Spatial variability in community composition on a granite breakwater versus natural rocky shores: Lack of microhabitats suppresses intertidal biodiversity

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ABSTRACT

Strong differences have been observed between the assemblages on artificial reefs and on natural hard-bottom habitats worldwide, but little is known about the mechanisms that cause contrasting biodiversity patterns. We examined the influence of spatial attributes in relation to both biogenic and topographic microhabitats, in the distribution and composition of intertidal species on both artificial and natural reefs. We found higher small-scale spatial heterogeneity on the natural reef compared with the study breakwater. Species richness and diversity were associated with a higher availability of crevices, rock pools and mussels in natural habitats. Spatial distribution of certain grazers corresponded well with the spatial structure of microhabitats. In contrast, the lack of microhabitats on the breakwater resulted in the absence of several grazers reflected in lower species richness. Biogenic and topographic microhabitats can have interactive effects providing niche opportunities for multiple species, explaining differences in species diversity between artificial versus natural reefs.

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1. Introduction

Urbanization has transformed different ecosystems throughout the world. It is an increasing problem as human populations are growing and expanding their activities and constructions into natural habitats (Airoldi et al., 2005; Bulleri and Chapman, 2010; Vitousek et al., 1997). Shorelines are highly attractive for residential development and for recreational activities (Airoldi et al., 2005; Bulleri, 2006; Connell and Glasby, 1999; Moschella et al., 2005). Many natural coastal habitats, which host a unique biodiversity legacy, are replaced with extensive and sometimes necessary infrastructure that changes the structure of seascapes and biodiversity patterns (Airoldi et al., 2005; Browne and Chapman, 2011; Chapman and Blockley, 2009; Connell and Glasby, 1999; Moschella et al., 2005). Coastal infrastructures, such as pipes, jetties, piers and "coastal armouring" (Chapman and Underwood, 2008, 2011), are used to protect shorelines or other infrastructures from waves and erosion. The most common artificial constructions are seawalls and breakwaters which can extensively cover coastlines around cities (Bulleri and Chapman, 2010). For example, in coastal cities like Sydney (Australia), as much as 50% of the intertidal shoreline is composed of structures like seawalls (Chapman and Bulleri, 2003). In California (USA), around 30% of the coastline supports artificial breakwaters as "ripraps" (Pister, 2009). These artificial structures serve as habitat for many intertidal and subtidal species, which seem to adapt to novel habitats according to their settlement and movement abilities. There is a great interest in understanding the colonization processes in order to take measures that improve biodiversity and natural services of these artificial habitats ("ecological engineering") (Browne and Chapman, 2011; Chapman and Blockley, 2009).

Studies conducted on vertical concrete seawalls and breakwaters (e.g. "Riprap"), have shown important differences in species composition between natural and artificial substrata (Chapman, 2003; Clynick et al., 2008; Vaselli et al., 2008a). These differences result from variable dominance of a few mobile species that quickly colonize novel habitats, with rare species usually being absent from them (Chapman, 2006, 2003). Differences in species composition between natural and artificial intertidal reefs have also been attributed to the lack of key microhabitats which can modify species interactions or behavior (Chapman and Blockley, 2009; Chapman, 2006; Klein et al., 2011; Martins et al., 2010; Moreira et al., 2007; Perkol-Finkel et al., 2012). For example, absence of rock pools on artificial reefs has been considered one of many (key) factors determining loss of biodiversity, because these microhabitats usually provide shelter from physical or biotic stress (Browne and Chapman, 2011; Chapman and Blockley, 2009; Firth et al., 2014,

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2013). Similarly, rock crevices can provide shelter for grazer species by reducing mortality under harsh environmental conditions; they commonly constitute a limited resource in intertidal habitats (e.g. Aguilera and Navarrete, 2011; Martins et al., 2010; Moreira et al., 2007; Williams and Morritt, 1995). In this way, microhabitat diversity enhances spatial heterogeneity, thereby favouring settlement and establishment of a diverse range of species (Burt et al., 2012; Martins et al., 2010; Moreira et al., 2007; Perkol-Finkel et al., 2012). Maintenance of microhabitats seems relevant to local diversity by facilitating "ecological engineering" in coastal ecosystems (Browne and Chapman, 2011; Burt et al., 2012; Chapman and Blockley, 2009; Chapman and Underwood, 2011; Firth et al., 2014; Martins et al., 2010; Moschella et al., 2005). Loss of species diversity on artificial reefs is not universal, and for some species assemblages they are considered a unique and important reef habitat (e.g. fish, Burt et al., 2011, 2012; Clynick et al., 2008), which could be related to their large-scale structural complexity (Burt et al., 2009, 2012). There is little knowledge, however, about the influence of spatial variation of topographic and biogenic habitats in causing contrasting biodiversity patterns between natural and artificial reefs (see Firth et al., 2014).

Breakwaters, as other coastal infrastructures, can be viewed as 'natural experiments' (Burt et al., 2011, 2012) where we can observe the dynamics of local communities in space and time. Breakwaters constructed from granite boulders are especially interesting because they are deployed randomly in the intertidal habitat, thereby generating a structurally complex landscape. Thus, breakwaters are expected to have higher topographic complexity at the meso-spatial scale (decimeters to meters) due to the spatial distribution and size structure of boulders, but they are expected to be more homogeneous at the micro-spatial scale (few centimeters) when compared to natural habitats. Consequently, while these artificial landscapes are expected to provide poor microhabitats for intertidal assemblages dominated by small (cm) invertebrates, they may provide suitable microhabitats for subtidal fish assemblages, commonly dominated by comparatively large (dm) fish species (Burt et al., 2011, 2009, 2012). The loss of spatial heterogeneity on breakwaters compared for example with natural rocky platforms is expected to affects sessile benthic intertidal assemblages, dominated by few species and with spatial distributions resembling the spatial complexity of these artificial habitats (Beck, 2006; Chapman and Underwood, 2008; Erlandsson et al., 2005; Underwood and Chapman, 1998). The spatial heterogeneity/complexity of artificial reefs might influence the effects of ecological engineering of these benthic communities and determine biodiversity patterns and the presence of rare or exotic species (Bulleri and Airoldi, 2005; Moschella et al., 2005; Vaselli et al., 2008a). The composition of resident intertidal communities on breakwaters has not been studied before in Chile, albeit these structures are becoming more common in northern and central Chile (i.e. from 18°S to 35°S, authors' unpublished results).

The purpose of this study was to examine the influence of spatial attributes of artificial and natural rocky reefs on biodiversity patterns of the intertidal assemblage, considering species composition and abundance on an artificial breakwater and in adjacent, natural habitats. Specifically, through intensive spatial and temporal monitoring of a local intertidal breakwater built with granite boulders and adjacent natural rocky platforms, we evaluated the spatial structure of dominant mobile and sessile species and community composition in the mid and high intertidal zone of both habitats. We also determined the spatial relationship of the dominant species with the large-scale complexity and small scale heterogeneity using the main topographic and biogenic microhabitat characteristics. In particular, we hypothesized that (a) species composition and diversity are higher in natural habitats compared with breakwaters due to the higher proportion of microhabitats in

the former, and thus (b) the spatial patterns of abundance of dominant species (i.e. grazers) is expected to resemble the spatial distribution of the main (topographic and/or biogenic) microhabitats. Even though the spatial structure of other artificial reefs can differ from our study breakwater, intensive spatial sampling of this habitat can help us to determine the underlying spatial mechanisms influencing species composition and abundance. Thus, this information can be useful to test for differences between artificial and natural reefs in other systems.

