Connectivity and patch area in a coastal marine landscape: Disentangling their influence on local species richness and composition

ANA INÉS BORTHAGARAY,[1,2,3]★ ALEJANDRO BRAZEIRO[3] AND LUIS GIMÉNEZ[4]

[1]*Instituto de Ecología y Biodiversidad (IEB), Casilla 653, Santiago, Chile,* [2]*Departamento de Ecología and Centro de Estudios Avanzados en Ecología y Biodiversidad (CASEB), Pontificia Universidad Católica de Chile, Alameda 340, Casilla 114-D, Santiago (Email: aborthagaray@bio.puc.cl),* [3]*Departamento de Ecología, Facultad de Ciencias, Montevideo, Uruguay; and* [4]*School of Ocean Sciences, Bangor University, Menai Bridge, Wales, UK*

Abstract   Landscape ecology emerged as a terrestrial discipline to evaluate the effect of spatial configuration of natural systems on ecological patterns. The advances in marine systems have been comparatively scarce perhaps as a consequence of a long-standing view about the greater dispersal potential of marine species and its effect on the spatial homogenization of marine landscapes. Herein we used an intertidal rocky system as a model to analyse the effect of landscape attributes on local species richness and composition. We evaluated the effect of patch area, landscape connectivity and salinity gradient on local species richness of macro-invertebrates, and the effect of geographic distance on species similarity. We sampled 19 rocky patches along the Uruguayan Atlantic coast one time during the spring of 2003. The relative contribution of the variables assessed on specific richness of sessile, mobile and total macrofauna was analysed with a stepwise multiple linear regression. For the mobile macrofaunal richness, we also incorporated the sessile macrofaunal richness as another independent variable. The effect of geographic distance on biological similarity was assessed by a Mantel test. We showed that landscape connectivity, as a descriptor of the average physical isolation of a biological community in the landscape, is an important factor explaining the community species richness for sessile macrofauna, what indirectly increases the mobile macrofaunal richness. The geographic distance between sites was negatively related to species similarity. We suggest that at the landscape scale, connectivity among sites can be important to understand the local structure of marine communities, particularly in rocky intertidal systems. Also the distance-decay of similarity in community composition provides a useful descriptor of how biological composition varies along a physical gradient. Our results contribute to reinforce the view that mesoscale connectivity (10^{1-2} km) in coastal marine landscapes plays a more important role in local community structure than previously assumed.

Key words: Atlantic coast, landscape connectivity, patch area, species composition, species richness.

INTRODUCTION

It is well known that species richness and composition of local communities reflect interactions between several distinct spatial processes operating at different spatial and temporal scales (Ricklefs 1987, 2004; Holt 1993; Schluter & Ricklefs 1993; Caley & Schluter 1997; Shurin & Srivastava 2005). Also the manifestation of spatial processes is shaped by different aspects of the landscapes attributes (e.g. topography, slope, soil, connectivity, size and shape of sites, see Rietkerk *et al.* 2004; Starzomski & Srivastava 2007). For that reason, the spatial features of the landscape attributes, where these communities are embedded, should be

considered in order to understand the structure and organization of local communities (e.g. Turner *et al.* 2001; Gonzalez 2005).

Since the theory of island biogeography of MacArthur and Wilson (1967), the patch area and the connectivity among patches are considered the main determinants of the number and composition of species in a locality (Rosenzweig 1995; Ricklefs & Lovette 1999; Tischendorf & Fahrig 2000; Johnson *et al.* 2003; Niegel 2003; Whaley *et al.* 2007). From this theory, landscape ecology has emerged as an ideal framework to address the importance of spatial configuration of natural systems, emphasizing the role of landscape attributes (e.g. connectivity) on ecological patterns and processes (Forman 1983; Turner 1989; Wiens *et al.* 1993; Turner *et al.* 2001; Wu 2007). A landscape is defined as a mosaic of patches connected

by a matrix that extend over tens of meters and 'that is spatially heterogeneous in at least one factor of interest' (Turner *et al.* 2001). In terrestrial systems this discipline has experienced a considerable development (McGarigal & McComb 1995; Fahrig 1997; McAlpine *et al.* 1999; Trzcinski *et al.* 1999; Villard *et al.* 1999; Schmiegelow & Mönkkönen 2002; Xu *et al.* 2002).

