Matching spatial scales of variation in mussel recruitment and adult densities across southwestern Atlantic rocky shores

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ABSTRACT

The recruitment of aquatic invertebrate larvae often differs in space and time thus contributing to variation in the abundance of adults. In the present study, we examined spatial scales of variation in mussel (*Brachidontes* spp.) recruitment and adult abundance across rocky intertidal areas in the Southwestern Atlantic. Recruitment and adult densities were compared between two regions separated ca. 700 km from each other, two locations (10–20 km from each other) within each region, and two sites (100–500 m from each other) within each location. Variance components analysis indicates that most variation in mussel recruitment and adult densities occurs at the scale of locations, irrespective of if mussel recruitment is quantified on mussel bed samples or artificial substrates (plastic mesh collectors). Increased mussel recruitment and adult densities at this scale are associated with higher time-averaged chlorophyll *a* concentration and wave exposure, which can potentially affect the supply of larvae to rocky shores by increasing their survival and delivery rates. There was close correspondence between the spatial patterns of variation in cumulative recruitment on natural substrates during the study period and the density of adults at its end. This suggests that differences in mussel abundance along Southwestern Atlantic rocky shores could be primarily determined by larval recruitment.

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1. Introduction

Larval recruitment to rocky shores often extremely varies in space and time (Bertness et al., 1996; Gaines and Roughgarden, 1985; Watson and Barnes, 2004). This is generally due to spatial and temporal variation in the reproductive output of species, as well as larval mortality and redistribution in the open oceanic waters (Gaines and Roughgarden, 1987; Marshall et al., 2009; Moran, 1999). Larval recruitment can significantly influence adult distribution and abundance (Gaines and Roughgarden, 1985; Minchinton and Scheibling, 1991). Furthermore, large-scale differences in recruitment can drive variation in post-settlement processes, such as competition and predation, with consequences for adult population size, species distribution, and overall community structure (Connolly et al., 2001; Menge, 2000).

Variation in recruitment from climatic, oceanographic, and biotic controls operate at a variety of scales (Menge and Menge, 2013; Navarrete et al., 2008b). Broad-scale climatic phenomena, like El Niño–Southern Oscillation, can directly affect species reproductive success generating inter-annual variations in recruitment (see Alvarado and

Castilla, 1996; Stenseth et al., 2002). Moreover, upwelling, winds, and wave action can influence the spatial distribution of larvae and their shoreward transport thus influencing settlement rates (Archambault and Bourget, 1999; Bertness et al., 1996; Vargas et al., 2004). At smaller spatial scales, recruitment and/or post-settlement survival can vary with wave exposure (McQuaid and Lindsay, 2007), tidal height (Lagos et al., 2005), heat and desiccation stress (Lathlean and Minchinton, 2012; Lathlean et al., 2012), stress amelioration by conspecifics (Lathlean et al., 2013), settlement cues (Navarrete and Castilla, 1990), predation on settling larvae (either by adult conspecifics or other organisms; Beadman et al., 2004; Comtet and Desbruyeres, 1998), food concentrations (Menge et al., 1999), or hydrodynamic perturbations caused by substrate roughness elements (Navarrete et al., 2008b).

The mussels *Brachidontes rodriguezii* and *Brachidontes purpuratus* (formerly *Perumytilus purpuratus*, see Adami et al., 2013) are the dominant organisms in the mid-intertidal level of rocky shores along the Argentinean coast (Arribas et al., 2013; Bertness et al., 2006; Penchaszadeh et al., 2007). They both are relatively small-sized mytilids (up to 55 mm length, most individuals less than 30 mm length; Alvarado and Castilla, 1996; Penchaszadeh, 1973). Both species coexist between 41° and 43°S, *B. rodriguezii* is absent southward of this range, and *B. purpuratus* is absent northward (Arribas et al., 2013; Trovant et al., 2013). *B. rodriguezii* was observed to recruit continuously during the year, with peaks during summer and autumn (Adami et al., 2008;

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Penchaszadeh, 1973). A similar temporal pattern of recruitment was observed for *B. purpuratus* in the southeastern Pacific (Navarrete et al., 2002).