2. Materials and methods

2.1. Community structure at the study site

The study was conducted on Península Cavancha, Iquique (20°14′S-70°0.9′W) which is located in the subtropical zone in northern Chile. In this locality, average maximum daily air temperature fluctuates from 26 °C during summer to 14.3 °C during winter. Coastal geomorphology at the study site corresponds to solid intertidal platforms comprising a mix of granitic and sedimentary intrusions. Here, the rocky intertidal community is characterized by mussel beds of *Perumytilus purpuratus*, which form dense patches from high to mid intertidal levels where chthamalid barnacles like *Jehlius cirratus* and *Notochthamalus scabrosus* are also abundant. These sessile invertebrates provide shelter and important microhabitats for multiple associated species due to their structural complexity (Beck, 2006; Erlandsson et al., 2005; Kostylev et al., 2005; Thiel and Ulrich, 2002). The mid-intertidal seaweed assemblage is characterized by opportunistic algae like *Ulva rigida*, *U. compressa*, *Pyropia* sp. and *Ulothrix flacca*, the brown algae *Petalonia fascia*, *Colpomenia sinuosa*, *Glossophora kunthii* and Ceramiales like *Centroceras clavulatum* and *Polysiphonia* spp. (Santelices, 1991, 1990). The corticated red alga *Mazzaella denticulata* is also abundant at mid-intertidal levels of exposed platforms. Low intertidal habitats are dominated by calcareous algae like *Lithothamnion* sp. and the kelp *Lessonia berteroana*. The intertidal grazer assemblage is characterized by scurrinid limpets like *Scurria viridula*, *S. araucana* and *S. ceciliana* which inhabit high to mid intertidal levels (Espoz et al., 2004). The limpet *S. viridula* is common on exposed platforms with steep slopes. *Lottia orbignyi* and the littorinid snails *Austrolittorina araucana* and *Nodilittorina peruviana* dominate the high intertidal level on most sheltered shores together with crabs like *Leptograpsus variegatus* and *Grapsus grapsus*. The sunstar *Heliaster helianthus* is the main predator in the rocky intertidal habitat (Navarrete and Castilla, 2003) together with some fish species which venture onto rocky platforms at high tide.

The artificial reef studied corresponds to a granite boulder breakwater (95 m long, average boulder size = 1.4 ± 0.11 m^2) built in 2005 to protect a pedestrian promenade and residential buildings from strong waves. The breakwater is facing towards the south-west and is influenced by strong wave action. Fishing or recreational activities are not observed as in other comparable artificial reefs (e.g. Pister, 2009), thus trampling effects are infrequent or absent. We selected this breakwater for the similarity with common granite breakwaters used at other coasts and for accessibility to conduct regular and intensive sampling. This allowed us to capture the main spatial features that influence species composition and abundance on this kind of artificial reef and natural adjacent rocky habitats.

2.2. Species diversity, abundance patterns and spatial structure

2.2.1. Sampling protocol for mobile and sessile organisms

In order to evaluate differences in community composition and spatial structure of dominant species between the breakwater and

natural adjacent (distanced ∼15 to 20 m from the breakwater) intertidal platforms, we estimated the abundance of intertidal species, i.e. the density of mobile animals and percentage cover of sessile organisms, and presence/absence of main topographic microhabitats like crevices and rock pools. We deployed 25–35 quadrats of 30 * 30 cm surface area that were separated from each other by 30 cm, at both the mid and high intertidal zones of the breakwater. On two adjacent natural rocky platforms (15–20 m long), on either side of the breakwater and distant from each other by approximately 150 m, we deployed 25–30 quadrats at the mid and high intertidal level as before. We took photographs using a digital camera positioned directly above each quadrat (Foster et al., 1991). Each photograph was cropped to include only the quadrat and analyzed using the program image J (http://imagej.nih.gov/ij/download.html). Percentage cover was quantified by projecting 25 dots randomly onto each photo and assigning a value of 4% to each organism that occurred in each dot. We also used a digital analysis of photographs using a high-pass filter method for abundance estimation of benthic organisms to improve our sampling (Pech et al., 2004). This method eliminates distortion caused by panoramic effects like shadows and changes in rock surface coloration, thus increasing geometric details of each photograph. However, since both photo quadrat and digital image analysis methods generate accurate and similar estimates when using fewer than 40 quadrats (Pech et al., 2004), we considered both methodologies as complementary. Samplings were conducted six times between March 2012 and April 2013 using the same protocol as described before.

2.2.2. Topographic complexity

We estimated the structural complexity level of the intertidal breakwater and natural adjacent platforms (i.e. spatial variation of each habitat in terms of abundance and distribution, see Beck, 2006; McCoy and Bell, 1991), considering the "chain method" procedure (Beck, 1998). This method consists in deploying a heavy iron chain and a tape across each transect where the quadrat sampling was conducted (see above). The chain links follow the shape of the rocks, and we used this value to estimate the ratio of the apparent distance (chain measurement). The tape only touched the highest parts of the rocks and thus represented the linear distance (tape) (Beck, 1998). Since quadrat sampling consisted of contiguous quadrats (see above), we followed the same protocol for chain-tape sampling. Thus, we used 51 and 20 1-m segments on the breakwater and natural adjacent platforms, respectively. We also measured granite boulder linear length and height, using a random sample of boulders present in the transect established on the breakwater at the mid and high intertidal level.

2.3. Statistical analyses

Differences between species composition on both the breakwater and on natural platforms were examined through a non-metric Multidimensional Scaling (nMDS) on untransformed Bray–Curtis distances using average density and cover for mobile and sessile species, respectively, for all sampling dates. Prior to analyses we removed species occurring in less than 5% of samples to reduce the potential influence of rare species acting as outliers (e.g. Clarke, 1993). Significant differences between groups were analyzed with PERMANOVA (Anderson, 2001) implemented with the package 'Vegan' in R (R-Core team 2014). Differences in species abundances, diversity and richness on the breakwater versus the corresponding values on the natural platforms were analyzed with a one-way ANOVA.

