle the components of variation in the spatially structured relationship between the recruitment of benthic invertebrate species with environmental variability operating at several nested spatial scales.

METHODS

Study area

The coast of northern Chile (~21–24° S; Fig. 1) is characterized by an almost linear coastline where a narrow band of coastal upwelling generates sustained offshore transport across the region (Marín et al. 2001). The only interruption of the linear coastline configuration is the Mejillones Peninsula (~23.5° S), which presents large embayment areas on its lee and windward sides. Our 12 study sites were distributed along the coastline south of the Mejillones Peninsula, inside the south-facing Antofagasta Bay, and the coastline north of the peninsula (Fig. 1b). Antofagasta Bay is exposed to the prevalent northwestern (equatorward) winds and is bounded by upwelling centers at Point Coloso, to the south of Antofagasta Bay, and at Point Tetas on the Mejillones peninsula, to the west (north of CER; Fig. 1b). The geographic setting of the bay determines the retention of surface waters inside the bay, resulting in a

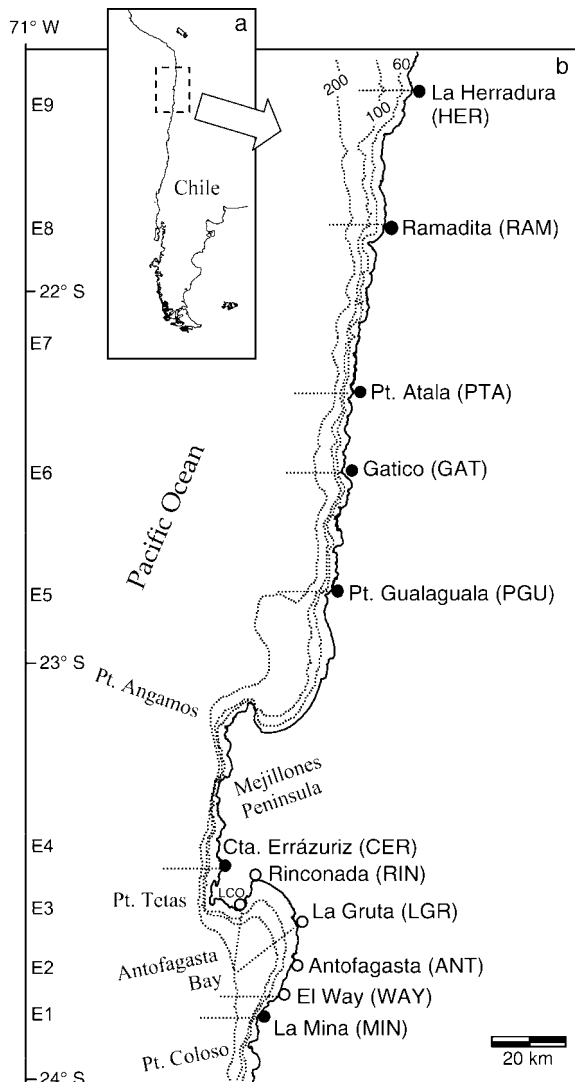


FIG. 1. (a) Study area along the coast of northern Chile upwelling ecosystem. (b) Location of sites along the open coast, the Mejillones Peninsula, and Antofagasta Bay. Solid circles indicate sites influenced by upwelling dynamics in the open coast; open circles correspond to sites located inside the Antofagasta Bay and not directly influenced by upwelling. The dotted lines in front of each site indicate the orientation of the bathymetric profile used to characterize the slope of the continental shelf and to assess the offshore distance of coastal fronts. E1 through E9 in front of each site on the left edge of the figure indicate the latitudes of the locations where we recorded the interpolated Bakun upwelling index.

“upwelling shadow” that is reflected as a persistent increase in the sea surface temperature inside the Antofagasta Bay as compared with the nearby recently upwelled waters (Castilla et al. 2002, Lagos et al. 2002, Piñones et al. 2007). The persistent upwelling observed along the open coast and the retention area inside the Antofagasta Bay represent contrasting mesoscale circulation regimes that may generate patchiness in the recruitment patterns of benthic species.

Barnacle recruitment

Study sites inside the Antofagasta Bay ($n = 5$) and on the open coast ($n = 7$) were monitored at biweekly (every other week) intervals (14.6 ± 2.2 days; mean \pm SD) from May 2000 to June 2001. We studied the barnacles *Jehlius cirratus* and *Notochthalmus scabrosus*, which are the dominant intertidal invertebrates in northern Chile (Camus and Lagos 1996). Larval recruitment rates were assessed using ten 10×10 cm Plexiglass settlement plates covered with an artificial substrate (Safety-Walk; 3M, St. Paul, Minnesota, USA) and anchored parallel to the inclination plane of the rocky substrate in order to follow local heterogeneity at scales of meters. Settlement plates were deployed along two 30–50 m long transects at the mid (~ 0.8 – 1.5 m above mean lower low water [MLLW]) and low (~ 0.3 – 0.5 above MLLW) intertidal zones of exposed rocky platforms at each site (Navarrete et al. 2002). Counts of all barnacle recruits in each plate were done under a dissection microscope. For periods of high recruitment, the count was estimated using a random subsample of 12 areas of 1 cm^2 . Regression analysis showed a significant adjustment between direct and estimated recruit counts (slope = 1.02 ± 0.03 SD; $n = 37$, $r^2 = 97.8$, $P < 0.0001$). The selected chthamalid barnacles recruit almost year-round in northern Chile with a increase during the austral spring–summer (Camus and Lagos 1996). The two species have planktotrophic larval development, with the naupliar stage lasting for 20 and 30 d for *J. cirratus* and *N. scabrosus*, respectively (Venegas et al. 2000). Thus, the larval dispersal of both species is expected to be influenced by several nearshore processes encompassing that larval duration. For each study site, recruitment rate of both species was averaged over time (July 2000–June 2001) and expressed as the mean number of individuals per day in 100 cm^2 . Recruitment rates of both species showed significant seasonal variation over the studied period (Lagos 2003). However, we found a systematic relationship between the local recruitment averaged over time and the s index (Lewontin 1966). The s index is commonly used to characterize temporal variation in abundance (see Steen et al. 1996) and was estimated as the standard deviation of log-transformed data of the biweekly estimates of local recruitment. Thus, averaged local variation in recruitment may be regarded as an embedded measure of temporal fluctuations in barnacle recruitment (see Fig. 2). This allowed us to reduce the dimensionality of the data set and make possible the use of the raw-data approach (Legendre 1993), where in order to take into account spatial autocorrelation, the spatial structure of the local mean recruitment takes the form of a polynomial of the x and y geographic coordinates of study sites (*Methods: Statistical analysis*).

Environmental variables

At each study site, we systematically recorded a comprehensive set of nine environmental correlates reported to drive patterns of larval transport, settlement,

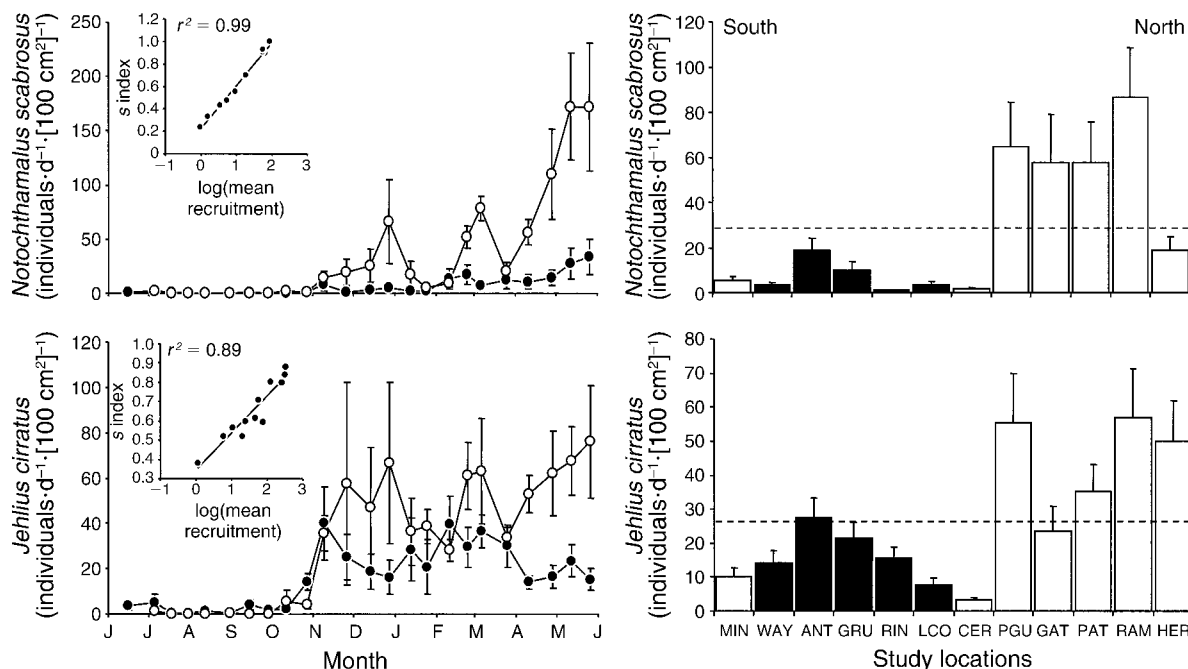


FIG. 2. Temporal and spatial variation in barnacle recruitment recorded inside the Antofagasta Bay (solid circles and bars) and in the open coast (open circles and bars). Insets show the coefficient of determination for the relationship between local recruitment averaged over time (July 2000–June 2001) with s index (standard deviation of log-transformed data of the biweekly estimates of mean recruitment). The horizontal dashed line indicates the regional mean in barnacle recruitment. Study locations are identified in Fig. 1.