Previous studies have shown that adult mussel densities vary across distinct locations in the Argentinean coast, either distant or neighboring ones (Arribas et al., 2013; Bertness et al., 2006; Kelaher et al., 2007). Evaluating what spatial scales contribute the most to variation in mussel densities and whether they match scales of variation in recruitment can shed light on possible causal relationships between both variables. In the present study, we evaluate if spatial variation in the density of adult mussels is related to the variation in mussel recruitment. By means of a hierarchical sampling design, we replicated small-scale measures of adult and recruit density across three spatial scales—i.e., hundreds of meters (sites), tens of kilometers (locations), and hundreds of kilometers (regions)—and investigated if the scales of variation in mussel recruitment and adult densities match each other. Additionally, we compared recruitment in natural substrates (i.e., mussel bed habitats) and in artificial ones (i.e., plastic-mesh pads commonly used in field estimates of mussel recruitment; e.g., Navarrete et al., 2002) to explore whether sampling methods can affect the detection of spatial variations. Last, we tested whether variations in mussel recruitment and adult density are related to each other and discuss whether they could be influenced by spatial variation in oceanographic factors such as chlorophyll *a* concentration and wave exposure.

2. Materials and methods

2.1. Study area and sampling design

The study was conducted at four locations (Fig. 1): Santa Elena (37° 51′S–57° 30′W; hereafter SE), Cabo Corrientes (38° 01′S–57° 31′W; hereafter CC), El Espigón (41° 07′S–63° 00′W; hereafter ES), and La Lobería (41° 09′S–63° 07′ W; hereafter LO). SE, ES, and LO are characterized by eroding cliffs and intertidal abrasion platforms composed of sedimentary rock (Bagur et al., 2013; Kokot et al., 2004). CC is located in the coastline of Mar del Plata (i.e., largest city along the Atlantic Argentinean coast; ca. 650,000 residents) and the intertidal substrate consists of large quartzitic blocks (Penchaszadeh, 1973). All locations have semidiurnal tides. SE and CC are microtidal areas (0.80 m mean tidal

Fig. 1. Locations sampled along Southwest Atlantic coast (37° 51′–41° 09′S). SE: Santa Elena, CC: Cabo Corrientes, ES: El Espigón, LO: La Lobería.

amplitude) while ES and LO are macrotidal (ca. 4 m amplitude; Bagur et al., 2013; Kokot et al., 2004; Penchaszadeh, 1973). Variations in chlorophyll *a* concentration and wave exposure across locations are shown in Table 1.

Locations in the provinces of Buenos Aires (i.e., SE and CC) and Río Negro (i.e., ES and LO) were aggregated into separate regions for the purposes of the hierarchical analysis. In addition, two sites were randomly selected at each location. In this way, we had a spatially hierarchical sampling design with pairs of sites (100–500 m distant from each other) nested within locations (10–20 km from each other), and pairs of locations nested within regions (ca. 700 km distance along the Argentinean coastline).

2.2. Field sampling

Mussel recruitment at each site was monitored from February 2010 to August 2011. Plastic-mesh collector pads (Tuffy ®, 7 cm diameter; *hereafter* Tuffy pads) were placed 1 to 3 m apart from each other at each site. Each individual Tuffy pad was attached to a dowel drilled into the rocks by means of washers and screws. Thirty-two Tuffy pads (i.e., four per site) were placed in the mid intertidal zone and replaced every 34–120 days. The mussels attached to Tuffy pads were removed in the laboratory (the pads were vigorously shaken in water that was then filtered through a 500 μm mesh) and counted. The mussels collected from Tuffy pads showed a range of sizes (up to 22 mm length). To avoid potential biases in recruitment estimates due to adult immigration into Tuffy pads (e.g., by lateral displacement; see Penchaszadeh, 1973), we have conservatively defined recruits as individuals of less than 3 mm length (most individuals collected from Tuffy pads were within this size range). Although both *B. rodriguezii* and *B. purpuratus* occur at ES and LO, it is impossible to visually distinguish between recruits of these species. Consequently, we have pooled both species when quantifying recruit density.

Recruitment in natural substrates was evaluated from cylindrical core samples of the mussel bed (10 cm diameter, 4 replicates per site) taken in the dates of Tuffy pad collection. As in the case of Tuffy pad sampling, only individuals smaller than 3 mm length were considered as recruits and, again, both mussel species were pooled when quantifying recruit density at ES and LO.

Spatial variation in the density of adult mussels was evaluated from the core samples taken at the beginning (February 2010) and the end of the sampling period (August 2011).