The spatial structure of both topographic and biogenic microhabitats and the dominant molluscan grazer species present on the breakwater and natural platform were analyzed using Moran's

I spatial correlograms (Fortin and Dale, 2005; Sokal and Oden, 1978), separately for each microhabitat and species. We used averaged pooled abundance data considering all sampling dates for analyses. As recommended (Erlandsson et al., 2005; Rossi et al., 1992), we only considered distances less than half the transect length to interpretation of spatial structure because correlograms do not capture spatial information at longer lags following the loss of degrees of freedom (few distance pairs) (Legendre and Fortin, 1989). To determine whether spatial autocorrelation coefficients were significant (at $\alpha = 0.05$), we used bootstrapping (Manly, 1997) considering Moran's I autocorrelation statistic (Moran's I) for the observed data against the distribution of values obtained by randomly sampling the data set and recalculating the coefficients 1000 times. Before examining individual significance values in the correlogram, we performed a global test by checking whether the correlogram contained at least one significant correlation after probabilities were adjusted using a Bonferroni correction for multiple tests ($\alpha = 0.05$/number of distance classes). All distance data were normalized to zero mean and unit variance to remove outliers before analyses. We examined the degree of positive/negative spatial association between the density of molluscan grazers and percent cover of sessile species constituting the main biogenic microhabitats, i.e. mussels and barnacles, and between density of grazers and presence/absence of the main topographic microhabitats, i.e. crevices and rock pools. In this case we used simple Pearson linear correlations (r). Significance was calculated through a t-test corrected for the effective degrees of freedom based on lag 1 autocorrelation estimates of Moran's I (Dutilleul, 1993). Differences in structural complexity between habitats, estimated through the "chain-tape method", were tested with one-way ANOVA.

3. Results

3.1. Species composition, diversity and richness

Differences in community composition between the breakwater and natural adjacent platforms were evident through the nMDS ordination (Fig. 1), which showed significant differences between these habitats (PERMANOVA; $F_{1,139} = 8.845$, $P = 0.001$). The species that most contributed to dissimilarity between the breakwater and natural platforms were the littorinid snail *N. peruviana* (dissimilarity = 15.0%), the barnacle *J. cirratus* (12.0%) and ulvoid algae like *U. rigida* and *U. compressa* (11.23%). Bare rock contributed with 15.0% of the differences between habitats for both mid and high intertidal levels.
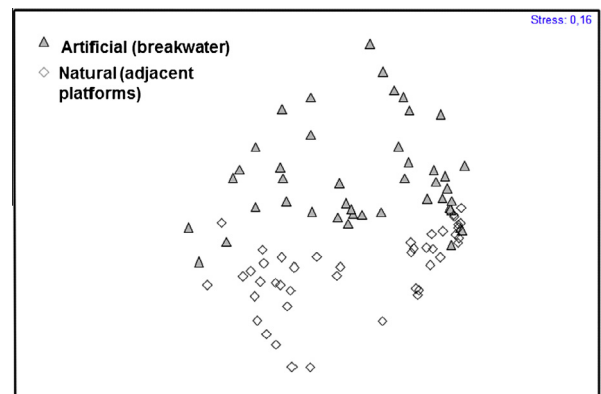

Fig. 1. Non-metric multidimensional scaling of intertidal assemblage composition (pooling seven sampling dates) recorded on artificial habitats (the study breakwater) and natural platforms.

Species diversity (Shannon index, H′) and species richness (number of species) were different between the breakwater and natural platforms at mid and high intertidal levels (Fig. 2a and b). We found that species diversity was significantly higher on the natural platforms compared with the breakwater for both intertidal levels (Fig. 2a, Table 1). The analyses also revealed that species diversity was higher at the high intertidal level, on natural platforms and the breakwater (Table 1; Fig. 2a). We observed higher species richness on the natural platforms compared with the breakwater, being higher at the mid intertidal level in both habitats (Fig. 2b).

3.2. Species abundance

We found important differences in abundance of sessile and grazer species at mid and high intertidal levels between the natural and artificial habitats (Fig. 3a–d). In the mid intertidal zone, the breakwater was characterized by lower cover of the chthamalid barnacle *J. cirratus* (average percentage cover ± SE = 9.7 ± 4.5%) and high abundance of ulvoids (*Ulva compressa* and *U. rigida*-mix) (19.4% ± 3.0%) and bare rock (13.5 ± 6.4%) when compared with natural platforms (average percentage cover ± SE; *J. cirratus* = 38.3 ± 4.6%; ulvoids = 12.5 ± 2.3%; bare rock = 7.4 ± 2.9%; Fig. 3a). We found that the mussel *P. purpuratus* was absent from the breakwater but reached an average cover of 15.0% on the natural platforms (Fig. 3a). The main biogenic microhabitats present on natural platforms were the mussel *P. purpuratus* and the chthamalid barnacle *J. cirratus*.

For the grazer species assemblage we also observed important differences between the natural habitat and the breakwater, which were driven by the abundances of gastropods like *Scurria* limpets
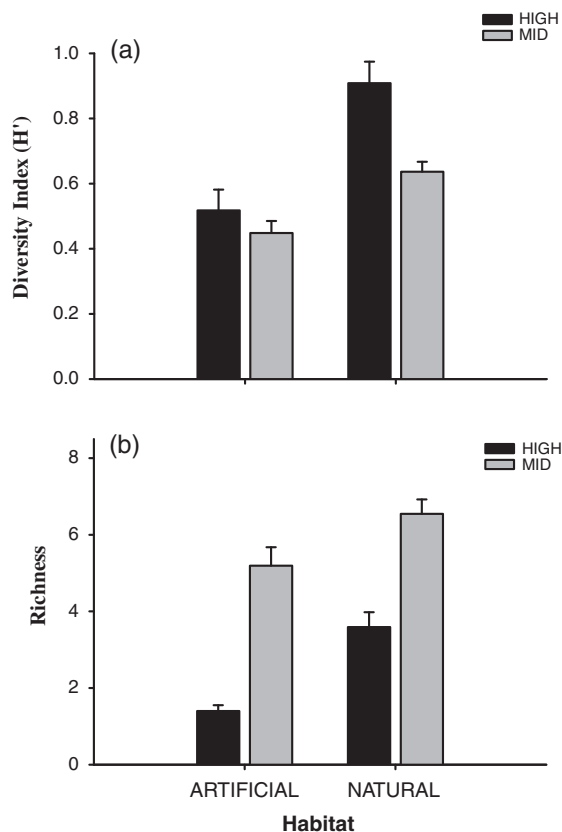

Fig. 2. Diversity (Shannon's index, H′) and species richness (species number) recorded in mid and high intertidal levels on the artificial (breakwater) and natural habitats.

Table 1
Two-way ANOVA for; a) species richness and b) Shannon's diversity index (H′) estimated for both artificial reef (breakwater) and natural platforms. Significant values (α<0.05) are presented in bold.

SV	df	SS	MS	F	P
(a) Species richness					
Habitat (H, artificial, natural)	1	70.204	70.204	20.37	**<0.001**
Level (L, mid, high)	1	253.7	253.7	73.83	**<0.001**
H * L	1	3.912	3.912	1.14	0.289
Residual	86	295.6	3.437		
(b) Diversity (H′)					
Habitat (H, artificial, natural)	1	3.31	3.31	31.04	**<0.001**
Level (L, mid, high)	1	3.253	3.253	30.5	**<0.001**
H * L	1	0.00062	0.00062	0.006	0.939
Residual	86	9.172	0.107		

and littorinid snails (Fig. 3b). *S. viridula* was absent on natural platforms and showed average densities of 0.25 indiv. * 900 cm^{-2} (SE = ± 0.716) on the breakwater (Fig. 3b). Contrarily, *S. ceciliana* and *S. araucana* were absent on the breakwater but showed an average density of 1.2 indiv. * 900 cm^{-2} (SE = ± 0.393) and 2.2 indiv. * 900 cm^{-2} (SE = ± 0.381) on natural platforms, respectively (Fig. 3b).