and recruitment (see Table 1). The first three correlates are regarded as mesoscale processes and were recorded as follows: (1) Sea surface temperature (SST). In each of the 12 study sites we recorded SST at 30-minute intervals from September 2000 to April 2001 using submersible temperature data loggers (Tidbit StowAway; ONSET, Pocasset, Massachusetts, USA) anchored at 1.5 m below sea level (see also Piñones et al. 2007). We used the daily mean to characterize SST adjacent to our study sites. (2) Coastal upwelling (UPW). We obtained the interpolated monthly Bakun upwelling index from the Pacific Fisheries Environmental Laboratories (data available online)⁶ for nine stations along 72° W (Fig. 1b) at the latitude of each site to estimate the magnitude of offshore transport (positive values, $\text{m}^3 \cdot \text{s}^{-1} \cdot 100 \text{ m}^{-1}$ of coastline). For sites located inside Antofagasta Bay, the upwelling index was linearly interpolated from data of stations E2, E3, and E4 (see Fig. 1b) and thus represented offshore conditions more than the localized effect of coastal upwelling. (3) For the period encompassing July 2000–July 2001, we used 155 daily satellite images of 1.1 km of nominal resolution for the study area from the Advanced Very-High Resolution Radiometer (AVHRR) to characterize the occurrence and offshore position of coastal fronts at each study site. Over each satellite image, frontal zones (operationally

defined as thermal differences $>1^\circ\text{C}$ among adjacent pixels) were localized by calculating the slope (as a percentage) among the four adjacent pixels (Rookcase model). The resulting image was reclassified (1 = presence and 0 = absence of front), with slopes between 60% and 80% interpreted as coastal fronts (Lagos et al. 2002). Reclassified images were additively overlapped, yielding the absolute frequency of fronts at each pixel of the study region. To quantify the influence of frontal offshore structures over recruitment we calculated the perpendicular distance between the site and the offshore location where the maximal frequency of front occurrences took place (FRONT). All image manipulations were carried out using IDRISI software v.2 (Eastman 1997).

To examine the influence of local-scale processes, we monitored six additional variables: (4) Foam lines (FOAM). We recorded the incidence of foam lines, which are visible as continuous lines of debris and flotsam surrounded by foam, located at the rear of the surf zone, positioned along $>100 \text{ m}$ off the coast of the study site. These very nearshore features suggest the existence of convergence zones delineating fronts separating different water masses (see McCulloch and Shanks 2003, Shanks et al. 2003). (5) Occurrence of surface slicks (SLICKS). These features appear as flat ocean surface zones surrounded by rough surface waters. Surface slicks were identified as proposed by

⁶ www.pfeg.noaa.gov

TABLE 1. Correlation coefficient of the relationships between environmental variables operating at different spatial scales with recruitment rates of intertidal barnacles (measured as individuals·d⁻¹·[100 cm²]⁻¹) and space (x coordinate UTM) across 12 sites on the northern Chile upwelling ecosystem.

Scale	Environmental variables	<i>Jehlius cirratus</i>	<i>Notochthamalus scabrosus</i>	Space	Authors
Meso	SST (°C)	-0.15	-0.37	-0.26	Farrell et al. (1991), Lagos et al. (2005)
	UPW (m ³ ·s ⁻¹ ·[100 m coastline] ⁻¹)	-0.80***	-0.78***	-0.89***	Connolly et al. (2001)
	FRONT (km)	0.03	-0.36	-0.19	Connolly and Roughgarden (1998), Roughgarden et al. (1988)
	WDIR (degrees)	0.29	0.17	0.31	Hawkins and Hartnoll (1982)
	WVEL (cm/s)	-0.81***	-0.69**	-0.85***	Farrell et al. (1991)
Local	FOAM (incidence)	-0.06	0.23	-0.05	Kingsford and Choat (1986), McCulloch and Shanks (2003)
	SLICK (incidence)	0.62**	0.67**	0.72**	Shanks and Wright (1987)
Small	SCS	0.03	-0.36	-0.07	This study
	<i>H</i>	-0.01	-0.05	-0.22	Archambault and Bourget (1996), Lagos et al. (2005)
	space (m)†	0.80***	0.74**		Belgrano et al. (1995a, b), Lagos et al. (2005)

Notes: SST = sea surface temperature; UPW = Bakun upwelling index at 72° W in front of each site; FRONT = distance to coastal front; WDIR = wind direction; WVEL = wind velocity; FOAM = incidence of surface foam lines; SLICK = incidence of surface slicks; SCS = slope of the continental shelf in front of each site; *H* = heterogeneity of the rocky platform (see *Methods* for details). The authors column indicates studies where a relationship between larval distribution and/or settlement/recruitment variations with environmental variables has been suggested.

** $P < 0.01$; *** $P < 0.001$.

† Note that space is across all scales.

Shanks and Wright (1987): located parallel to the shoreline and traveling in trains to the shore. Observation of foamlines and slicks lasted for 5 min before and after the replacement of recruitment plates (~25 min.). It must be pointed out that the occurrence of these variables can be underestimated because slicks are internal wave convergence zones which may occur on every, or at least during, many changes of the tide during the biweekly sampling interval. We also recorded (6) Wind direction (WDIR) and (7) velocity (WVEL) using a portable anemometer (Airguide, Windial, Chicago, Illinois, USA) to characterize the wind orientation (degrees) and velocity (cm/s) at the site. All wind records were done in the afternoon, and the hour depended on when we visited the site (~12:00–19:00 hours); 4–10 wind measures were carried out on each visit, and we used the mean of the maximum values to characterize wind conditions at each site. Finally, (8) to assess the role of coastal geomorphology, we constructed a digital bathymetric model for the study area by digitizing marine charts from the Chilean Navy Hydrographic and Oceanographic Service (SHOA). For each site we calculated the distance from the coastline to 60, 100, and 200 m at each study site and estimated the slope of the continental shelf (SCS) using linear regression (with intercept restricted to 0, coastline depth). Additionally, to examine within-site topographic factors that act at scales of meters and are largely independent of the processes outlined above, we examined (9) the heterogeneity of the rocky substrate (*H*). At each site, the rocky platform where recruitment plates were deployed was characterized as the ratio $H = C/L$, where *C* is the distance recorded by a graduated

chain laid over the substrate and *L* is the distance measured linearly ($H = 1$ for flat surfaces; Archambault and Bourget 1996, Lagos et al. 2005). *H* was calculated for five vertical and four horizontal transects using the position of plates as the extremes. The mean of all these *H* measurements was used as the local topographic heterogeneity.

Statistical analysis

First, the relationship between barnacle recruitment across sites with the subset of environmental correlates and spatial structure of study sites (*x* coordinates) was estimated using the Pearson correlation with significance adjusted using a Bonferroni correction. Second, the independent contribution of each environmental variable to the spatial variation in barnacle recruitment was assessed using the squared semi-partial correlation with type II square sum error (sr^2) in a multiple regression model (Tabachnik and Fidell 1989, SAS Institute 1996). This correlation characterizes the *pure* effect of each environmental variable on the spatial variation in barnacle recruitment by taking into account all the other variables (Freckleton 2002). Thus, observed sr^2 is usually smaller than or equal to the more familiar determination coefficient (r^2). In our study, the additive effects of sr^2 for all environmental variables were lower than the full multiple regression model (*Results*), suggesting a case of *shared variance* (Tabachnick and Fidell 1989) resulting from the *combined effect* of several variables over the spatial variation in barnacle recruitment and highlighted the need for directed analysis fitting regression models using a restricted subset of environmental variables.