Applications of a landscape approach to the study of marine ecosystems are still few (Irlandi *et al.* 1995; Ault & Johnson 1998; Turner *et al.* 1999; Hovel *et al.* 2002; Pittman & McAlpine 2003; Pittman *et al.* 2004; Cowen *et al.* 2006). One possible reason of this disparity between terrestrial and marine systems is the idea about the greater physical connectivity of marine ecosystems (Jones *et al.* 1992) and the potential for long-distance dispersal of marine larvae (Scheltema 1986; Kinlan & Gaines 2003). In addition, species with direct development may disperse by rafting (Thiel & Gutow 2005). Under these views, the distance among local patches, as proxy of landscape connectivity, should not play a significant role in the assemblage of local communities as a consequence of a considerable spatial homogenization. However, in the last years an increasing body of evidence demonstrated that larval dispersal may be appreciably shorter than previously assumed (Palumbi 2003; Miller & Shanks 2004; Cowen *et al.* 2006; Becker *et al.* 2007; but see Kinlan & Gaines 2003). For example, Cowen *et al.* (2006) reported for reef fish species that the ecologically important larvae dispersal distances are on the scale of 10–100 km. These results suggest that the level of homogenization of marine landscapes is not as high as previously assumed.

In addition, the perception of the spatial configuration of habitat may depend on the species (Nekola & White 1999) leading to a species- or functional group-specific effect of patch area or landscape connectivity on local richness and composition (see Collins & Glenn 1991; Broitman *et al.* 2001; Marquet *et al.* 2004; Baguette & Dyck 2007). For example, along the intertidal landscape mobile species (e.g. peracarid crustaceans, gastropod molluscs) are affected by bioengineer sessile organisms such as mussels (Prado & Castilla 2006) while sessile species may be affected by both bioengineer effects and space competition (Gascoigne *et al.* 2005). According to that view, we should expect a stronger area effect on the sessile macrofauna in relation to the mobile macrofauna. However, if we consider the degree of connectivity among patches this effect could vary, because the influx of larvae between pairs of sites increase the similarity in community composition of nearby sites (Oliva & González 2005).

If connectivity and patch area vary among local communities at landscape scale (10^1–10^2 km), then colonization and extinction rates, and therefore species richness and composition should also vary (see MacArthur & Wilson 1967; Brown & Kodric-Brown 1977). To assess this general hypothesis, we analysed the effect of landscape attributes on rocky intertidal communities from the Uruguayan coast. Specifically, we evaluated the effect of patch area, landscape connectivity and salinity gradient on local species richness of macro-invertebrates, and the effect of geographic distance on species similarity. Rocky intertidal systems represent an ideal marine model to evaluate the role of patch area and landscape connectivity on local communities because of the following reasons. First, it is a well defined system with discrete rocky patches separated by sandy arcs; it can be therefore identified in the coastal landscape. Second, the connection among local communities, principally due to larval dispersal, may be important. Third, the space as limiting resource for sessile organisms plays an important role in the community organization (Raffaelli & Hawkins 1996).

Apart from the analysis using the richness and composition of the whole community, we disaggregated the data in two species functional groups, sessile and mobile macrobenthos, and tested effects of connectivity and patch area per group. In rocky intertidal communities these functional groups, with contrasting biology, are easily identified and allow disaggregation the overall patterns at the community level.

MATERIAL AND METHODS

Study system

The Uruguayan coast, of about 670 km in length, is strongly affected by the fresh water discharge of the Río de la Plata into the Atlantic Ocean (Fig. 1). The Río de la Plata is a funnel-shaped, coastal plain, microtidal estuary that drains the second largest basin of South America (Framiñan & Brown 1996; Nagy *et al.* 1997) and provides the major source of freshwater run-off in the south-west Atlantic. The impact of freshwater run-off is highly variable depending on wind forcing and river discharge (Guerrero *et al.* 1997; Möller *et al.* 2008). During the austral winter the nearshore current pattern is characterized by a balance between onshore and offshore winds generating a main north-easterly drift of the estuarine waters along the Uruguayan coast (Guerrero *et al.* 1997). This estuarine plume may reach the Brazilian coast as far as 23–28°S (Campos *et al.* 1999; Möller *et al.* 2008). However, during summer, onshore winds become dominant resulting in a southward drift along the Argentine coast and consequently shelf waters penetrate up to Punta del Este, Uruguay (Guerrero *et al.* 1997).
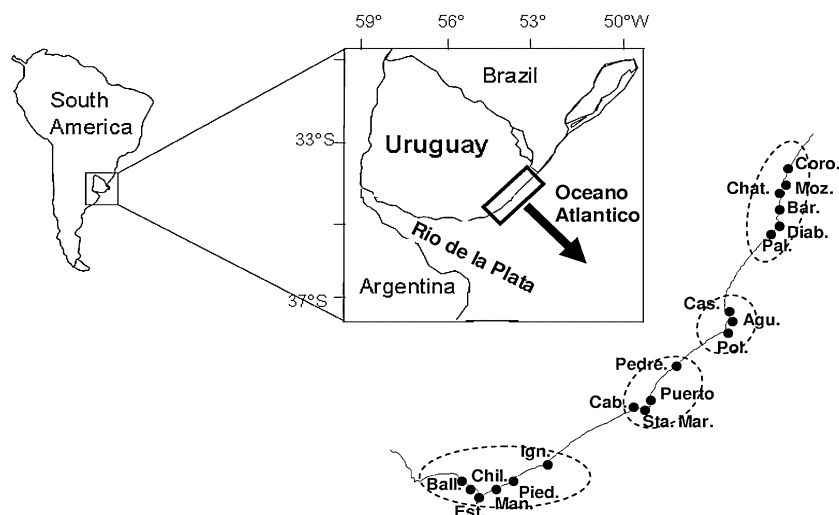
Fig. 1. Geographic location of the 19 rocky points sampled along the Uruguayan Atlantic coast. The dashed lines indicate the natural aggregations considerate to calculate the neighbourhood connectivity. Abbreviations of sites are: Ball., Punta Ballena; Chil., Punta del Chileno; Est., Punta del Este; Man., Punta Manantiales; Pied., Punta Piedras; Ign., José Ignacio; Cab., El Cabito; Sta.Mar., Cabo Santa María; Puerto, Puerto de la Paloma; Pedre., La Pedrera; Pol., Cabo Polonio; Agu., Punta Aguda; Cas., Cabo Castillo; Pal., Punta Palmar; Diab., Punta del Diablo; Bar., Punta del Barco; Chat., Punta Cerro Chato; Moz., Punta de la Moza; Coro., Punta Coronilla.