2.3. Data analysis

Hierarchically nested ANOVA (Underwood, 1997) was used to test for scales of variation in (a) cumulative recruitment during the 18-month sampling period (measured either from Tuffy pads or natural substrate samples) and (b) adult mussel density at its end. As earlier mentioned, factors included regions, locations nested within regions, and sites nested within locations and regions (all random factors). While two levels of each factor were included in the original sampling design, all Tuffy pad replicates were lost at a site in CC, and thus, an unbalanced nested analysis was necessary in this case. Recruit counts in Tuffy pads were ln(x) transformed to meet the assumptions of homogeneity of variances (Underwood, 1997). Variance components were used to evaluate the contribution of each spatial scale to the total variance of the data set (see O'Leary and Potts, 2011). Residual maximum likelihood (REML) was used to estimate variance components since this method is suitable both for balanced an unbalanced designs and prevents negative estimates that may otherwise occur when variability at one spatial scale is less than would be predicted from the variability observed on a smaller scale (Fletcher and Underwood, 2002).

Pearson correlations (Neter et al., 1991) were used to test for site-scale association between cumulative recruitment in natural mussel beds and Tuffy pads. Multiple regression (Neter et al., 1991) was used
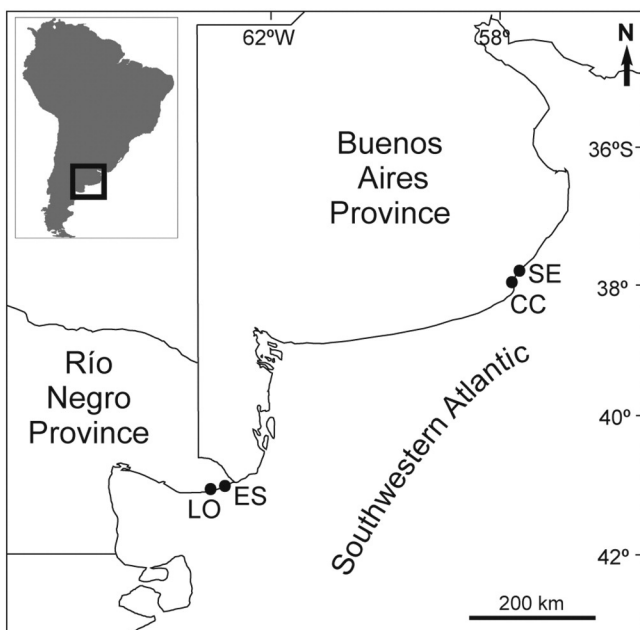
Table 1
Mean (SD) chlorophyll *a* concentration (mg m^{-3}) and wave exposure index at the four Locations considered in this study. SE: Santa Elena, CC: Cabo Corrientes, ES: El Espigón, LO: La Lobería.

Variable	SE	CC	ES	LO	Description
Chl-*a* concentration	3.80 (1.02)	3.06 (0.75)	3.16 (0.99)	3.07 (0.96)	Chlorophyll *a* concentration (mg. m^{-3}) was estimated from satellite images (NOAA; http://oceancolor.gsfc.nasa.gov). We used standard mapped images (SMIs) of monthly satellite-derived chlorophyll *a* concentration from MODIS Aqua for the period May 2010 to August 2011. The images have a spatial resolution of approximately 4 km. The global SMI data were subsampled from the region bounded by 33 to 43° S and 49 to 65°W. Satellite data were extracted ca. 2 km from the coast.
Wave exposure index	8.96	7.29	4.79	7.62	Wave exposure at the different locations was quantified with an exposure index using local wind data and nautical charts according to Thomas (1986). The formula for this index is W × (F modified by CS), where W is the wind energy, F is the fetch in nautical miles (100 nautical miles maximum) and CS is the extent in nautical miles of water <6 m deep bordering the shore (used as the critical depth).

to evaluate the degree to which variation in adult mussel density at the end of the recruitment monitoring period were related to variations in initial adult densities and cumulative mussel recruitment (either in natural beds and Tuffy pads). Collinearity was evaluated by means of the variance inflation factor (VIF; Neter et al., 1991). Extra sum of squares was used to test whether an independent variable could be dropped or should be retained in the multiple regression model (Neter et al., 1991).