In the high intertidal zone bare rock was more abundant on natural platforms compared with the breakwater where periphyton (microalgae and cyanophytes) was also abundant (Fig. 3c). The mobile assemblage on the breakwater was numerically dominated by the littorinid snails *A. araucana* and *N. peruviana* (4.0 ± 1.70 indiv. * 900 cm^{-2} and 15.0 ± 5.59 indiv. * 900 cm^{-2}, respectively), and to a lesser extent by *L. orbignyi* while *Scurria ceciliana* and *Siphonaria lessoni* were absent here (Fig. 3d). On the natural platforms, *E. peruviana*, *S. ceciliana* and *S. lessoni* reached densities of 56.7 indiv. * 900 cm^{-2} (± 7.78), 4.78 indiv. * 900 cm^{-2} (SE = ± 1.34) and 4.8 indiv. * 900 cm^{-2} (SE = ± 0.091), respectively. In this habitat the limpet *L. orbignyi* was not observed and *N. peruviana* reached low densities (0.95 ± 1.61 indiv. * 900 cm^{-2}, Fig. 3d).

3.3. Landscape complexity and topographic microhabitat availability

Meso-scale topographic (meter to dozens of meters) complexity was higher on the breakwater compared with the natural platforms (one-way ANOVA, Table 2, Fig. 4a), indicating that topographic complexity at the large scale was significantly higher on the artificial reef.

The main topographic microhabitats (found at the scale of dm to several m) on the natural platforms and to a lesser extent on the breakwater were crevices and rock pools. In the mid intertidal zone, the availability of crevices across the entire transects was significantly different between natural platforms and the breakwater (Fig. 4, Table 3). Rock pools were absent on the breakwater but were observed in 24.0% (±0.336) of the quadrats on the natural platforms (Fig. 4a). At the high intertidal level, crevices were also significantly more abundant on the natural platforms compared with the breakwater (Table 3). Rock pools were absent on the breakwater at the high level, but were common on the natural platforms (52.0% ± 11.17, Fig. 4b) (see Table 3).

3.4. Grazers and microhabitat spatial structure

Spatial distribution patterns of different grazer species, and both biogenic and topographic microhabitat varied according to species, habitat type and intertidal level (results summarizing in Table 4). At the mid intertidal level, scurrinid limpets like *S. viridula*
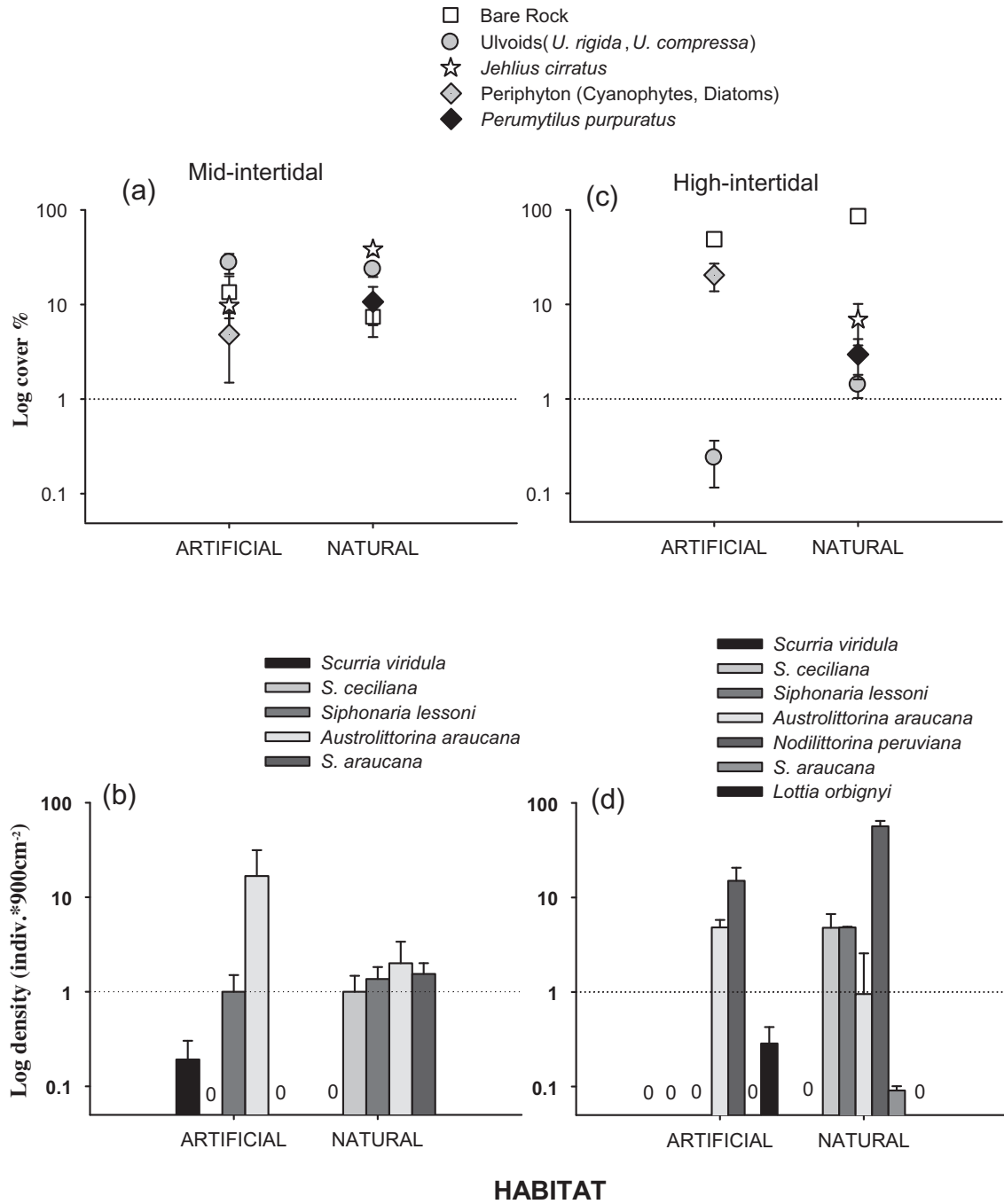
Fig. 3. Percentage cover (%) of the main sessile invertebrate and algae species, bare rock, and density of molluscan grazers found in mid and high intertidal levels on the artificial (breakwater) and natural habitats.

were abundant on the breakwater and *S. ceciliana* on the natural platforms (see above), and both species showed significant non-random distribution patterns (Fig. 5a–c; black triangle and white circle correspond to significant Moran's *I* values for the breakwater and natural platforms, respectively). The spatial structure of *S. ceciliana* followed a gregarious distribution at scales ranging from 30 to 60 cm (lag 1) with a patch size of about 160 cm (where the correlogram change from positive to negative, Fig. 5a). *S. viridula*, found only on the breakwater, showed a patchy distribution only at the smallest spatial scale resolved (i.e. 30–60 cm), corresponding to the scale of one or two quadrats (Fig. 5b). Contrarily, *S. araucana*, found only on the natural platforms, showed a random distribution

pattern with negative and non-significant Moran's *I* values (denoted as "x" in the correlograms) at the smaller scales and only a positive and significant value at scales of about 200–220 cm (Fig. 5c). Similarly, the pulmonate limpet *S. lessoni*, which was abundant in both habitats, showed no significant distribution patterns (Fig. 5d), indicating a random distribution across the platforms and the breakwater.