Although during extreme events (e.g. El Niño) the Río de la Plata could influence the environmental conditions of all Uruguayan coast, it is possible to distinguish, under normal conditions, an estuarine (estuarine coast) and an oceanic sector (Atlantic coast). Our study was conducted in the Atlantic coast of Uruguay (about 300 km), where rocky shores represent a prominent feature of the coastal landscape. These communities are isolated from the nearest rocky communities of the region. At the south, the nearest rocky patches are located in the estuarine coast, where the species pool is a small subgroup of the one of the Atlantic coast (Brazeiro et al. 2006), and secondly the Argentinean rocky shores located further south and separated by the Río de la Plata (maximum width 230 km). Thus, potential species migrations from the south would not affect species richness or composition of the studied local communities. Towards the north, the nearest rocky shores are located at a distance of about 700 km (Torres, Brazil, 29°19′36″S, 49°46′03″O).

The physiognomy of the Atlantic coast of Uruguay is dominated by large sandy beaches separated by discrete rocky headlands (called hereafter rocky patches). The rocky patches have a clustered distribution (Fig. 1), and are characterized by smooth slopes (<30°) and narrow widths (15–23 m). They are in general fully exposed to wave action, and show a classical vertical zonation scheme (Stephenson & Stephenson 1949), in which three zones can be identified: a high intertidal zone dominated by a cyanobacterial film; a middle intertidal zone dominated by barnacles; and a low

zone characterized by a dense cover of mussels and/or macro-algae (Scarabino et al. 1975; Maytía & Scarabino 1979; Neirotti 1981; Batallés et al. 1985). In this work we focus on the assemblages of the middle and low intertidal zones.

Sampling

We sampled the main rocky patches of the Atlantic coast, consisting in 19 rocky headlands, (Fig. 1), during the spring of 2003. These patches form four clusters along the coastal landscape (Fig. 1). Depending on the patch area a variable number of quadrats of 20×20 cm (between 10 and 40 quadrats) were randomly sampled, equally distributed within the middle intertidal and the low intertidal. All the macrobenthic organisms (invertebrates) within the quadrats were collected and fixed (formalin 10%) for posterior identification and quantification in the laboratory. We also determined water salinity (was Horiba U-10 Multiparameter sensor). Although records of three sites were lost, we could use distance as a surrogate of salinity for the analysis because there is a significantly positive correlation between salinity and geographic distance, measured from the site Punta Ballena (point zero, see Fig. 2).

Estimations of connectivity and patch area

Because of the pattern of coastal circulation of the study area (see Section *Study system*), we consider that
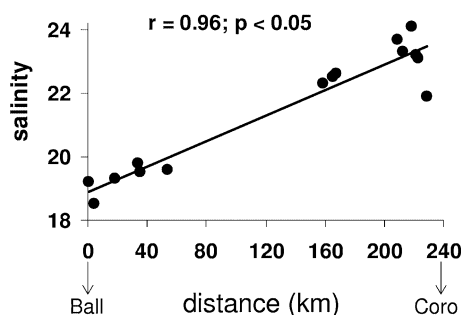
Fig. 2. Positive correlation between the salinity gradient and the geographic distance taking the first site studied as a reference point until the last one (Punta Ballena = 0 km; Punta Coronilla = 240 km). Abbreviations of sites as in Fig. 1.