Fig. 2. Mean (SD) density of mussel recruits (ind. m^{-2}) in Tuffy pads and natural substrate at each sampling location and date. Note the different scales in the Y-axes of the top and bottom panels.

3. Results and discussion

As in previous studies on *B. rodriguezii* and *B. purpuratus* (Adami et al., 2008; Navarrete et al., 2002), mussel recruitment was observed here to occur all year round (see Fig. 2). Despite continuous recruitment at all sites, peaks were observed in some cases (e.g., March and June 2011 at SE and CC; Fig. 2). Similar temporal trends in recruitment were observed when considering estimates from natural mussel beds and Tuffy pads (Fig. 2). Yet, both methods gave markedly different estimates at some locations (see Figs. 2 and 3) and, accordingly, the site-scale recruitment estimates obtained from each method were not significantly correlated ($r = 0.31$, df = 5, $p > 0.05$). Invertebrate recruitment onto Tuffy pads can be lower than recruitment on natural substrate (see Navarrete et al., 2008a). Here we observed inconsistency among locations in the relative magnitude of the recruitment estimates obtained by means of each method. For instance, Tuffy pad estimates of recruitment at SE were 2–3 times higher than estimates from natural substrate, meanwhile natural substrate estimates at LO were nearly twice those from Tuffy pads (see Fig. 3). This suggests that there were location-specific factors aside from larval supply that affected recruitment on either substrate. For instance, larval recruitment onto natural substrates can be affected by the density of adult conspecifics (Alvarado and Castilla, 1996; Hidas et al., 2013). On the other hand, and in contrast to natural substrates, artificial substrates like Tuffy pads provide an attachment site that is free from any potential influence of adult conspecifics (Ricciardi et al., 1997). Nonetheless, both substrates can potentially—and differentially—be affected by the characteristics of the surrounding setting (e.g., rock topography, flow characteristics, sedimentation, biota) or the recruitment of non-target organisms (e.g., algal overgrowth; Jenkins et al., 2000; Menge et al.,
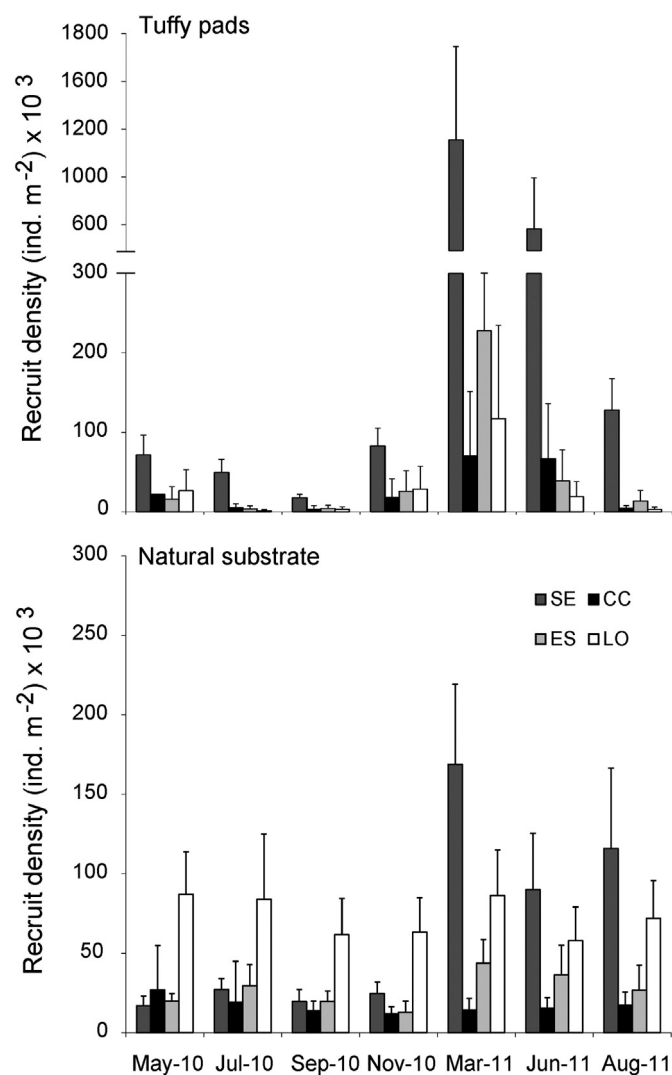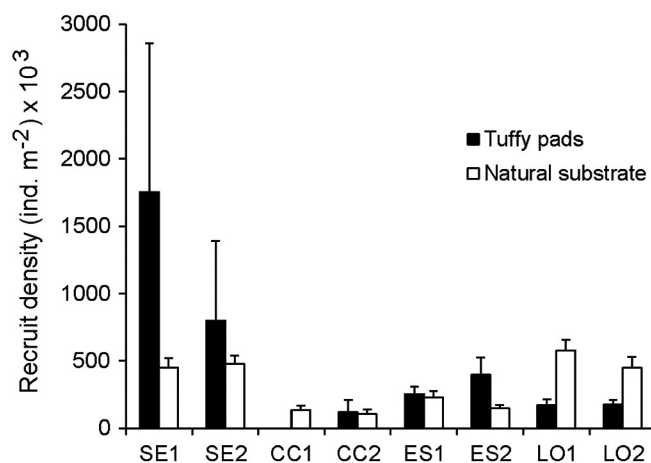