Spatial analyses

The previously discussed analyses do not take into account the spatial autocorrelation in recruitment and environmental variables, but variation in a given ecological variable, such as larval recruitment, may result from spatial autocorrelation of the variable itself (e.g., aggregated settlement, Crisp and Meadows 1962; spatial coherence of the larval pool, Pineda 2000), from the relationship between larval recruitment with another variable that is spatially structured (e.g., mesoscale upwelling, Lagos et al. 2005) or from relationship of both variables that are independent of space. As suggested by Legendre (1993), we examined the spatial variation in the recruitment rate of both intertidal barnacles by partitioning it into four components: (a) spatial non-environmental, the component of spatial variation in larval recruitment that is not shared with the environmental variables studied; (b) spatially structured environmental, the spatial structure of recruitment that is shared with environmental variables; (c) nonspatial environmental, the spatial variation in recruitment that can be explained by environmental variables independent of any spatial structure; and (d) unexplained residual, the component of the variation in recruitment that is independent from the set of environmental variables studies and its spatial structure (i.e., other ecological variables not included in analysis, such as spatial variation in post-settlement mortality). The spatial structure in the barnacle recruitment rate for each regression analysis was modeled using a third-order polynomial, which can extract any broad-scale spatial trend:

$$R = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3 \quad (1)$$

where R is the recruitment rate in the site, x and y represent UTM coordinates (meters) of that site, and b_1 to b_9 are parameters. The intercept (b_0) was eliminated through centering of x and y prior to analysis and other nonsignificant parameters were removed by hand. The x and y coordinates were sufficient to represent the spatial trend of sites ($P < 0.02$). The r^2 between recruitment rates and spatial coordinates was used as measure of the component of spatial variation in recruitment explained by a combination of a non-environmental spatial (space only) and the spatially structured environmental components ($a + b$). The r^2 of the relationship between barnacle recruitment and the different environmental variables was used as measure of the variation explained by a combination of the spatially structured environmental component and the non-spatial environmental (environment only) component ($b + c$). This combination of spatial variation components corresponds to the recruitment–upwelling relationship but includes confounding effects of space and environment (Connolly and Roughgarden 1998, Connolly et al. 2001). The variation in barnacle recruitment explained by compo-

nents ($a + b + c$) was determined from a regression model incorporating both the environmental and the spatial variables. The variation accounted for by each of the components was estimated by subtraction among corresponding r^2 . For multiple regressions, the presence of multicollinearity among variables did not allow the use of automatic model selection, and environmental variables were entered by hand to examine their effect on r^2 with respect to the rest of variables and the previous model. The adequate model was also identified by inspecting the normality of residuals. The Akaike information criterion (AIC) was used to rank the models parsimoniously (SAS Institute 1996). In the *Results* section we present the bivariate, and the two- and three-parameter models that showed a significant fit after the Bonferroni correction.

In order to examine the spatial structure of recruitment rates and environmental variables, we estimated the Moran's I autocorrelation index (Sokal and Oden 1978) for 10 even distance classes covering the full spatial extent of the study area. However, only eight distance classes are presented, as distances <30 km and >240 km only occur among sites located inside the Antofagasta Bay and between sites located in the extremes of the study region, respectively. The elimination of these distance classes did not affect I for other distance classes where significance was assessed using a sequential Bonferroni correction. Spatial correlograms were computed using SAAP 4.3 (Wartenberg 1989).

RESULTS

Although recruitment of the barnacles *Jehlius cirratus* and *Notochlamalus scabrosus* showed important temporal variation over the studied period, spatial variation across sites was systematically related to the temporal fluctuation (s index) in recruitment at the corresponding site (Fig. 2). Large spatial variation in recruitment rates of the two barnacle species was observed, with higher magnitudes at sites on the open coast than those located inside the Antofagasta Bay. One site, located toward the northern extreme of our study region (RAM; Fig. 1b), showed the highest recruitment rates for both Chthamaliid species (Fig. 2). The site that exhibited the lowest magnitude in the recruitment rates of *N. scabrosus* was located inside the Antofagasta Bay (RIN), while for *J. cirratus* the lowest rate of recruitment was observed on the open coast immediately north of the bay at the Mejillones Peninsula (CER; Figs. 1 and 2). In terms of the regional oceanography and geomorphology, the recruitment rates of both species showed a decreasing trend from northern sites located on the open coasts (RAM), followed by recruitment rates on sites located toward inner sections of the Antofagasta Bay (ANT, GRU), and a further decrease in barnacle recruitment in sites located nearby to the limits of the bay (WAY, LCO) and to upwelling centers associated to Point Coloso from the south (MIN) and Point Tetras in the Mejillones Peninsula (CER; see Figs. 1b and 2).

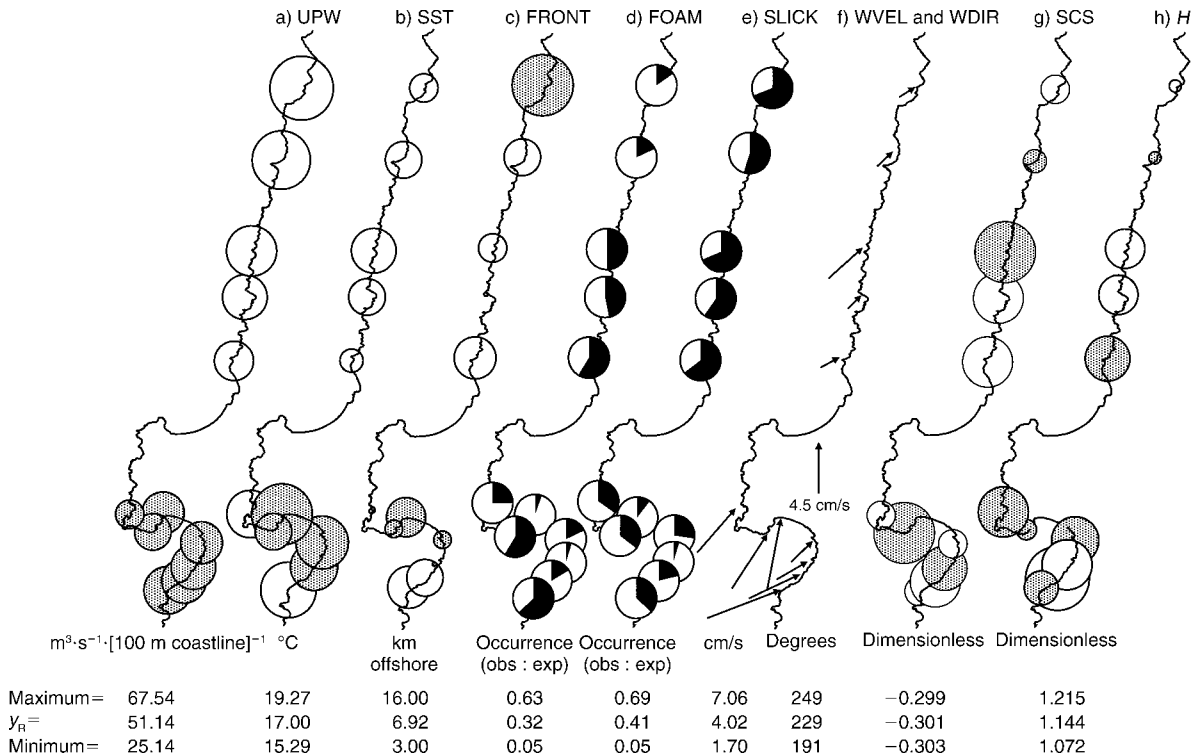


FIG. 3. Posting map of the environmental variables (a–h: UPW = Bakun upwelling index at $72^{\circ}W$ in front of each site; SST = sea surface temperature; FRONT = distance to coastal front; FOAM = incidence of surface foam lines; SLICK = incidence of surface slicks; WVLE = wind velocity; WDIR = wind direction; SCS = slope of the continental shelf in front of each site; H = heterogeneity of the rocky platform [see *Methods* for details]). All variables are centered to their regional means (y_R). The size of circles in each site is proportional to the absolute difference of the variable with respect to the regional mean; thus small circles are roughly similar to the regional mean, and solid and open circles indicate values higher and lower than the regional mean (y_R), respectively. The length of the labeled arrow (4.5 cm/s) should be used as a reference scale for the intensity of wind velocity in each location. In the case of (d) FOAM and (e) SLICK, the black area represents proportional occurrence (observed : expected ratio). Below each map the maximum and minimum values observed for the corresponding variable across sites are noted, along with the y_R value.

The upwelling index (UPW) and sea surface temperature (SST) showed values above the regional mean at the sites located inside Antofagasta Bay with respect to those located on the open coast (Fig. 3a, b) and tended to decrease toward the northern section of the study region. Similarly, three of the four sites showing distances to the position of coastal fronts (FRONT) above the regional mean were located in the interior of the Antofagasta Bay (LCO, RIN, and LGR; Figs. 1b and 3c) and one was situated on the northern extreme of the study region (RAM; Fig. 3c). The observation of local-scale oceanographic variables showed a similar spatial distribution than the mesoscale variables. The lowest number of foam line occurrences (FOAM; Fig. 3d) was observed at sites inside the Antofagasta Bay and with high numbers recorded at the sites in the periphery of the bay (LCO and MIN; Figs. 1b and 3d), and variable occurrence elsewhere. A similar pattern was observed for surface slicks (SLICKS; Fig. 3e) which had a high occurrence at sites adjacent to open coastal waters (>0.5) and low occurrence inside Antofagasta Bay and surrounding

areas (<0.4 ; Fig. 3e). Wind velocity (WVLE) was higher in sites located at or near the known upwelling centers (CER in Mejillones Peninsula and MIN at Pt. Coloso; Figs. 1b and 3f). Wind direction (WDIR) at the open coast sites showed values similar to the regional mean ($229^{\circ}SW$), while inside the Antofagasta Bay, the dominant wind direction was $\sim 240^{\circ}$ (i.e., more perpendicular to the coastline; Fig. 3f). The slope of the continental shelf (SCS) showed a less coherent spatial distribution with maximum slope inside both Antofagasta Bay and at sites on the open coast (Fig. 3g). The topographic heterogeneity of the rocky platforms (H ; Fig. 3h) was very variable with values of H lower and higher than the regional mean in sites located inside the Antofagasta Bay and in the open coast.