all habitat patches are physically well connected. In consequence, habitat patches should receive pelagic stages from any other patch, irrespective of the inter-patch distance. Therefore we used geographic distance among patches as proxy of connectivity. For species richness analyses, two indices were used: (i) landscape connectivity, that is, the average distance from the focal patch to each of the others 18 patches, and (ii) neighbour connectivity, that is, the average distance from the focal patch to the nearest neighbour patch. The neighbour patches were defined as those that naturally form clusters with the focal patch (see Fig. 1). We calculated a third metric, the geographic distance between patches, that is, a matrix of geographic distance between pairs of patches, in order to assess the effects of connectivity on species similarity among patches. Given that tidal amplitude and platform slope are similar along the Uruguayan Atlantic coast, we used the coastal perimeter of each rocky patch as an index of its area. The estimations of both the patch area (i.e. patch perimeter) and the three connectivity metrics were done using aerial photographs and digital maps (scale: 1:50 000), with the help of image analysis software.

Data analysis

All the analyses were conducted for total macrofauna as well as for sessile and mobile groups separately. We also considered the fauna of the whole patch and each intertidal level separately in order to test the effect of intertidal level on our community attributes.

The importance of landscape attributes on species richness was evaluated by stepwise multiple linear regressions. Landscape features (patch area, landscape connectivity, neighbour connectivity and salinity) were used as independent variables and local specific richness as dependant variable. Landscape connectivity and neighbour connectivity were used in separated

models but only the ones that explain higher percentage of total variance of the dependant variable (i.e. higher r^2) were reported. Cochran's C-test was used to check the assumption of homogeneity of variances and when necessary, data were log-transformed to remove heterogeneous variances. In the analysis of the mobile macrofauna, the species richness of the sessile macrofauna was incorporated as another independent variable. Previous papers show that sessile species are important in structuring assemblages of mobile invertebrates (Cerda & Castilla 2001; Gutierrez *et al.* 2003; Prado & Castilla 2006; Borthagaray & Carranza 2007). For the mobile richness analysis the model without the sessile species richness as independent variable was also evaluated in order to be compared with the one that consider the sessile species richness as independent variable. In this case, only the total model that explains the highest proportion of total variance for the mobile species was reported.

Differences in species richness between the intertidal levels studied (middle intertidal and low intertidal) were evaluated by means of a two-way analysis of variance (ANOVA, Zar 1999), with intertidal level and faunal group representing the factors and species richness the dependent variable.

The influence of landscape connectivity on species composition was assessed through the relationship between the biological and the geographic distance matrices by a Mantel test. The biological distance matrix was obtained by applying the Jaccard coefficient to the matrix of species composition per site. The significance values of the observed correlation were estimated using the RELATE module of the PRIMER community analysis program (Clarke & Warwick 1994). The null hypothesis of no association between the biological and the geographic distance matrices was rejected if no more than 5% of the randomly generated associations exceeded the observed value.

RESULTS

A total of 52 species (or operative taxonomic units) of benthic invertebrates, distributed in seven major taxa were found in the 19 patches sampled (Table 1). These were: 23 crustaceans (four sessile and 19 mobile), 12 molluscs (six sessile and six mobile), five cnidarians, nine polychaetes, one pycnogoniid, one nemertean and one platyhelminth.

Local species richness

For the whole patch, total species richness was affected by landscape connectivity and salinity gradient although there was a considerable portion (40%) of unexplained variance (Table 2a). For the sessile

Table 1. Mean (±SD) and upper and lower values of the number of species per patch and tidal levels (low zone and middle zone (N: number of quadrats sampled in each case)