At the high intertidal level of the breakwater and natural platforms the littorinid snail *A. araucana* and *N. peruviana* and the limpet *S. ceciliana* were the dominant grazer species (see Fig. 3). The limpet *S. ceciliana*, observed only on natural platforms, showed a patchy distribution at small spatial scales i.e. 30–60 cm at this
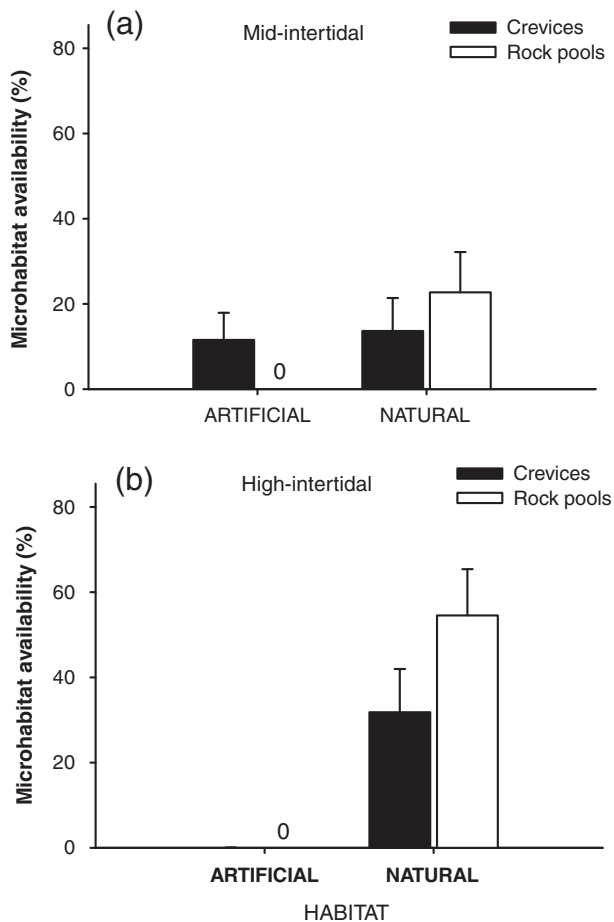
Fig. 4. Availability of the main topographic microhabitats, crevices and rock pools, present in mid and high intertidal levels on the artificial (breakwater) and natural habitats.

Table 2
One-way ANOVA to test differences in structural complexity (Chain-index) between the artificial breakwater and natural habitats. Significant values ($\alpha < 0.05$) are presented in bold.

SV	df	SS	MS	F	P
Habitat (artificial, natural)	1	19.83	19.83	16.84	**0.001**
Error	69	81.29	81.29		

Table 3
One-way ANOVA for differences in crevice incidence present on the artificial breakwater and natural platforms in mid and high intertidal levels. Significant values ($\alpha < 0.05$) are presented in bold.

SV	df	SS	MS	F	P
Mid-intertidal					
Habitat	1				
(artificial, natural)		0.966	0.966	20.83	**<0.001**
Error	96	4.452	0.046		
High-intertidal					
Habitat (artificial, natural)	1	23.17	23.17	9.34	**0.0039**
Error	41	101.65	2.48		

intertidal level. The correlogram for *A. araucana* showed a gradient-like pattern across the breakwater, which indicates a change in abundance around 160–220 cm (i.e. the point where the correlogram changes from positive to negative, Fig. 5e). This spatial structure suggests that large patches of snails were interspersed across

the breakwater, but a random distribution was found for this species on the natural platforms (Fig. 5f). Similarly, a random distribution pattern was found for *N. peruviana* in both habitats (Fig. 5g). As described above, the most important biogenic microhabitats were beds of the mussel *P. purpuratus*, which were present only on natural platforms (see above), and the chthamalid barnacle *J. cirratus* observed on both natural platforms and on the breakwater. At mid-intertidal levels, mussels showed significant positive values of the correlogram at scales of about 30–60 cm (lag 1) and negative values at scales of 230–360 cm (lags 4-6, Fig. 6a). This indicates a patchy distribution for this species, with an average patch size of about 160–180 cm (where the correlogram changes from positive to negative). The chthamalid barnacle *J. cirratus* showed a random distribution in the natural habitat, with a significant positive value only at scales of about 200–240 cm (Fig. 6b). Topographic microhabitats present in the mid-intertidal zone were found almost exclusively on natural platforms. Crevices showed significant values at lag 1 (30–60 cm) and a negative value at lag 5 (280–320 cm, Fig. 6c), indicating a patchy distribution pattern at the smaller scale (see Table 4). In contrast, rock pools showed a random distribution with no characteristic spatial scale (Fig. 6d). At high intertidal levels, the mussel *P. purpuratus* showed a random distribution pattern (Fig. 6e). The barnacle *J. cirratus* showed a significant value at the smallest scales on the breakwater, indicating a patchy distribution, but a random pattern was observed on natural platforms (Fig. 6f). No significant values at any distance lag were observed for topographic microhabitats, indicating a random distribution pattern for both crevices and rock pools across natural platforms at this intertidal level (Fig. 6g & h, and see Table 4).

3.5. Spatial associations

Spatial correlation analyses of the main grazer species, and both biogenic and topographic microhabitats were variable on both natural platforms and the breakwater, and between the mid- and high intertidal level (see Table 5 for summary). Since topographic microhabitats and the mussel *P. purpuratus* were low or absent on the breakwater, we did not consider them for analyses at any intertidal level for this habitat. Overall, we found a significant positive relationship between *S. ceciliana* and *P. purpuratus* on the natural platforms in the mid and high intertidal zone (Table 5). No significant spatial relationships were observed with the other grazer species (Table 5). *A. araucana* and *N. peruviana* showed positive and significant associations with the barnacle *J. cirratus* on natural platforms in the mid and high intertidal zone, respectively. On the breakwater, we found also positive spatial association for some grazer species and *J. cirratus*. *S. lessoni* and *A. araucana* showed a positive and significant association with this biogenic microhabitat (barnacles) in the mid intertidal zone (Table 5). Overall, we found no significant relationship of the grazer species with any topographic microhabitat, neither crevices nor rock pools on natural platforms (Table 5).

4. Discussion

Our study showed consistent differences in species composition, abundance and diversity patterns between the artificial boulder breakwater and natural adjacent platforms. Natural habitats had higher species diversity and richness compared with the breakwater, consistent with the broad evidence suggesting artificial reefs reduce biodiversity of benthos (Bulleri and Chapman, 2010; Moschella et al., 2005). More importantly, we found that overall species diversity and richness were related to the availability and spatial distribution of microhabitats, especially presence of biogenic microhabitats like mussels and barnacles, independently

Table 4
Summary of grazer and microhabitat spatial distributions, based in autocorrelation analyses (Moran's *I* Correlograms), found in mid and high intertidal levels on the study breakwater and the natural platforms. Spatial structure classification according to Fortin and Dale (2005).