Fig. 3. Mean (SD) cumulative mussel recruitment per area unit (ind. m^{-2}) on artificial plastic mesh collectors (Tuffy pads) and natural substrate at each sampling site during the 18-month study period.

Table 2
Hierarchically nested ANOVA testing spatial scales of variation in cumulative mussel recruitment in artificial plastic mesh collectors (Tuffy pads) and natural substrate (Mussel beds) during the 18-month period. Tuffy pad data were ln(x) transformed to meet the assumption of homogeneity of variances.

| Source | Tuffy pads | | | Mussel beds | | |
	df	MS	F	df	MS	F
Regions	1	1.14	0.13	1	27844993732	0.06
Locations (Reg.)	2	8.85	15.10*	2	446044596118	36.20**
Sites (Reg. × Loc.)	3	0.59	1.70	4	12320501849	3.61*
Residual	21	0.35		24	3417249516	

* $p < 0.05$.
** $p < 0.01$.

Table 3
Hierarchically nested ANOVA testing spatial scales of variation in adult mussel density at the end of the recruitment monitoring period.

| | Adult density | | |
Source	df	MS	F
Regions	1	3612500000	0.41
Locations (Reg.)	2	8872413181	29.92*
Sites (Reg. × Loc.)	4	296572376	2.02
Residual	24	147071720	

* $p < 0.01$.

1994). Differences in the relative magnitude of recruitment estimates obtained by each method may be associated to variation across locations in environmental and biotic features that differentially affect the suitability of the substrate for settling larvae or its probability of encounter.

Cumulative mussel recruitment during the study period was not significantly different across regions (Table 2). However, significant differences were found between locations within each region (considering both Tuffy pads and natural substrate) and sites within locations and regions (considering only natural mussel beds; Table 2, Fig. 3). Most variation in cumulative mussel recruitment occurred here at the scale of locations (71 and 87% of variation in Tuffy pads and natural mussel bed areas, respectively; Fig. 4). Variations in larval recruitment at a scale like this (tens of kilometers) are generally associated to differences in larval supply rates (Hidas et al., 2013; Jenkins et al., 2000). Larval supply can vary because of differences in local larval production and oceanographic factors that affect the size of the larval pool and the fluxes of larvae toward the intertidal zone (Bertness et al., 1992; Jenkins et al., 2000). Spatial variations in the settlement of benthic invertebrates are often strongly influenced by local wind conditions (which affect the transport of larvae shoreward; see Bertness et al., 1996), near-shore pelagic productivity (Menge et al., 1997), and wave exposure (Bertness et al., 2006; Broitman et al., 2008). In our study, locations within each single region were similar as regard to orientation and prevailing wind conditions (see Fig. 1). Nonetheless, locations showing the highest cumulative recruitment at each region were characterized either by a higher time-averaged chlorophyll *a* concentration (ES, if considering Tuffy pad recruitment), a higher wave exposure index (LO, if considering recruitment on natural substrates), or both (SE, irrespective of settlement substrate; see Table 1 and Fig. 3). Larger larval pools are expected to occur with increased chlorophyll *a* concentration because phytoplankton is an important food source for developing larvae (Jenkins et al., 2000). In addition, increased wave-exposure is expected
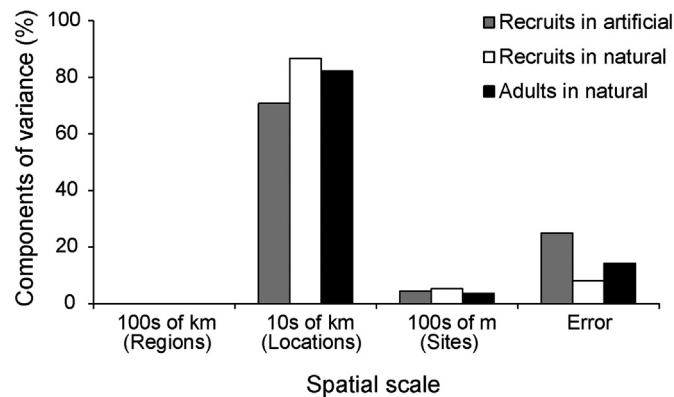
to cause larger larval fluxes to intertidal rocky shores (Gaines and Bertness, 1993). Thus, differences in phytoplankton production and wave exposure across locations could be contributing to location-scale variations in mussel recruitment.