	Mean (±SD)	Lower	Upper	N
a) Whole patch				
Punta Ballena	4.89 ± 2.85	1	11	28
Punta del Chileno	9.50 ± 2.63	6	14	20
Punta del Este	10.45 ± 3.10	5	17	40
Punta Manantiales	9.50 ± 3.85	4	15	8
Punta Piedras	10.75 ± 1.26	2	5	8
Punta José Ignacio	10.52 ± 4.16	1	18	28
El Cabito	11.64 ± 5.94	1	20	14
Cabo Santa María	11.47 ± 6.32	3	20	20
Puerto de la Paloma	12.15 ± 6.44	3	22	20
La Pedrera	14.85 ± 6.31	2	25	20
Cabo Polonio	13.33 ± 5.75	4	24	28
Punta Aguda	12.90 ± 5.46	5	25	20
Cabo Castillo	12.63 ± 11.32	3	51	19
Punta Palmar	12.15 ± 4.51	5	19	20
Punta del Diablo	14.65 ± 3.06	9	20	17
Punta del Barco	10.70 ± 5.05	2	22	20
Punta Cerro Chato	8.80 ± 3.68	5	17	10
Punta de la Moza	12.30 ± 4.41	6	20	20
Punta Coronilla	13.05 ± 5.12	3	20	20
b) Low intertidal				
Punta Ballena	5.93 ± 2.73	2	11	14
Punta del Chileno	8.60 ± 2.12	6	12	10
Punta del Este	11.40 ± 3.03	7	17	20
Punta Manantiales	11.50 ± 2.65	9	15	4
Punta Piedras	10.75 ± 2.06	8	13	4
Punta José Ignacio	12.93 ± 3.32	8	18	14
El Cabito	16.71 ± 2.63	12	20	7
Cabo Santa María	15.80 ± 4.54	7	20	10
Puerto de la Paloma	16.00 ± 5.79	3	22	10
La Pedrera	20.20 ± 2.35	17	25	10
Cabo Castillo	16.44 ± 3.40	11	21	9
Punta Palmar	15.70 ± 2.67	11	19	10
Punta del Diablo	15.50 ± 2.78	12	20	8
Punta del Barco	14.60 ± 3.24	10	22	10
Punta Cerro Chato	9.60 ± 4.56	6	17	5
Punta de la Moza	16.10 ± 2.02	14	20	10
Punta Coronilla	9.30 ± 4.06	3	17	10
c) Middle intertidal				
Punta Ballena	3.86 ± 2.66	1	9	14
Punta del Chileno	10.40 ± 2.88	6	14	10
Punta del Este	9.50 ± 2.95	5	15	20
Punta Manantiales	7.50 ± 4.12	4	12	4
Punta Piedras	3.75 ± 1.26	2	5	4
Punta José Ignacio	12.93 ± 3.32	1	18	14
El Cabito	6.57 ± 3.10	1	10	7
Cabo Santa María	6.67 ± 4.15	3	14	10
Puerto de la Paloma	8.30 ± 4.60	4	15	10
La Pedrera	9.50 ± 3.87	2	13	10
Cabo Polonio	8.54 ± 2.96	4	13	14
Punta Aguda	9.00 ± 2.54	5	12	10
Cabo Castillo	9.20 ± 14.79	3	51	10
Punta Palmar	8.60 ± 2.80	5	13	10
Punta del Diablo	13.89 ± 3.26	9	19	9
Punta del Barco	6.80 ± 3.08	2	11	10
Punta Cerro Chato	8.00 ± 2.83	5	11	5
Punta de la Moza	8.50 ± 2.22	6	13	10
Punta Coronilla	16.80 ± 2.78	13	20	10

Table 2.   Proportion of the variance explained (r^2) of the specific richness by the patch area, landscape connectivity and salinity gradient

	Total richness		Sessile richness		Mobile richness	
	r^2	P	r^2	P	r^2	P
a) Whole patch						
Landscape connectivity	0.370	0.005	0.300	0.010	0.030	0.190
Patch area	0.090	0.088	0.180	0.020	n.i.	n.i.
Salinity gradient	0.130	0.062	0.120	0.090	n.i.	n.i.
Sessile richness					0.690	0.000
b) Low intertidal						
Landscape connectivity	0.500	0.000	0.370	0.006	0.080	0.037
Patch area	0.160	0.007	0.150	0.023	n.i.	n.i.
Salinity gradient	0.100	0.050	0.140	0.050	n.i.	n.i.
Sessile richness					0.690	0.000
c) Middle intertidal						
Landscape connectivity	n.i.	n.i.	0.070	0.220	0.060	0.170
Patch area	0.250	0.027	0.120	0.110	n.i.	n.i.
Salinity gradient	0.180	0.039	0.200	0.050	n.i.	n.i.
Sessile richness					0.450	0.001

For the mobile macrofauna the sessile richness was also considered as a predictor variable. In all the cases the r^2 values and P values by each factor are indicated. (n.i. means that the factor was not included by the model as a significant predictor of the richness variance).

species, richness was explained by landscape connectivity and patch area while for mobile species, the only significant variable was the richness of sessile species (Table 2a). Landscape connectivity was better predictor of total ($r^2 = 0.37$) and sessile ($r^2 = 0.30$) macrofauna than salinity or patch area, suggesting that patches better connected harbour a higher number of species. The effect of the salinity gradient was significant only for the total macrofaunal richness ($r^2 = 0.13$, $P = 0.05$). The positive relation between the species richness and the patch area was only significant for the sessile macrofauna ($r^2 = 0.18$, $P = 0.02$).