Both intertidal barnacles showed significant relationships with three environmental variables: negative relationships with UPW and WVLE, and positive with SLICKS (Table 1). These environmental variables as well as barnacle recruitment also showed spatial trends along the studied coast, reflected by their significant

TABLE 2. Coefficients of determination for the relationship between recruitment of intertidal barnacles and environmental variables over 12 sites in northern Chile.

Species	Environmental variable	Proportion of variation in barnacle recruitment, r^2				
		Total ($a + b + c$)	Space only (a)	Spatially structured environmental variation (b)	Environment only (c)	Spatially structured environmental variation and environment ($b + c$)
<i>Notochthamalus scabrosus</i>	UPW	0.61*	0.01	0.53	0.08	0.60**
	WVEL	0.57*	0.10	0.44	0.04	0.48*
	SLICK	0.57*	0.12	0.41	0.04	0.45*
<i>Jehlius cirratus</i>	WVEL	0.79**	0.13	0.60	0.06	0.66**
	UPW	0.73*	0.10	0.63	0.01	0.64**
	SLICK	0.72**	0.34	0.39	0.01	0.38*

Notes: For the ($b + c$) components, r^2 corresponds to the regression model including all environmental variables. Total component ($a + b + c$) corresponds to the regression including both environmental variables and spatial coordinates. Abbreviations are as in Table 1.

* $P < 0.05$; ** $P < 0.01$.

association with space (Table 1). The relationships between recruitment rates and the rest of the environmental variables were nonsignificant and with opposite trends between species (e.g., FOAM and SCS; Table 1).

When we examined significant bivariate relationships, taking into account their spatial structure, we found that the spatially structured environmental variation (component b) accounted for a much larger proportion of spatial variation in recruitment rates than the environmental only component (c) and the spatial only component (a ; Table 2). A three-dimensional representation of the linear relationship between barnacle recruitment and the most important environmental correlates while controlling for spatial structure helps to clarify this result (Fig. 4). In this figure, we use the x coordinate to represent the space because it graphically minimize clustering of data inside the Antofagasta Bay and along the open coast, and it also reflects the gradual decrease in recruitment across sites (i.e., open coast > inner bay > border's bay > upwelling centers; see Figs. 1b and 2). In the case of *N. scabrosus*, it can be seen that UPW and space jointly determine the slope of the linear plane describing their shared influence over recruitment ($r^2_{(a+b+c)} = 0.61$, Fig. 4a). However, variation in recruitment of *J. cirratus* was tightly associated with space, reflected as a stronger influence than UPW on the inclination of the linear plane ($r^2_{(a+b+c)} = 0.74$, Fig. 4b). Thus, the negative relationship of *J. cirratus* with UPW ($r = -0.80$, Table 1) may arise from the shared but inverse correlation of both variables with space ($r_{\text{sp-UPW}} = -0.89$, $r_{\text{sp-Jc}} = 0.80$; see Table 1). Partialling out the component of variation of environmental variables with respect to the spatial structure, we found that in the case of *J. cirratus* the influence of the space-only component was 10-fold ($a = 0.1$) more important than for *N. scabrosus* ($a = 0.01$; see Table 2). Similar patterns of association showed the SLICK influence over spatial variation in recruitment of *J. cirratus*, since the inclination of the plane is dominated by the influence of space (Fig. 4f). Finally, WVEL and space jointly determine the slope of the linear plane describing their

shared influence over recruitment of both barnacles (Fig. 4c, d). Thus, the observed relationship with UPW, WVEL, and SLICK emerges from the gradual variation in barnacle recruitment across space that is shared with all variables and is quantified by the spatially structured environmental component (b).

When we included all environmental variables in the regression model, the estimation of sr^2 showed that only FRONT had a significant and negative relationship with the spatial variation in the recruitment rates of *N. scabrosus* (FRONT, $sr^2 = 0.19$; Table 3). On the other hand, UPW, SST, WDIR, FRONT, and H showed significant relationships with the spatial variation in recruitment rates of *J. cirratus* (Table 3). The additive pure effects of each environmental variables (*N. scabrosus*, $\Sigma sr^2 = 0.24$; *J. cirratus*, $\Sigma sr^2 = 0.65$) were lower than the variation explained by a full multiple regression model (*N. scabrosus*, $r^2 = 0.99$, $P = 0.025$; *J. cirratus*, $r^2 = 0.99$, $P = 0.026$; Table 3). The difference between the variance explained by the sum of sr^2 and the r^2 in the complete model can be interpreted as overlapping contributions to spatial variation in barnacle recruitment rates by two or more environmental variables that result in an inflated r^2 (Tabachnick and Fidell 1989, see *Methods*).

Multiple regression models including two and three parameters and taking into account spatial autocorrelation showed that restricted combinations of mesoscale (UPW, FRONT, WVEL, WDIR) and local variables (SST, FOAM, and SLICK, but see later results about the characteristic spatial scale of surface slick occurrence) had the ability to explain a large amount of variation in the spatial pattern of recruitment rates for both species. The inclusion of a third parameter did not increase substantially the variance explained by the model (Table 4). In all regression models, the component describing spatially structured environmental variation (b) explained >50% and >60% of spatial variation in recruitment of *N. scabrosus* and *J. cirratus*, respectively (Table 4). In all models, the space-only component (a) explained a very low proportion in the

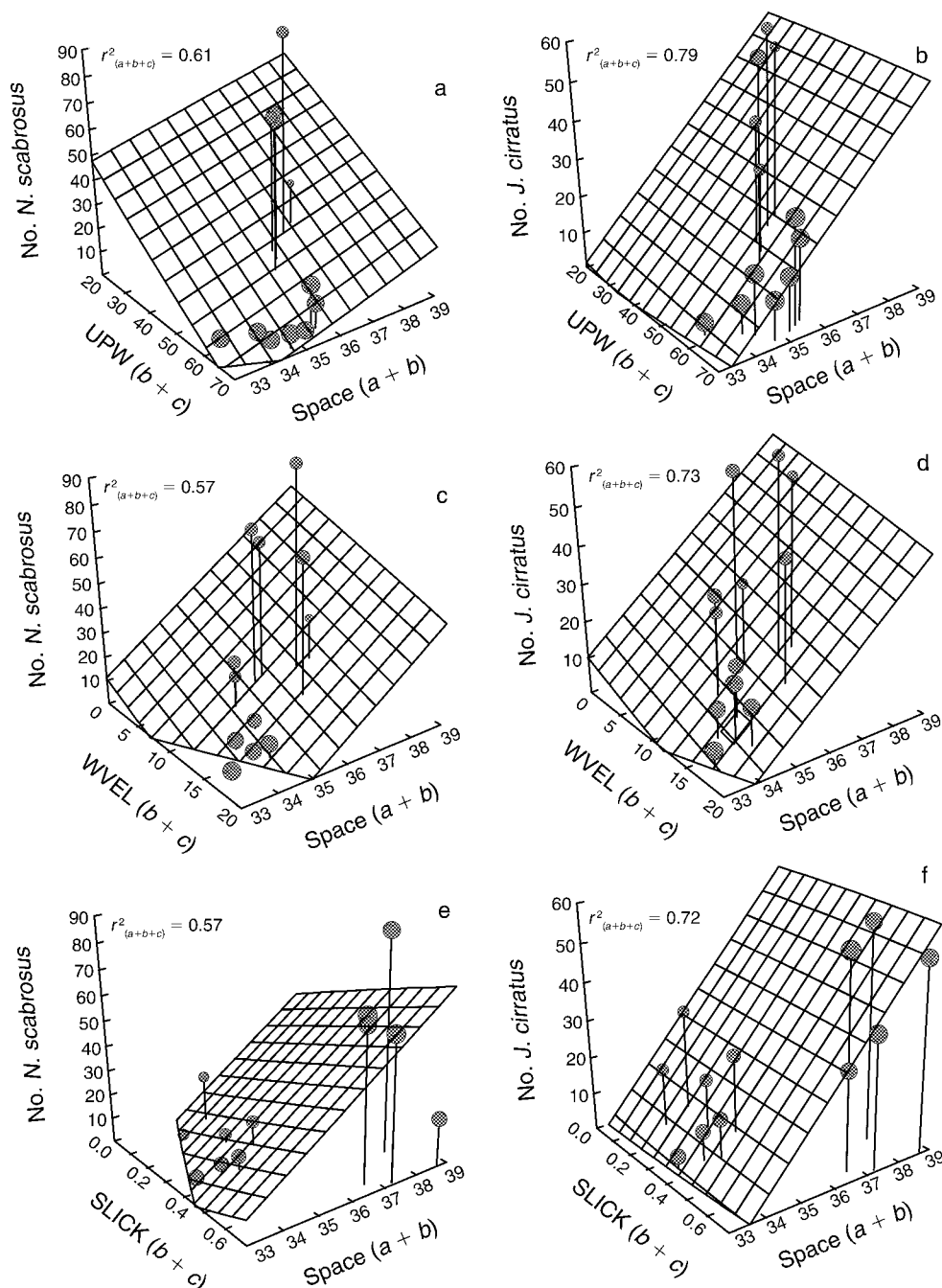


FIG. 4. Three-dimensional representation of the relationship between the recruitment of *Notochthamalus scabrosus* and *Jehlius cirratus* and the most important environmental variables (UPW, WVWL, and SLICK), including the influence of the spatial structure represented as an x coordinate (UTM; $\times 10^5$ m east). The coefficients of determination (r^2) in the figures correspond to the total variation explained by environmental and spatial variables (combination of components $a + b + c$; see *Methods* and Table 2).

spatial variation of barnacle recruitment, suggesting that the environmental variables included in the analysis were appropriate to explain spatial variation in recruitment rates of both barnacles' species.