Grazer species	Habitat type			
	Natural		Breakwater	
	Mid	High	Mid	High
Scurria ceciliana	Aggregated	Aggregated	–	–
S. viridula	–	–	Aggregated	–
S. araucana	Random	–	–	–
Siphonaria lessoni	Random	Random	–	–
Nodilittorina peruviana	–	Random	–	Random
Austrolittorina araucana	–	Trend-like	–	Random
Microhabitats (biogenic, topographic)				
Perumytilus purpuratus	Patchy	Random	–	–
Jehlius cirratus	Random	Random	Random	Patchy
Crevices	Patchy	Random	–	–
Rock pools	Random	Random	–	–

of "between-habitat" differences in large scale complexity, while on the artificial reef biogenic microhabitats were fewer and less extensive than on the natural platforms. The small-scale distribution of the dominant molluscan grazers in natural habitats resembles the spatial distribution of topographic microhabitats or biogenic shelters like mussel beds or barnacle patches. Our results highlight the importance of small-scale spatial heterogeneity generated by diverse microhabitat availability in determining differences in species diversity and abundance distribution between natural and artificial reefs. Here we discuss the main spatial mechanisms determining differential species coexistence in both habitats. In particular we explore the importance of microhabitat availability and species spatial distribution patterns in determining contrasting biodiversity patterns on artificial versus natural reefs.

Important differences in species composition have been observed between natural and artificial habitats in intertidal systems worldwide (see Bulleri and Chapman, 2010 for review). These differences have been attributed to the dominance of few species which adapt quickly to artificial habitats like breakwaters, while other habitat-specialist species are usually absent (Chapman, 2006). Some studies suggest differences in species composition between natural and artificial intertidal reefs could be related to presence of microhabitats like crevices or rock pools in the latter compared with the former (Browne and Chapman, 2011; Chapman and Blockley, 2009; Firth et al., 2014, 2013; Klein et al., 2011; Martins et al., 2010; Moreira et al., 2007). Spatial heterogeneity at small scales can improve diversity because more types of microhabitats can fulfil the habitat requirements of multiple species (Beck, 2006; McCoy and Bell, 1991; McGuinness and Underwood, 1986; Meager et al., 2011). Our study showed that topographic microhabitats like crevices and rock pools were much more abundant on natural platforms than on the adjacent breakwater. Similarly, the mussel *P. purpuratus,* considered an "ecosystem bioengineer" (*sensu* Jones et al., 1994), was present only on natural platforms at the study site. The other species capable of generating a biogenic microhabitat considered in our study, *J. cirratus*, was present on both the natural platforms and the breakwater. Thus, topographic and biogenic microhabitat diversity was markedly higher on natural platforms when compared with the breakwater which allow multiple niche opportunities for different species (Jones and Boulding, 1999).

Geomorphology of natural adjacent platforms comprises of a mix of granitic and sedimentary intrusions while breakwater boulders consisted exclusively of granite. Likely, slight differences in microtopography (few mm) between these habitats may affect the settlement potential of some species. For example, absence of mussel beds on the breakwater might be related to different ability/preferences of invertebrate larvae to settle on the surface of the granite boulders, which possibly have a smoother surface structure than natural rocky platforms (Carl et al., 2012). Since we did not consider the micro-spatial scale (few mm) in our study, we can only speculate about this possibility. Future studies should examine potential differences in settlement rates in both habitats and the effect of substratum microtopography or geochemistry on larval attachment to the substratum.

As crevices and rock pools constitute shelters against physical or biotic stress for different grazer species, they usually enhance settlement and species co-occurrence (Aguilera and Navarrete, 2011; Garrity, 1984; Harper and Williams, 2001; Moreira et al., 2007; Williams and Morritt, 1995). For example, many molluscan grazers use crevices in intertidal habitats for shelter during diurnal low tides (e.g. chitons, limpets), leading to a direct positive relationship between density of some species and the availability of these microhabitats (Aguilera and Navarrete, 2011; Jones and Boulding, 1999; Martins et al., 2010). Nonetheless, we observed no significant relationship of grazer species with rock pools or crevices. We found limpet species had patchy and gregarious distributions, but no strong spatial association was observed between behavioral aggregations and topographic complexity (see summary Table 4). Species like the pulmonate limpet *S. lessoni* have been observed to use crevices for shelter during nighttime, but our sampling was conducted during daytime (i.e. 10:00 to 18:00) when this species is expected to be actively foraging outside shelters (Aguilera and Navarrete, 2011). Other species, like littorinid snails, forage during daytime and we indeed observed no direct relationship with any potential shelters, neither crevices nor rock pools or mussels. Thus, we did not capture well the behavioral spatial structure for these species.

Abundances of littorinid snails were higher on the breakwater where crevice availability was low and rock pools were absent. Thus, we probably failed to detect a direct association between abundances of these species and the availability of topographic variables due to the time when we conducted the samplings. It is also possible that these species are not obligatory users of small scale shelters, which should be examined in future studies.