The pattern observed at the low intertidal for the total and sessile macrofauna was similar to the one described above for the whole patch (total macrofauna: $r^2 = 0.76$ and sessile macrofauna $r^2 = 0.66$, Table 2b). For the total macrofauna, the highest proportion of variance was explained by the landscape connectivity ($r^2 = 0.50$) followed by the patch area ($r^2 = 0.16$). For the sessile macrofauna, landscape connectivity explained a small proportion of variance ($r^2 = 0.37$) but still higher than the one of patch area ($r^2 = 0.14$). The salinity gradient explained a low percentage of variance in both richness of total and sessile species ($r^2 = 0.10$ and $r^2 = 0.15$ respectively). The richness of mobile species was mainly predicted by the richness of sessile macrofauna ($r^2 = 0.69$, $P < 0.0001$, Table 2b); the landscape connectivity played a significant but small role ($r^2 = 0.08$).

For the middle intertidal, the independent variables explained a lower percentage of variance as compared with the low intertidal and the whole patch (total
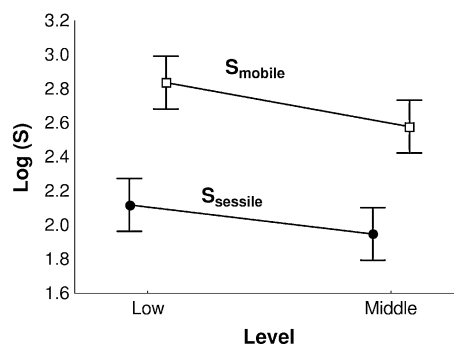
Fig. 3.   Variation in mean specific richness log-transformed between macrofaunal groups (sessile and mobile) and tidal levels (low zone and middle zone). Vertical bars denote 0.95 confidence intervals.

macrofauna: $r^2 = 0.43$ and sessile macrofauna $r^2 = 0.39$, Table 2c). For the total macrofauna, the patch area and the salinity gradient significantly explained respectively the 25% and 18% of the richness. For the sessile macrofauna, patch area was not significant while the salinity gradient explained 20% of the variance. The percentage of richness of mobile species explained by the sessile macrofauna was 45%.

The species richness was significantly higher in the low intertidal than in the middle intertidal (Fig. 3, $F_{(1,72)} = 7.6$, $P < 0.05$), while the richness of sessile species was significantly lower than that of the mobile species (Fig. 3, $F_{(1,72)} = 75.34$, $P < 0.05$). The nonsignificant level $\times$ faunal-group interaction suggested that the effect of the intertidal level effect on the species