Spatially structured environmental variation (b) was clearly the most important explanatory component of environmental variability on the spatial variation in the

recruitment rates of both intertidal barnacles. Spatial correlograms of recruitment rates and the most important environmental variables in the bivariate relationships helped to quantify the scales of spatial autocorrelation (Fig. 5). Recruitment rates of *N. scabrosus* had significant, positive spatial autocorrelation at distance classes shorter than 70 km, decayed beyond 90 km, and showed

TABLE 3. Influence (*pure*) of each environmental variable upon spatial variation in recruitment of intertidal barnacles (squared semi-partial correlation, sr^2) over 12 sites of the northern Chile upwelling ecosystem.

Species and variable	df	Parameter	SE	$t(H_0: b = 0)$	P value	sr^2
<i>Notochthamalus scabrosus</i>						
FRONT	1	-4.87	0.65	-7.46	0.02*	0.157
UPW	1	-2.47	0.62	-3.93	0.06	0.043
SLICK	1	-106.32	43.57	-2.44	0.13	0.017
WVEL	1	-2.23	1.12	-1.98	0.19	0.011
FOAM	1	37.96	20.91	1.81	0.21	0.009
WDIR	1	-0.28	0.23	-1.23	0.34	0.004
H	1	32.27	33.13	0.97	0.43	0.003
SST	1	0.36	4.15	0.08	0.94	0.000
SCS	1	-323.64	1415.09	-0.22	0.84	0.000
<i>Jehlius cirratus</i>						
UPW	1	-2.95	0.39	-7.52	0.02*	0.165
SST	1	17.91	2.6	6.88	0.02*	0.138
WDIR	1	1.06	0.14	7.32	0.02*	0.156
H	1	95.81	20.73	4.62	0.04*	0.062
FRONT	1	-1.75	0.4	-4.29	0.05*	0.054
WVEL	1	2.8	0.7	3.98	0.06	0.046
SLICK	1	-76.4	27.27	-2.8	0.11	0.023
SCS	1	-1752.42	885.7	-1.97	0.19	0.011
FOAM	1	22.49	13.09	1.71	0.23	0.009

Notes: The fit of the multiple regression models was $r^2 = 0.994$ for *N. scabrosus* ($P = 0.0250$) and $r^2 = 0.994$ for *J. cirratus* ($P = 0.0259$); Σsr^2 , the sum of sr^2 for all variables included in the model, was 0.244 for *N. scabrosus* and 0.654 for *J. cirratus*.

* $P < 0.05$.

significantly negative long-range autocorrelation that persisted from distance classes larger than 100 km up to 190 km. *J. cirratus* showed a similar pattern but with significant positive correlations restricted to distances shorter than 70 km and negative relationships at distances larger than 180 km. Spatial correlograms of UPW, WVEL, and SLICKS confirmed their shared spatial structure with recruitment rates with positive autocorre-

lation at distances classes <70 km and significant negative correlations at distance classes >160 km.

DISCUSSION

The spatial variation in the recruitment rates of intertidal barnacles *Jehlius cirratus* and *Notochthamalus scabrosus* in northern Chile showed a mesoscale spatial structure with a characteristic length of ~60–70 km. A

TABLE 4. Coefficients of determination, for regression models including two and three parameters, in the relationship between barnacle recruitment and environmental variables.

Species, variables included in models with best fit	Proportion of variation in barnacle recruitment, r^2					
	AIC	Total ($a + b + c$)	Space only (a)	Spatial structured environmental variation (b)	Environment only (c)	Spatial structured environmental variation and environment ($b + c$)
<i>Notochthamalus scabrosus</i>						
UPW and FRONT	62.3	0.873***	0.002	0.533	0.338	0.871***
UPW and WVEL	74.2	0.653**	0.000	0.535	0.118	0.653**
UPW and FOAM	75.2	0.637*	0.013	0.522	0.102	0.624**
<i>Jehlius cirratus</i>						
UPW and WVEL	57.4	0.796**	0.023	0.700	0.073	0.773***
UPW and SST	60.9	0.784**	0.088	0.635	0.061	0.696**
UPW and WDIR	61.4	0.734**	0.051	0.672	0.011	0.683**
<i>N. scabrosus</i>						
UPW, FRONT, and SST	50.1	0.960***	0.000	0.535	0.425	0.960***
UPW, FRONT, and WDIR	62.4	0.920***	0.030	0.505	0.385	0.890***
UPW, FRONT, and FOAM	62.7	0.888**	0.000	0.535	0.353	0.888***
<i>J. cirratus</i>						
UPW, WVEL, and FRONT	58.7	0.810*	0.023	0.700	0.087	0.787**
UPW, WVEL, and WDIR	58.9	0.796*	0.013	0.710	0.073	0.783**
UPW, WVEL, and SLICK	59.1	0.801*	0.021	0.702	0.078	0.780**

Notes: Abbreviations are as in Table 1. All models were significant after a Bonferroni correction. AIC = Akaike Information Criteria for models including the corresponding subset of environmental variables.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

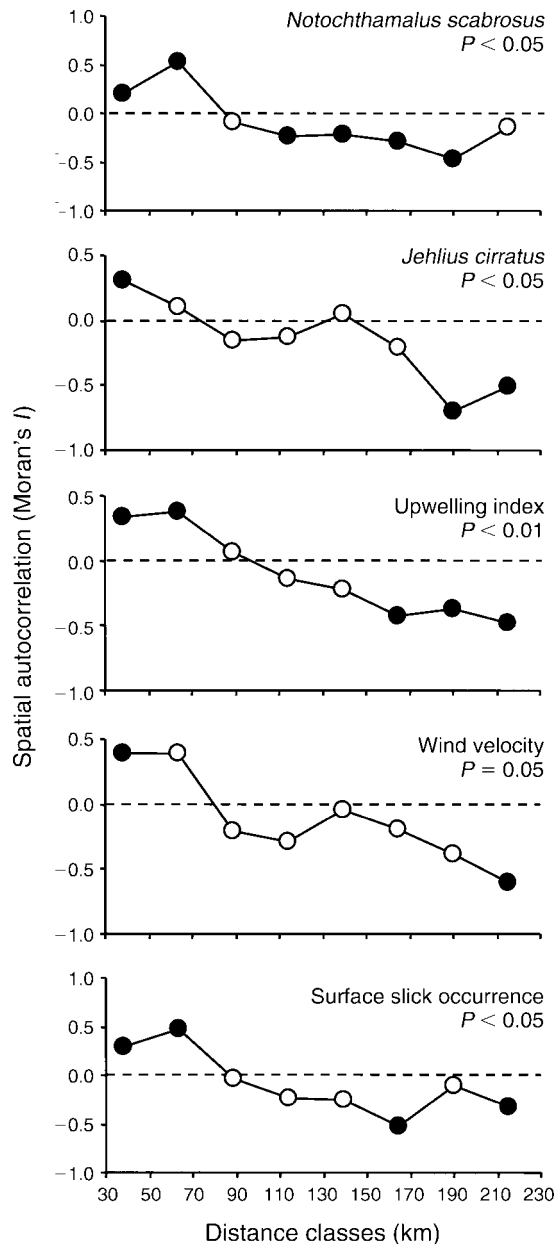


FIG. 5. Spatial structure in the recruitment of intertidal barnacles *Notochthamalus scabrosus* and *Jehlius cirratus* and environmental variables with Moran's I used as the estimator of spatial autocorrelation. Solid and open circles indicate significant and nonsignificant Moran's I coefficients after a sequential Bonferroni correction, respectively. In all cases, the Moran's I values were standardized between 1 and -1 by dividing them by the range. P values indicate the significance of the overall correlogram.

large amount of the variation in the spatial distribution of recruitment rates could be explained by a combination of spatially structured environmental processes as evidenced by the high r^2 observed in bivariate relationships between recruitment rates and mesoscale nearshore process (Bakun upwelling index [UPW], wind

velocity [WVEL], and incidence of surface slicks [SLICKS]). Through their influence on patterns of nearshore circulation, these environmental variables may generate spatially autocorrelated patterns of recruitment characterized in our study system. The powerful influence of the spatially structured environmental component of variation on barnacle recruitment rates may rule out other measurement such as the (*pure*) influence of each environmental variable determined through sr^2 , but does not take into account the spatial structure. Thus, the influence of the studied environmental correlates of barnacle recruitment is through their inherent geographic structure. That is a very general result because similar conclusions have been reached in several ecological studies examining biological responses in association with environmental gradients such as the spatial variation in diversity of terrestrial plants (Borcard et al. 1992, Lichstein et al. 2002), avian diversity (van Rensburg et al. 2002), abundance distribution of meroplanktonic larvae (Belgrano et al. 1995a, b), and latitudinal gradients of diversity of benthic crustaceans (Astorga et al. 2003). In all of these studies, the spatially structured environmental variation was the most important component influencing the spatial variation observed in the ecological process examined.