We found a consistent spatial relationship of the limpet *S. ceciliana* and the mussel *P. purpuratus* at mid-intertidal levels in the natural habitats. Similarly, we found significant and positive relationships of littorinid snails with the chthamalid barnacle *J. cirratus* at mid intertidal levels in natural habitats, and for the limpet species *S. lessoni*, and this barnacle on the artificial reef. The gregarious distribution of *S. ceciliana* resembles the distribution of the mussel because the limpet occupies them as habitat for shelter and foraging (Santelices and Martínez, 1988). Previous studies showed that mussel beds are an important microhabitat for multiple invertebrate species of variable sizes, which find shelter and/or food
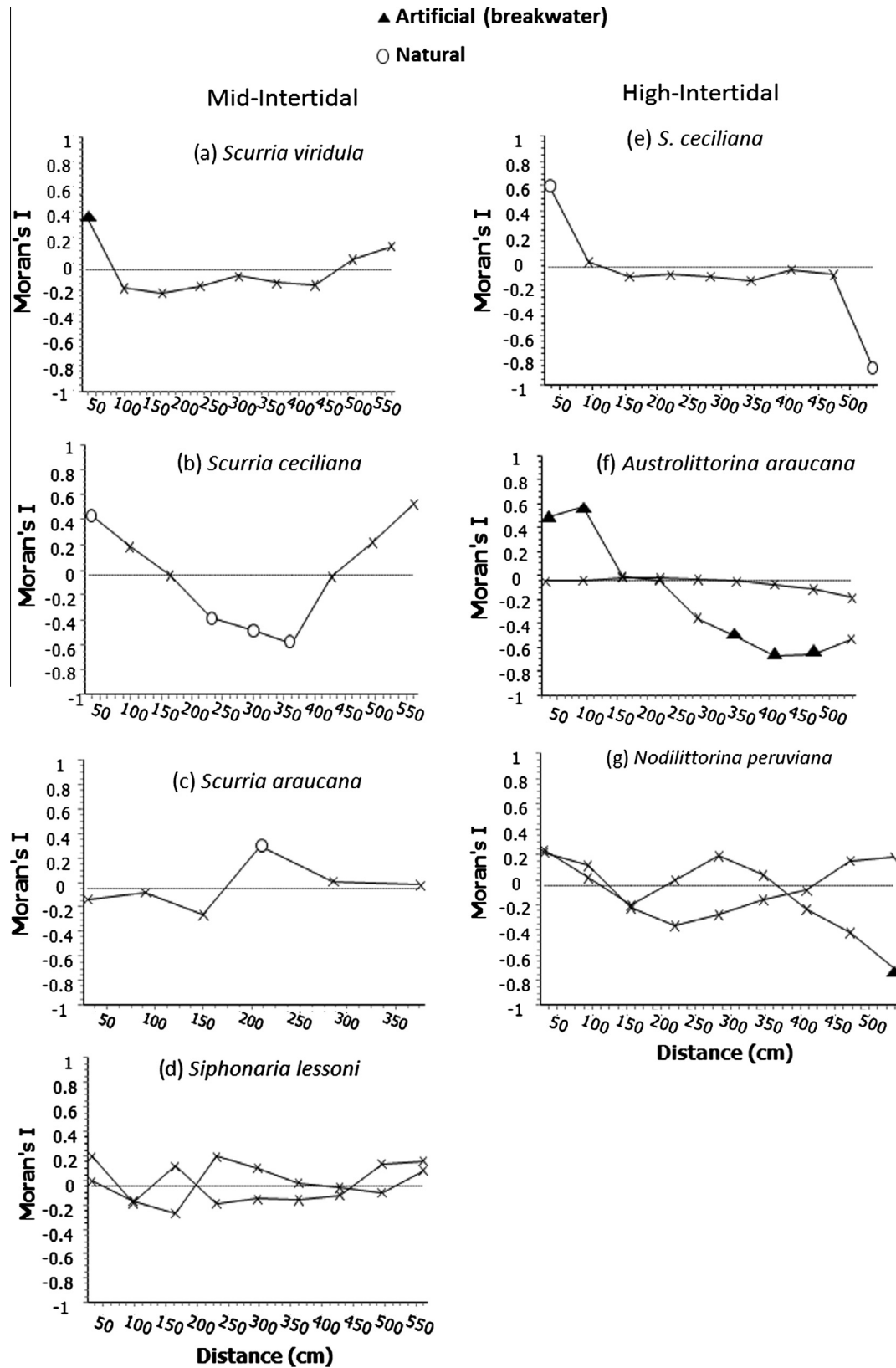
Fig. 5. Moran's *I* spatial correlograms of the main moluscan grazers found in mid (a–d) and high (e–g) intertidal levels on the breakwater (black triangle) and natural (white circle) habitats.

within the mussel matrix (Prado and Castilla, 2006; Thiel and Ulrich, 2002). Thus, this species is considered an "ecosystem engineer" in rocky intertidal habitats (Kelaher et al., 2007; Prado and Castilla, 2006). In this context, we observed that rare or less abundant grazer species (e.g. keyhole limpets, chitons), polychaetes, and sessile organisms like ascidians, anemones or coralline algae
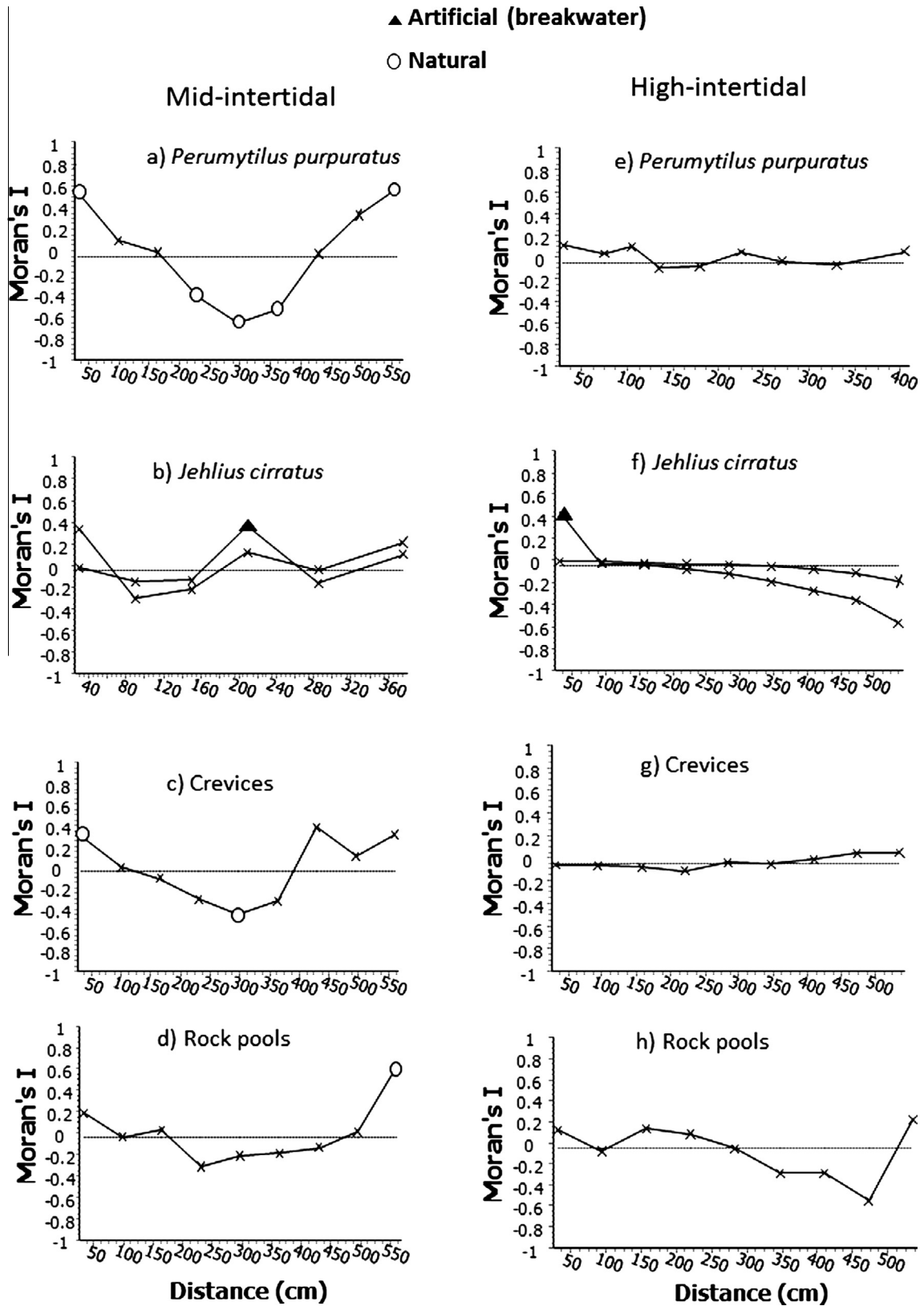
Fig. 6. Moran's *I* spatial correlograms for biogenic (a, b, e, f) and topographic (c, d, g, h) microhabitats present on the breakwater black triangle and natural platforms white circle), in mid (a–d) and high (e–h) intertidal levels.

were present only in this microhabitat on the natural platform. Since we did not remove the mussel matrix in our sampling, we likely underestimated other rare species present in this microhabitat, thereby biasing our estimation of species richness (Prado and Castilla, 2006; Thiel and Ulrich, 2002). Overall, our results suggest that absence of mussel beds on the breakwater results in a net decrease of species richness and consequently diversity patterns (see Valdivia and Thiel, 2006 for similar effects of mussel removal).