a) Whole Patch

b) Low intertidal
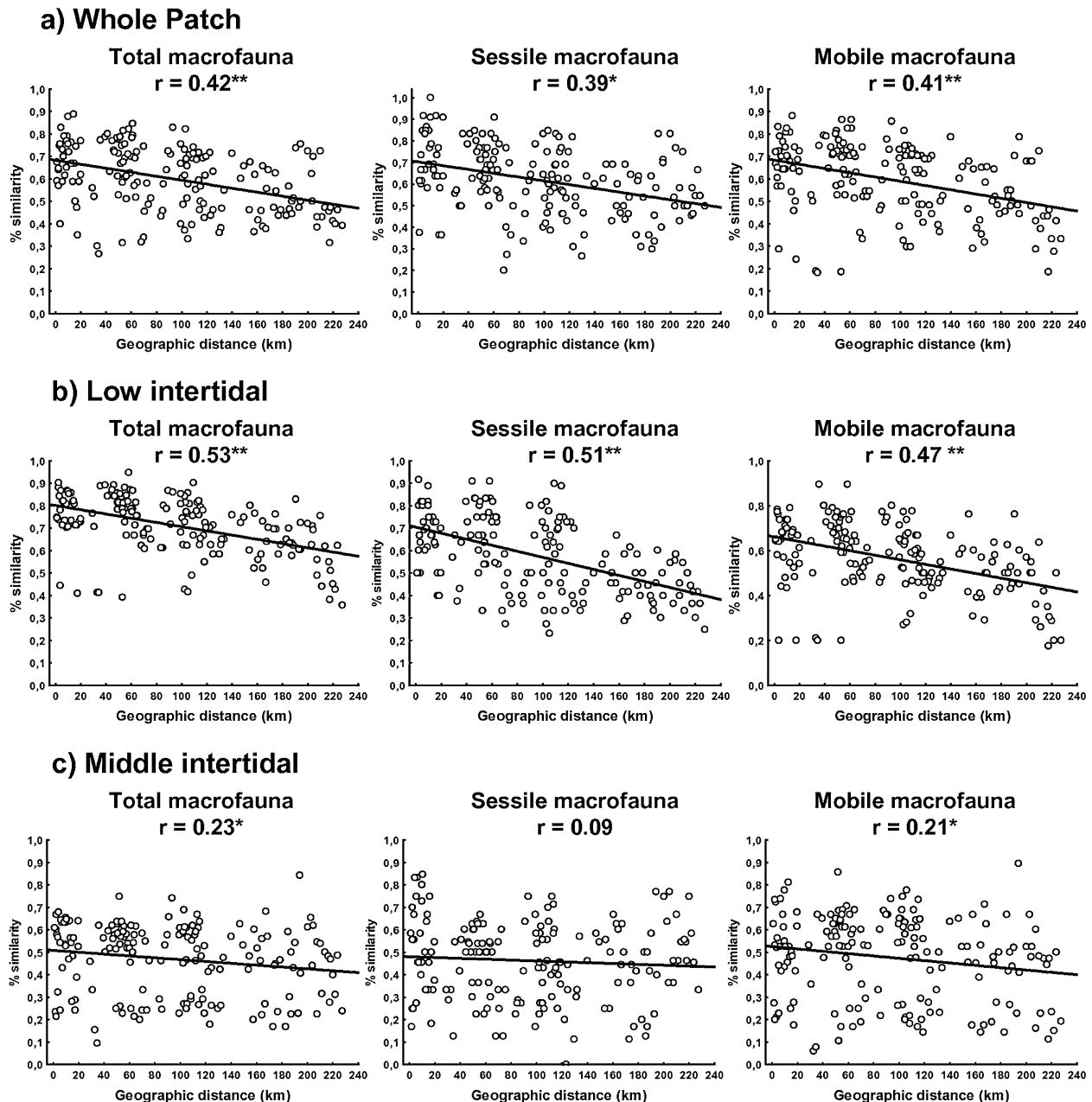

c) Middle intertidal

Fig. 4. Patterns of distance-decay of similarity resulting from the relationship between the biological and the geographic distance matrices. The biological distance matrix was obtained by applying the Jaccard coefficient to the matrix of species composition per site. Significance values of correlations were obtained from 999 random permutations (**$P < 0.01$ and *$P < 0.05$).

richness was independent of the functional group (Fig. 3, $F_{(1,72)} = 0.32$, $P = 0.57$).

Species composition

The Mantel test showed that connectivity, as geographic distance between pairs of patches, affected the species composition between local communities (Fig. 4). Geographic distance between sites was negatively related to similarity for all the cases, except for the sessile macrofauna at the middle intertidal level (Fig. 4c).

The decay of similarity with increasing distance (i.e. the relation between species similarity and geographic distance) was stronger for the low than for the middle intertidal irrespective of whether richness was considered for the total macrobenthos or for each functional

group separately (Fig. 4b,c). The effects observed at the whole patch reflected the one observed at the low intertidal level (Fig. 4a).

DISCUSSION

Understanding the factors underlying the spatial pattern distribution of species is one of the central themes in ecology (Fortin & Dale 2005; Tuda 2007). However, little is known about the effect of landscape configuration on marine community structure (Pittman *et al.* 2004). Here, we showed that for a rocky intertidal community the geographic distance, as proxy of landscape connectivity, is an important factor to explain the species richness and composition. We also found a linear decrease in species similarity with increasing geographic distance regardless of the functional group considered. These patterns of decay are consistent with several studies dealing with different systems and organisms (Nekola & White 1999; Green *et al.* 2004; Oliva & González 2005; Thompson & Townsend 2006; Soininen *et al.* 2007).

Landscape heterogeneity in intertidal rocky shores

In a broad sense, landscape connectivity encompasses all features (e.g. geographic proximity, presence of barriers) affecting the displacement of organisms among habitat patches within the landscape (Baguette & Dyck 2007). Because benthic species of coastal systems can spend days to months as planktonic larval stages (Grantham *et al.* 2003; Shanks *et al.* 2003), larval dispersion may contribute to high landscape connectivity among marine communities (Roughgarden *et al.* 1988; Caley *et al.* 1996; Swearer *et al.* 2002). Moreover, in rocky habitats nearly 42% of species had planktonic feeding larvae and only 15% had nonplanktonic larvae (Grantham *et al.* 2003). However, the strong relationship between geographic distance and species richness or composition supports the hypothesis that landscape connectivity is not as high as previously thought. Our results are therefore consistent with an alternative view suggesting that mean dispersal distances of invertebrate larvae (25–150 km: Palumbi 2003) or rafting should not produce a high level of homogeneity.

For coastal mussels Becker *et al.* (2007) showed that larvae can be retained within 20–30 km of their natal origin. This may explain the spatial segregation of the three species of mussels that dominate the assemblage of sessile species in the Uruguayan Atlantic coast (*Brachidontes rodriguezii*, *Perna perna* and *Mytilus edulis platensis*). On the other hand, several species of the mobile macrofauna have direct development (see Grantham *et al.* 2003) and may remain near the natal origin. Such are the cases of the amphipods (eight species) and isopods (two species) found in this study. Moreover, many of these peracarid crustaceans provide parental care of their offsprings (Thiel 1997, 1999), contributing to a limited dispersal during the early life stages.