Adult mussel densities at the end of the recruitment monitoring period were significantly different only at the scale of locations (Table 3, Fig. 5). As in the case of cumulative recruitment, locations accounted for most spatial variation in adult densities (82%; Fig. 4). Matching scales of variation in recruitment and adult densities may simply indicate that processes operating at the same scale control both the recruitment and subsequent survival of mussels or, more specifically, that recruitment is the chief determinant of adult mussel densities (i.e., mortality after recruitment would be proportionally similar across locations). In this latter case, adult densities and preceding recruitment should be positively related to some degree. In this regard, our results from regression analysis indicate that adult mussel densities at the end of the monitoring period were positively related to cumulative mussel recruitment on natural mussel beds but unrelated with cumulative mussel recruitment on Tuffy pads (Table 4, Fig. 6A). Certainly, variations across locations (and sites) in cumulative recruitment on natural substrates and adult densities closely mirrored each other (see Figs. 3 and 5), which suggests that post-recruitment processes might not noticeably contribute to spatial variation in adult densities (i.e., adult mussel densities would thus be primarily controlled by recruitment). In this context, lack of relationship between final adult densities and preceding cumulative recruitment on Tuffy pads may well indicate biases in the mussel recruitment estimates obtained by this means.

Initial adult densities were also positively related to variation in final adult densities across locations (Fig. 6B). Single regression models with initial adult density as independent variable explained ca. 60% variation in final adult densities (Table 4). Yet, cumulative mussel recruitment on natural substrate was a better predictor of final adult densities (83% explained variability in single regression models; Table 4). The multiple regression model including cumulative recruitment in natural substrate and initial adult densities as independent variables (VIF: 1.45; i.e., no collinearity) was the most parsimonious one in explaining variation in
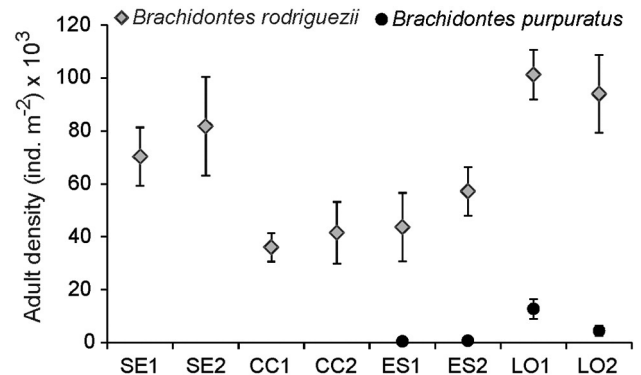

Fig. 4. Components of variation (%) in mussel adult densities and recruitment at each spatial scale. Recruitment on natural substrates and artificial plastic mesh collectors (Tuffy pads) is analyzed separately.

Fig. 5. Mean (SD) density (ind. m^{-2}) of adult mussels (*Brachidontes rodriguezii* and *B. purpuratus*) at each sampling site at the end of the study period.

Table 4

Regression models relating adult densities at each location at the end of the study period (dependent variable) with cumulative recruitment during the same period and initial adult densities (independent variables) when considering (A) recruitment estimates from natural substrate (NS; $n = 8$) and (B) recruitment estimates from Tuffy pads (TP; $n = 7$). Daggers indicate the most parsimonious models in each case.