Variation in barnacle recruitment rates along the study region was associated with the dynamics of coastal upwelling circulation. Thus, the spatial structure of recruitment rates may reflect the interaction between coastal geomorphology and the regional gradient in upwelling intensity, which determines that different oceanographic regimes are observed inside and around the Antofagasta Bay and the open coast. The complex interaction between processes operating at different spatial scales implies that no single environmental correlate will perform uniformly across all sites. Notwithstanding, our analysis suggests that models based on combinations of mesoscale, nearshore processes with others operating at different spatial scales may have considerable explanatory power. For instance, the model selection criteria detected the postulated mechanistic relationship between the intensity of coastal upwelling, the proximity of offshore frontal structures, and the recruitment of intertidal barnacles (Roughgarden et al. 1988, 1991, Connolly and Roughgarden 1998). These studies suggest that planktonic larvae become entrained in the surface Ekman layer during coastal upwelling, which may result in their offshore transport and accumulation in the coastal front separating the cool upwelled water from the warmer oceanic waters mass. When the upwelling-favorable winds stop (i.e., downwelling conditions), the coastal front is advected onshore or alongshore (Send et al. 1987). Larval transport (Wing et al. 1995, 1998, Shanks et al. 2000) and corresponding recruitment events of intertidal species, such as barnacles (Farrell et al. 1991, Roughgarden et al. 1991), have been observed in association

with these upwelling–relaxation cycles. Although this larval transport mechanism is highly idealized (Narvaez et al. 2006; see also Shanks and Brink 2005), it has been shown that offshore frontal structures have an important role on the spatial distribution of meroplanktonic larvae (Wing et al. 1995, 1998, Shanks et al. 2000, 2003) and may also influence settlement and recruitment patterns (Roughgarden et al. 1991, McCulloch and Shanks 2003). It should be pointed out that negative evidence about the role of the upwelling–relaxation cycle as a mechanism of distribution of larvae in the nearshore zone and subsequent recruitment has also been reported. For instance, Shanks (1998) found little evidence of upwelling–downwelling conditions over larval recruitment and suggests a more important role of internal tides. In addition, Shanks and Brink (2005) showed that larvae with slow swimming abilities do not behave as passive particles, and they were not swept offshore/onshore during upwelling/downwelling events, respectively. Instead, behavioral responses such as the depth-keeping behaviors similar to those displayed by other animals concentrated at the convergence fronts may maintain larvae close to the shore despite upwelling–downwelling conditions. In the central Chile upwelling ecosystem, a similar behavioral mechanism has been suggested by Poulin et al. (2002) to explain how gastropod larvae may avoid offshore transport. More studies are needed to understand the generality and relative role of behavioral responses in decoupling the postulated recruitment–upwelling hypotheses.

The negative relationship between UPW and recruitment rates agrees with our finding that the recruitment rates of both species of barnacles were high in the region where intermittent offshore transport occurs (open coast). In fact, it has been reported that poleward flow along this open coast constrains the upwelling circulation, which is restricted to a narrow area and the coastal fronts are located inshore (Marin et al. 2001, Lagos et al. 2002, Rojas et al. 2002). Thus, both factors (weak offshore UPW and short distance to FRONT [distance to coastal front]) may interact to increase the barnacle recruitment. Recent studies indicate that Antofagasta Bay represents a retention zone (Castilla et al. 2002, Lagos et al. 2002, Lagos 2003). In stark contrast with several studies of recruitment in embayment vs. open areas (Gaines and Bertness 1991, Archambault and Bourget 1999, Mace and Morgan 2006, McQuaid and Phillips 2006), we found that recruitment rates of both barnacle species were lower inside the bay when compared with the open coast. We suggest that this unexpected relationship may be attributable to the presence of an “upwelling trap” (Piñones et al. 2007). Forced by surface circulation patterns from the upwelling center at Pt. Coloso (south of the bay; Fig. 1), the water inside the bay is separated from the upwelled water by a persistent frontal zone located at the mouth of the bay (Castilla et al. 2002, Lagos et al. 2002, Lagos 2003). This frontal structure can also entrap meroplanktonic larvae, and if the temporal persistence of the front

exceeds the pelagic larval duration of barnacles it may yield the negative effect observed in barnacle recruitment rates (see also Graham and Largier 1997). In addition, during upwelling conditions, water flows across the mouth of the bay and there is a *prograde* front (see Graham 1993) separating the upwelling water from the warm water landward in the bay, whereas the *upwelling* front is located on the seaward side of the upwelled waters. Under this circulation pattern, it may be expected that during relaxation events, the prograde front does not propagate toward the shore, and instead the warm waters enclosed inside the bay should move seaward. This effect may further diminish the reduced opportunities of recruitment for larvae entrained in the frontal structure. The contrast between observed results and expectations could be examined through the direct and simultaneous sampling of larval distribution in the plankton and benthic recruitment during upwelling–downwelling conditions inside the bay. Lastly, FRONT was the only environmental correlate for which its *pure* effect was significant for both barnacle species (Table 3). Thus, our results may also reflect the importance and generality of frontal circulation in coastal ecosystems (Roughgarden et al. 1988, 1991, Connolly and Roughgarden 1998).

Upwelling is a wind-induced process (Smith 1995). Thus, a relationship between WDIR (wind direction) and WVEL and barnacle recruitment rates may arise due to the circulation mechanism described previously. This relationship has been reported in several studies. For instance, Belgrano et al. (1995a, b) demonstrate that spatial variation of planktonic larvae is explained by the spatially structured wind velocity and direction. Similarly, Wing et al. (1995) related the spatial variation in recruitment of *Cancer* crabs with wind-driven upwelling dynamics in the California coast, which Botsford (2001) had previously reported to be negative and coherent across interannual scales. Our results are in broad agreement with such findings since both species showed significant negative bivariate associations with WVEL. Even though the *pure* contribution of WVEL on barnacle recruitment rates did not reach statistical significance (Table 3), its effect is clearly enhanced in combination with UPW (Table 4).

As ecological studies have progressively shifted their focus to large spatial scales (Connolly et al. 1998, Jenkins et al. 2000, Navarrete et al. 2005), few studies have emphasized the importance of local-scale nearshore process over spatial distribution of larvae and subsequent recruitment (but see Shanks 1983, Shanks and Wright 1987, Wolanski and Hamner 1988, Kingsford 1990, Castilla et al. 2002, Shanks and McCulloch 2003, Shanks et al. 2003). The positive influence of SLICK on barnacle recruitment rates is in agreement with previous studies showing that larvae can be transported onshore in these convergence zones (Shanks 1983, Shanks and Wright 1987) and that this transport mechanism may explain spatial variation in barnacle recruitment (Shanks 1995). We defined SLICKS as a local-scale nearshore

process (see *Methods* and Table 1). In contrast with our own assumptions SLICKS showed a clear mesoscale spatial structure (Fig. 5). This suggests that SLICKS, just as UPW and WVWL, can introduce similarities among nearby locality and have the potential to influence barnacle recruitment across vast sections of the coast along our study region. Although internal waves are not produced homogeneously across the coastline, as they are refracted by the bottom topography (Shanks 1995), and surface slicks associated with convergence zones are obliterated by strong wind (Shanks and Wright 1987), it does not imply that onshore transport in convergence zones vanishes. Instead, internal wave activity may have a pervasive and widespread local- to mesoscale influence over recruitment to benthic habitats. In fact, the requisites for internal wave propagation (tidal currents, a change in bottom topography, water column stratification; Shanks 1995) have been reported in regions of the southern (Strub et al. 1998, Vargas et al. 2004) and northern Eastern Pacific upwelling ecosystems (Shanks 1983, Rosenfeld 1990, Storlazzia et al. 2003). Regardless of the lack of oceanographic information about internal waves and corresponding larval distributions in the study zone, there is no reason to rule out their influence over the observed patterns of barnacle recruitment. In particular, although (1) spatial variation of SLICKS was correlated with recruitment rates and (2) spatially structured variation of SLICKS explained an important portion of the spatial variation in recruitment of both barnacles, we found that (3) SLICKS were almost absent as environmental correlates of barnacle recruitment in the two or three parameters models, suggesting a single (instead of *combined*) and spatially structured influence upon spatial variation in barnacle recruitment. This implies that studies designed at the mesoscale may be the most fruitful way to characterize the relative role of internal waves and upwelling dynamics on the spatial variation of recruitment to benthic populations.