In general, the tendency observed in the whole patch coincided with that found at the low intertidal, suggesting that the mechanisms setting the local richness and composition at the low level override the other potential mechanisms operating at the middle intertidal. This could be associated with the higher number of species observed in the low level compared with the middle level for both functional groups analysed. However, the potential mechanism accounting the observed pattern seems to be the same regardless the intertidal level considered because of only the magnitude of the factors considered to explain the species richness varied between the intertidal levels. This results contrast with the explanations given to the classical vertical zonation scheme in intertidal systems (Stephenson & Stephenson 1949). Under a classic scenario, at a local scale physical factors and biological interaction dominate the structure of the middle and low intertidal level, respectively. However, when it changes to a landscape scale, the same mechanisms may be operating on the community structure regardless the intertidal level. Thus, the vertical pattern seems to be more dependent on the functional group considered.

Potential mechanisms accounting for the observed patterns

In a landscape context, the mechanisms that account for community structure could be mainly grouped within the niche theory, based on the differences among species and those focused in neutral process, based in the similarity among species. On one hand, neutral theory (Hubbell 2001) predicts that at local scales the richness and composition is the result of individual immigration from the regional species pool and zero-sum local dynamics. This theory explicitly ignores differences between individuals in response to local ecological conditions, based on the assumption of ecological equivalence among all the individuals (Hubbell 2001). In contrast, niche theory suggests that community structure result from local process such as competition or species-specific responses to physical disturbance regime (Nekola & White 1999; Leibold *et al.* 2004).

The mechanisms that account for the community structure may be different depending on whether sessile or mobile species are considered. This would be consistent with Cadotte (2007) who suggests that

neutral- and niche-based mechanisms of coexistence can operate simultaneously. For sessile rocky shore species, several authors emphasize that a lottery effect of establishment should predominate (Chesson & Warner 1981; Tokeshi 1999; Johnson *et al.* 2003; Thompson and Townsend 2006) because these organisms are often limited by space (Raffaelli & Hawkins 1996). This implies that an increase in surface patch area, in absence of a habitat effect, represents additional opportunities for sessile species to recruit to the community (Johnson *et al.* 2003). In this sense, the pattern of variation in richness and composition of sessile species reported here is consistent with a lottery model and therefore with a neutral theory. Thus, when dispersal is limited, in the neutral theory, nearby sessile communities should show similar biological composition due to the geographic proximity regardless of physical conditions or species differences in response to local conditions.

On the other hand, the richness of mobile species may be more dependent on the local conditions of the habitat. While higher richness of sessile species should increase mobile species richness by increasing habitat heterogeneity, the distance decay of similarity in community composition would be the consequence of the decay in environmental similarity with distance. Rocky intertidal sessile species act as physical bioengineers (sensu Jones *et al.* 1994) modifying the nature and complexity of the substrate, providing habitat for mobile macrofauna (Broitman *et al.* 2001; Cerda & Castilla 2001; Gutierrez *et al.* 2003; Castilla *et al.* 2004; Prado & Castilla 2006; Kelager *et al.* 2007; Voultsiadou *et al.* 2007). In particular, the mussel beds play a central role as bioengineers for mobile species of the rocky intertidal coast of Uruguay (Borthagaray & Carranza 2007). Specific groups of organisms are favoured in mussel beds depending on their physiological abilities (Tokeshi & Romero 1995). For example, for amphipods and isopods mussel beds constitute refuges from water movement and desiccation (Bain 1991; Piel 1991; Genzano 2002); polychaetes are able to colonize the sediment trapped by mussel beds (Prado & Castilla 2006). Other studies report negative interactions between mussel beds and mobile macrofauna (Iwasaki 1995; Ragnarsson & Raffaelli 1999). Thus, mussel beds may enhance species richness, but also may act as a biological filter to the establishment of mobile macrofauna.

In summary, this paper shows that at the landscape scale, connectivity among sites can be important to understand the local structure of a marine community, in particular in the rocky intertidal zone. Further than its biological and environmental traits, it is also necessary to invoke its geographic location in relation with the other patches that form the marine landscape where it is embedded. The average geographic distance of a patch to the other patches of the seascape, as proxy of patch connectivity, contribute significantly to explain the community structure, in particular in the low intertidal zone. More connected patches tend to harbour more rich communities by increasing the number of sessile species, what indirectly improve the condition to mobile ones, and more connected (between them) local communities tend to be more similar in species composition than more distant communities. These results contribute to reinforce the view that mesoscale connectivity (10^{1-2} km) in coastal marine landscapes plays a more important role in local community structure than previously assumed. Understanding the role of marine landscape attributes to determine emergent diversity patterns represents a major challenge to future research.

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