Independent variables	r^2	MS	df	F
(A) Recruitment (NS)	0.83	1.59×10^8	6	29.36[**]
Initial adult densities	0.62	3.53×10^8	6	9.93[*]
Recruitment (NS) + initial adult densities[†]	0.95	6.19×10^7	5	43.01[**]
(B) Recruitment (TP)	0.00	8.93×10^8	5	1.64×10^{-3}
Initial adult densities[†]	0.57	3.79×10^8	5	6.76[*]
Recruitment (TP) + initial adult densities	0.81	2.11×10^8	4	8.57[*]

[*] $p < 0.05$.
[**] $p < 0.01$.

adult densities (Table 4). Thus, variation in final adult densities across locations seems to result from combined influences of variation in recruitment and initial adult densities.

4. Conclusion

Our results indicate that most spatial variation in mussel recruitment and adult abundance occurs at a scale of tens of kilometers. Variation at a larger scale (hundreds of kilometers) is negligible despite noticeable differences in oceanographic factors (e.g., sea-surface temperature, tidal amplitude, coastal circulation) within our study range (Arribas et al.,

2013; Piola and Rivas, 1997). Enhanced mussel recruitment at a tens of kilometers scale is associated to increased chlorophyll *a* concentration and wave exposure, which can potentially affect the supply of larvae to rocky shores by increasing their survival and delivery rates (Jenkins et al., 2000; McQuaid and Lindsay, 2007). Close correspondence between the spatial patterns of variation in adult densities and preceding recruitment in the mussel bed suggests that differences in mussel abundance along Southwestern Atlantic rocky shores would be primarily determined by larval recruitment. Despite that, post-settlement process could still affect local mussel densities by controlling the survival of recruits. Since mussels are the dominant organisms on these shores in terms of percentage cover of the rock substrate and creation of habitat to other organisms (Bertness et al., 2006; Borthagaray and Carranza, 2007), variations in mussel recruitment may have important consequences for the recruitment and survival of other organisms and, in turn, for rocky shore community structure (see Koivisto et al., 2011).
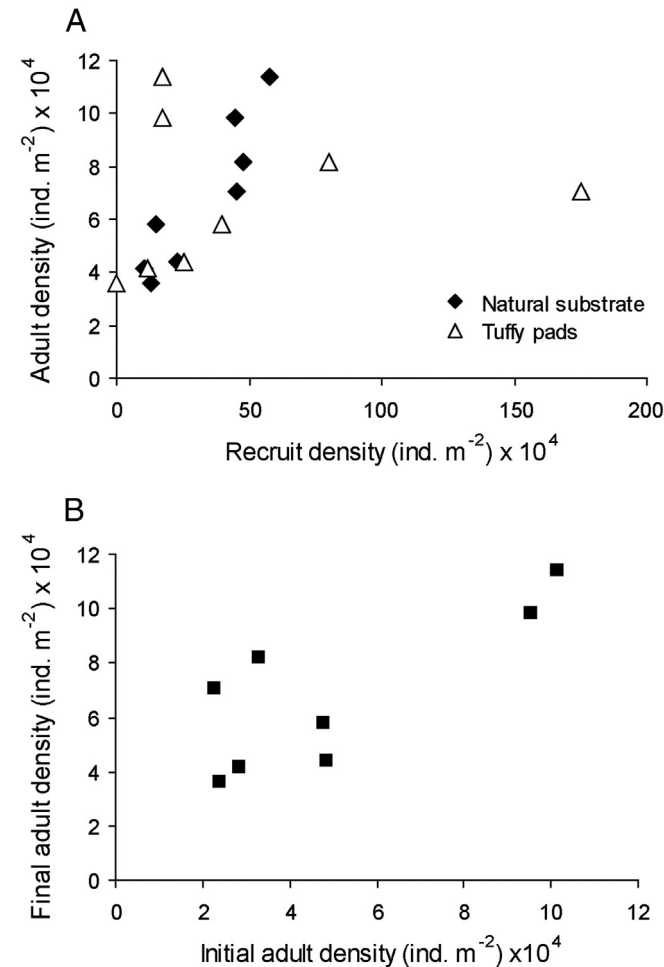
Fig. 6. Relationships between mean adult densities at the end of the study period and (A) cumulative recruitment estimates from natural substrate and Tuffy pads during the previous 18 months, and (B) adult densities at the beginning of the study period.

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