Topography at the local and at the small scale, SCS (slope of continental shelf in front of each site) and *H*, respectively, were not associated with the observed spatial variation in barnacle recruitment rates. However, in spite of the low resolution of the local variables examined, platform heterogeneity (*H*) had a significant, *pure* contribution to the spatial variation of *J. cirratus* (Table 3) but did not show a significant spatial structure, indicating a potential role in producing stochastic patterns at within-site or local scales. In addition, when spatial autocorrelation was taken into account, a small proportion of the variation in recruitment rates was explained by the *pure* spatial component of environmental correlates which would be indicative of the importance of other environmental variables, not regarded in the study but with a shared spatial structure. A plausible explanation for the observed spatial patterns in barnacle recruitment could be the influence of spatial variation in post-settlement process operating within

sites. For instance, it has been shown that settling larvae actively select between rock types, which can drive patterns of pre- and post-settlement mortality associated with rock warming and desiccation (Menge 2000, Guichard et al. 2001). Conversely, Jeffery (2003) reported that, even in the presence of predators, post-settlement mortality does not override the role of settlement over the determination of spatial distribution of barnacles among localities. These different results suggest that, in spite of the fact that local variables may have an influence across our study region, the particular nature of the local rocky platform may yield different pathways of mortality for settlers within each locality. For instance, Pineda (1994) showed that post-settlement mortality of the barnacle *Chthamalus* spp. is a spatially structured process over scales of a few 100s of meters, which agrees with findings of Lagos et al. (2005) that local topography influences the settlement of Balanid barnacles, but it did not affect the mesoscale spatial variation in settlement and recruitment of Chthamalid barnacles. Notwithstanding, if local topography may be regarded as a surrogate measure associated with substratum temperature and dessication, which influences spatial variation in post-settlement mortality (Menge 2000, Guichard et al. 2001) and small-scale flows that generate within-site, small-scale patchiness in settlement (Guichard and Bourget 1998, Guichard et al. 2001), then its relative role, at least over spatial variation in recruitment of *J. cirratus*, cannot be ruled out.

In the intertidal of northern Chile, the recruitment rates of *J. cirratus* and *N. scabrosus* appear to be a spatially structured mesoscale process. Accordingly, as in other marine and terrestrial ecosystems, spatially structured environmental components of the variables as UPW, WVWL, and SLICKS, explained a large proportion of spatial variation in barnacle recruitment and seem to modulate its characteristic spatial scale. As such, spatial autocorrelation must be taken into account in the study of the recruitment–environment relationships across space. Our study also pointed out the importance of frontal structures as drivers of spatial variation in recruitment along the studied coast. These results indicate that barnacle recruitment is likely a function of several nearshore circulation processes. In addition, platform heterogeneity (*H*) showed a *pure* and non-spatially structured influence over recruitment of *J. cirratus*. Thus, the influence of local and within-site, small-scale factors over spatial variation in barnacle recruitment should be interpreted cautiously. Lastly, our results highlight the importance of spatially structured variation in inner-shelf and very nearshore processes, providing clues about the spatial scales at which simultaneous monitoring of physical–biological interactions in the coastal ocean could be performed. Further, because of the ecological dominance of barnacles (Camus and Lagos 1996), and species with similar life cycles as mussels (Navarrete et al. 2005), its environmentally driven recruitment patterns could determine

the dynamics of the intertidal metacommunity by affecting the spatial dynamics of species with which they interact (Guichard et al. 2004, Holyoak et al. 2005). As such, spatially explicit approaches, integrating process and factors operating from local to regional or biogeographic scales may provide important insights on the functioning of coastal ecosystems and will greatly aid future management and conservation initiatives.

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LITERATURE CITED

- Aiken, C., S. A. Navarrete, M. Castillo, and J. C. Castilla. 2007. Along-shore larval dispersal kernels in a numerical ocean model of the central Chilean coast. *Marine Ecology Progress Series* 339:13–24.
- Archambault, P., and E. Bourget. 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Marine Ecology Progress Series* 136:111–121.
- Archambault, P., and E. Bourget. 1999. Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. *Journal of Experimental Marine Biology and Ecology* 238:161–184.
- Astorga, A., M. Fernández, M. Boschi, and N. A. Lagos. 2003. Two oceans, two taxa and one mode of development: latitudinal diversity patterns of South American crabs and test for possible causal processes. *Ecology Letters* 6:420–427.
- Barth, J. A., S. D. Pierce, and R. L. Smith. 2000. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep Sea Research II* 47:783–810.
- Belgrano, A., P. Legendre, J. M. Dewarumez, and S. Frontier. 1995a. Spatial structure and ecological variation of meroplankton on the Belgian–Dutch coast of the North Sea. *Marine Ecology Progress Series* 128:43–50.
- Belgrano, A., P. Legendre, J. M. Dewarumez, and S. Frontier. 1995b. Spatial structure and ecological variation of meroplankton on the French–Belgian coast of the North Sea. *Marine Ecology Progress Series* 128:51–59.
- Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution* 14:427–432.
- Bolker, B. M., S. W. Pacala, and C. Neuhauser. 2003. Spatial dynamics in model plant communities: what do we really know? *American Naturalist* 162:135–148.
- Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055.
- Botsford, L. 2001. Physical influences on recruitment to California current invertebrates populations on multiple scales. *ICES Journal of Marine Science* 10:1–11.
- Broitman, B. R., C. A. Blanchette, and S. D. Gaines. 2005. Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California. *Limnology and Oceanography* 50:1473–1479.
- Caley, M., M. Carr, M. Hixon, T. Hughes, G. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine population. *Annual Reviews of Ecology and Systematics* 27:477–500.
- Camus, P., and N. A. Lagos. 1996. Variabilidad espacial y temporal del reclutamiento de ensambles de especies intermareales sésiles del norte de Chile. *Revista Chilena de Historia Natural* 69:193–204.
- Castilla, J. C., N. A. Lagos, R. Guíñez, and J. Largier. 2002. Plankton retention mechanism in the nearshore with emphasis on embayments: a review. Pages 179–203 in J. C. Castilla and J. Largier, editors. *The oceanography and ecology of the nearshore and bays in Chile*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- Connolly, S. R., B. A. Menge, and J. Roughgarden. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in northeast Pacific ocean. *Ecology* 82:1799–1813.
- Connolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* 151:311–326.
- Cowen, R. K., C. B. Paris, and J. L. Fortuna. 2006. Scaling connectivity in marine populations. *Science* 311:522–527.
- Crisp, D., and P. Meadows. 1962. The chemical basis of gregariousness in cirripedes. *Proceedings of the Royal Society London B* 156:500–520.
- Eastman, R. 1997. IDRISI for Windows users guide, version 2.0. Clark lab for cartography technology and geographic analysis. Clark University, Worcester, Massachusetts, USA.
- Ebert, T., and M. Russell. 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnology and Oceanography* 33:286–294.
- Ebert, T., S. Schroeter, J. Dixon, and P. Kalvass. 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. *Marine Ecology Progress Series* 111:41–52.
- Farrell, T., D. Bracher, and J. Roughgarden. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* 36:279–288.
- Freckleton, R. P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *Journal of Animal Ecology* 71:542–545.
- Gaines, S. D., and M. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579–580.
- Graham, W. M. 1993. Spatio-temporal scale assessment of an “upwelling shadow” in northern Monterey Bay, California. *Estuaries* 16:83–91.
- Graham, W., and J. L. Largier. 1997. Upwelling shadows as nearshore retention sites: the example of Monterey Bay. *Continental Shelf Research* 17:509–532.
- Guichard, F., and E. Bourget. 1998. Topographic heterogeneity, hydrodynamics, and benthic community structure: a scale-dependent cascade. *Marine Ecology Progress Series* 171:59–70.
- Guichard, F., E. Bourget, and J. L. Robert. 2001. Scaling the influence of topographic heterogeneity on intertidal benthic communities: alternative trajectories mediated by hydrodynamics and shading. *Marine Ecology Progress Series* 217:27–41.
- Guichard, F., S. A. Levin, A. Hastings, and D. Siegel. 2004. Toward a dynamic metacommunity approach to marine reserve theory. *BioScience* 54:1003–1011.
- Harris, J. M., G. M. Branch, B. L. Elliott, B. Currie, A. Dye, C. D. McQuaid, B. Tomalin, and C. Velasquez. 1998. Spatial

- and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *South African Journal of Marine Science* 33:1–11.
- Hawkins, S. J., and R. G. Hartnoll. 1982. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *Journal of Experimental Marine Biology and Ecology* 62: 271–83.
- Hoffman, E., and T. Powell. 1998. Environmental variability effects on marine fisheries: four case histories. *Ecological Applications* (Supplement) 8:S23–S32.
- Holyoak, M., M. A. Leibold, N. Mouquet, R. D. Holt, and M. F. Hoopes. 2005. Metacommunities. A framework for large-scale community ecology. Pages 1–31 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Jeffery, C. J. 2003. Determination of abundance and distribution of an intertidal barnacle: settlement or post-settlement mortality? *Marine Ecology Progress Series* 246:291–305.
- Jenkins, S., et al. 2000. Spatial and temporal variation in settlement and recruitment of intertidal barnacle *Semibalanus balanoides* (L.) (Crustacea: Cirripedia) over a European scale. *Journal of Experimental Marine Biology and Ecology* 243: 209–225.
- Kingsford, M. J. 1990. Linear oceanographic features: a focus for research on recruitment processes. *Australian Journal of Ecology* 15:391–401.
- Kingsford, M. J., and J. H. Choat. 1986. Influence of surface slicks on the distribution and onshore movements of small fish. *Marine Biology* 91:161–171.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020.
- Lagos, N. A. 2003. Dinámica espacial del reclutamiento de cirripedios intermareales: una aproximación empírica a la formación de patrones espacio-temporales en el acople bento-oceánico. Tesis de Doctorado. Pontificia Universidad Católica de Chile, Santiago, Chile.
- Lagos, N. A., I. Barria, and P. Paolini. 2002. Upwelling ecosystems in northern Chile: integrating benthic ecology with oceanography through remote sensing. Pages 117–141 in J. C. Castilla and J. Largier, editors. *The oceanography and ecology of the nearshore and bays in Chile*. Ediciones Universidad Católica de Chile, Santiago, Chile.
- Lagos, N. A., S. A. Navarrete, F. Véliz, A. Masuero, and J. C. Castilla. 2005. Meso-scale spatial variation in settlement and recruitment of intertidal barnacles along central Chile. *Marine Ecology Progress Series* 290:165–178.
- Lagos, N. A., F. Tapia, S. A. Navarrete, and J. C. Castilla. 2007. Spatial synchrony in recruitment of intertidal benthic invertebrates along the central Chile coast. *Marine Ecology Progress Series* 350:29–39.
- Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13:71–89.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.
- Lewontin, R. C. 1966. On the measurement of relative variability. *Systematic Zoology* 15:141–142.
- Lichstein, J., T. Simons, S. Shriner, and K. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs* 73:445–463.
- Mace, A. J., and S. G. Morgan. 2006. Larval accumulation in the lee of the small headland: implications for the design of marine reserves. *Marine Ecology Progress Series* 318:19–29.
- Marín, V., R. Escribano, L. Delgado, G. Olivares, and P. Hidalgo. 2001. Nearshore circulation in a coastal upwelling site off the northern Humbolt current system. *Continental Shelf Research* 21:1317–1329.
- McCulloch, A., and A. Shanks. 2003. Topographically generated fronts, very nearshore oceanography and the distribution and settlement of mussel larvae and barnacle cypris. *Journal of Plankton Research* 25:1427–1439.
- McQuaid, C. D., and T. E. Phillips. 2006. Mesoscale variation in reproduction, recruitment and population structure of intertidal mussels with low larval input: a bay/open coast comparison. *Marine Ecology Progress Series* 327:193–206.
- Menge, B. 2000. Recruitment vs. post-recruitment processes as determinants of barnacle population abundance. *Ecology* 70: 265–288.
- Menge, B. A., C. Blanchette, P. Raimondi, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. *Ecological Monographs* 74:663–684.
- Narvaez, D. A., S. A. Navarrete, J. Largier, and C. A. Vargas. 2006. Onshore advection of warm water, larval invertebrate settlement, and relaxation of upwelling off central Chile. *Marine Ecology Progress Series* 309:159–173.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285.
- Navarrete, S. A., B. R. Broitman, E. A. Wieters, G. Finke, R. Venegas, and A. Sotomayor. 2002. Recruitment of intertidal invertebrates on the southeast Pacific: interannual variability and the 1997–1998 El Niño. *Limnology and Oceanography* 47:971–802.
- Navarrete, S. A., E. A. Wieters, B. R. Broitman, and J. C. Castilla. 2005. Benthic–pelagic coupling and the oceanographic control of species interaction. *Proceedings of the National Academy of Sciences (USA)* 102:18042–18051.
- Nekola, J. C., and P. S. White. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26:867–878.
- Palma, A. T., L. M. Pardo, R. Veas, C. Cartes, M. Silva, K. Manríquez, A. Diaz, C. Muñoz, and F. P. Ojeda. 2006. Coastal brachyuran decapods: settlement and recruitment under contrasting coastal geometry conditions. *Marine Ecology Progress Series* 316:139–153.
- Pineda, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107:125–138.
- Pineda, J. 2000. Linking larval settlement to larval transport: assumptions, potentials, and pitfalls. *Oceanography of the Eastern Pacific* 1:84–105.
- Piñones, A., J. C. Castilla, R. Guíñez, and J. L. Largier. 2007. Nearshore surface temperatures in Antofagasta Bay (Chile) and adjacent upwelling centers. *Ciencias Marinas* 33:37–48.
- Poulin, E., A. T. Palma, G. Leiva, D. Narvaez, R. Pacheco, S. A. Navarrete, and J. C. Castilla. 2002. Avoiding offshore transport of competent larvae during upwelling events: the case of the gastropod *Concholepas concholepas* in central Chile. *Limnology and Oceanography* 47:1248–1255.
- Rojas, P., R. Escribano, and V. Marín. 2002. The influence of coastal upwelling on fish larvae distribution off Mejillones Peninsula, northern Chile. *Fisheries Oceanography* 11:233–244.
- Rosenfeld, L. 1990. Baroclinic semidiurnal tidal currents over the continental shelf off northern California. *Journal of Geophysical Research* 95:22153–22172.
- Roughan, M., A. J. Mace, J. L. Largier, S. G. Morgan, J. L. Fischer, and M. L. Carter. 2005. Subsurface recirculation and larval retention in the lee of a small headland: a variation on the upwelling shadow theme. *Journal of Geophysical Research* C 110:C10027. [doi: 10.1029/2005JC002898]
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.
- Roughgarden, J., T. Pennington, and S. Alexander. 1991. Collision of upwelling fronts with the intertidal zone: the causes of recruitment pulses in barnacle populations of central California. *Acta Oecologica* 12:35–51.

- SAS Institute. 1996. SAS/STAT User's Guide. Release 6.03 edition. SAS Institute, Cary, North Carolina, USA.
- Send, U., R. C. Beardsley, and C. D. Winant. 1987. Relaxation from upwelling in the coastal ocean dynamics experiment. *Journal of Geophysical Research* 92(C):1683–1698.
- Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fished shoreward. *Marine Ecology Progress Series* 13:311–315.
- Shanks, A. L. 1995. Mechanism of cross-shelf dispersal of larval invertebrates and fishes. Pages 324–367 in L. MacEdward, editor. *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, Florida, USA.
- Shanks, A. L. 1998. Abundance of post-larval *Callinectes sapidus*, *Penaeus* spp., *Uca* spp., and *Labinia* spp. collected at an outer coastal site and their cross-shelf transport. *Marine Ecology Progress Series* 168:57–69.
- Shanks, A., and L. Brink. 2005. Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. *Marine Ecology Progress Series* 302:1–12.
- Shanks, A., J. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnology and Oceanography* 45:230–236.
- Shanks, A. L., A. McCulloch, and J. Miller. 2003. Topographically generated fronts, very nearshore oceanography and the distribution of larval invertebrates and holoplankters. *Journal of Plankton Research* 25:1251–1277.
- Shanks, A., and W. Wright. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. *Journal of Experimental Marine Biology and Ecology* 114:1–13.
- Smith, R. 1995. The physical processes of coastal upwelling systems. Pages 39–64 in C. P. Summerhayes, K. Emeis, M. V. Angel, R. Smith, and B. Zeitzschel, editors. *Upwelling in the ocean: modern processes and ancient records*. John Wiley and Sons, Hoboken, New Jersey, USA.
- Soininen, J., R. McDonald, and H. Hillebrand. 2007. The distance decay of similarity in ecological communities. *Ecography* 30:3–12.
- Sokal, R., and N. Oden. 1978. Spatial autocorrelation in biology. 1. Methodology. *Biological Journal of the Linnean Society* 10:199–228.
- Steen, H., R. A. Ims, and G. A. Sonnerud. 1996. Spatial and temporal patterns of small-rodent population dynamics at a regional scale. *Ecology* 77:2365–2372.
- Storlazzi, C. D., M. A. McManus, and J. D. Figurskib. 2003. Long-term, high-frequency current and temperature measurements along central California: insights into upwelling/relaxation and internal waves on the inner shelf. *Continental Shelf Research* 23:901–918.
- Strub, T., J. Mesias, V. Montecinos, J. Rutland, and S. Salinas. 1998. Coastal ocean circulation off western South America. *The Sea* 11:273–313.
- Tabachnik, B., and L. Fidell. 1989. Using multivariate statistics. Harper Collins, New York, New York, USA.
- van Rensburg, B. J., S. L. Chown, and K. J. Gaston. 2002. Species richness, environmental correlates, and spatial scale: a test using south African birds. *American Naturalist* 159:566–577.
- Vargas, C. A., D. A. Narvaez, A. Piñones, R. Venegas, and S. A. Navarrete. 2004. Internal tidal bore warm fronts and settlement of invertebrates in Central Chile. *Estuarine, Coastal and Shelf Science* 61:603–612.
- Venegas, R., V. Ortiz, and S. A. Navarrete. 2000. Larval development of the intertidal barnacles *Jehlius cirratus* and *Nothochlamys scabrosus* (Cirripedia: Chthamaloidea) under laboratory conditions. *Journal of Crustacean Biology* 20:495–504.
- Wartenberg, D. 1989. SAAP 4.3: Spatial Autocorrelation Analysis Program. Exter Software, Setauket, New York, USA.
- Wing, S., L. Botsford, S. Ralstonm, and J. Largier. 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling systems. *Limnology and Oceanography* 43:1710–1721.
- Wing, S., J. Largier, L. Botsford, and J. Quinn. 1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. *Limnology and Oceanography* 40:316–329.
- Wolanski, E., and W. Hamner. 1988. Topographically controlled fronts in the ocean and their biological influence. *Science* 241:177–181.