Table 5

Summary of spatial associations between grazer species and both biogenic and topographic microhabitats in the mid and high intertidal levels on natural platforms and the breakwater, +: positive association; −: negative association; 0: non-significant association; *:non-tested, i. e. there were few data for analyses. Pearson's r-statistic and P-value are shown in parenthesis, significant ($\alpha = 0.05$) are presented in bold.

Grazer species	Natural								Breakwater	
	Perumytilus purpuratus		*Jehlius cirratus*		Crevices		Rock pools		*Jehlius cirratus*	
	Mid	High	Mid	High	Mid	High	Mid	High	Mid	High
Scurria ceciliana	+ (**r = 0.936, P = 0.003**)	+ (**r = 0.363; P = 0.036**)	0 (r = 0.037, P = 0.831)	*	0 (r = −0.536, P = 0.138)	0 (r = 0.105; P = 0.657)	0 (−0.531, P = 0.088)	− (**r = −0.529; P = 0.048**)	*	*
S. viridula	*	*	*	*	*	*	*	*	0 (r = 0.237, P = 0.181)	*
S. araucana	0 (r = 0.267, P = 0.165)	*	0 (r = 0.213, P = 0.394)	*	0 (r = −0.102, P = 0.610)	*	0 (r = 0.116, P = 0.558)	*	*	*
Siphonaria lessoni	0 (r = −0.165, P = 0.324)	*	0 (r = −0.037, P = 0.862)	*	0 (r = 0.004, P = 0.189)	*	0 (r = −0.084, P = 0.983)	*	+ (**r = 0.446, P = 0.035**)	*
Nodilittorina peruviana	0 (r = −0.177; P = 0.344)	0 (r = 0.452; P = 0.085)	− (**r = −0.415, P = 0.048**)	+ (**r = 0.546, P = 0.008**)	0 (r = 0.075, P = 0.670)	0 (r = 0.208, P = 0.369)	0 (r = 0.355, P = 0.093)	0 (r = −0.128; P = 0.617)	0 (r = −0.203, P = 0.239)	0 (r = 0.230, P = 0.349)
Austrolittorina araucana	0 (r = −0.052; P = 0.824)	0 (r = 0.139; P = 0.619)	+ (**r = 0.404, P = 0.030**)	0 (r = 0.201, P = 0.591)	0 (r = −0.295, P = 0.160)	0 (r = −0.156, P = 0.618)	0 (r = −0.066, P = 0.766)	0 (r = −0.199, P = 0.378)	+ (**r = 0.593, P = 0.003**)	0 (r = −0.047, P = 0.835)

We also found higher abundances of chthamalid barnacles on natural platforms compared with the breakwater. The spatial distribution of *J. cirratus* was patchy on natural platforms, and this pattern was positively related to densities of small grazers like littorinid snails. Even though on the breakwater the spatial distribution of barnacles was random, its presence was related with density of *A. araucana* and *S. lessoni*, which could find shelter or food on them (Jones and Boulding, 1999). Therefore, it seems to be an interactive effect of the diverse microhabitat types, especially biogenic ones, on overall species diversity patterns which can account for strong differences between natural habitats and the artificial reef.

Food availability could be also a factor determining differences between artificial and natural habitats. In this context, microalgae are considered one of the main food items for multiple grazer species in this (Aguilera et al., 2013) and in other systems (Bustamante et al., 1995; Coleman et al., 2006; Jenkins et al., 2001). We found relatively higher periphyton cover, i.e. microalgae, cyanophytes, on the breakwater compared with natural platforms. Possibly low densities of grazers on the breakwater account for higher periphyton cover, a hypothesis that requires further examination. Overall, within the grazer guild it seems that spatial heterogeneity related to the presence of diverse microhabitats rather than food availability is the main factor determining species coexistence in both natural and artificial habitats.

Some studies have observed that artificial reefs like breakwaters can increase fish abundance compared with natural habitats (Burt et al., 2011, 2009, 2012; Clynick et al., 2008). Increase in large scale (dozens of meters) structural complexity caused by the simple presence of a breakwater seems to influence fish assemblage composition providing habitats for sheltering or food (Burt et al., 2009, 2012). In our study, we found littorinid snails sheltering amidst or under granite boulders. Similarly, other species like *L. orbignyi* and *S. viridula*, both species absent on natural platforms, were found underneath or on the side of boulders on the breakwater. This suggests that the structural complexity of the breakwater, determined by granite boulder spatial and size distribution, can provide suitable microhabitats for some grazer species by offering shelter during diurnal low tides, an aspect in need of further examination.

As suggested by previous studies and our own results, maintenance of microhabitats seems to be relevant to maintain local diversity patterns on artificial reefs (i.e. "ecological engineering"; Browne and Chapman, 2011; Chapman and Blockley, 2009; Chapman and Underwood, 2011; Firth et al., 2014; Moschella et al., 2005). Because the abundance and extension of artificial reefs like breakwaters is increasing in many coastal countries, including Chile (Bulleri and Chapman, 2010, Authors' unpublished results), it is urgent to generate a specific framework to study and monitor these habitats (e.g. Browne and Chapman, 2011; Chapman and Underwood, 2011; Firth et al., 2014). Even though we only considered one breakwater in our study, intensive sampling of this habitat helped us to determine the spatial structure of more dominant species and the influence of spatial heterogeneity/complexity which can be relevant for determining differences between natural and artificial reefs in other systems. Our findings suggest that including knowledge on the spatial variation of species and both topographic and biogenic microhabitats, at small and larger scales, can help determine the specific mechanisms underlying differences in species composition between natural and artificial reefs. Higher topographic and biogenic microhabitat availability (as commonly found in natural habitats) can provide shelter from desiccation stress during resting periods for grazer species (Jones and Boulding, 1999; Meager et al., 2011), or can offer suitable settlement areas, e.g. sessile and mobile invertebrates or algae. The presence of biogenic microhabitats in particular can enhance spatial heterogeneity thus determining diversity patterns at different scales. On the other hand, dominance of some species on the breakwater can be associated to large spatial scale attributes of the breakwater like spatial distribution, slope, and/or size of granite boulders (McGuinness and Underwood, 1986). Previous findings that suggest the increase, decrease or even no effect of artificial reefs on species diversity as compared to adjacent natural habitats (Airoldi et al., 2005; Burt et al., 2011, 2012; Chapman, 2006, 2003; Connell and Glasby, 1999; Pister, 2009) may be a direct consequence of spatial heterogeneity/complexity differing between these habitats at various ecologically relevant scales (Meager et al., 2011). This spatial variation could have important consequences for coexistence and biodiversity patterns at the landscape level and can be used as an engineering tool to improve artificial reef structure.

References

Aguilera, M.A., Navarrete, S., 2011. Distribution and activity patterns in an intertidal grazer assemblage: influence of temporal and spatial organization on interspecific associations. Mar. Ecol. Prog. Ser. 431, 119–136.

Aguilera, M.A., Valdivia, N., Broitman, B., 2013. Spatial niche differentiation and coexistence at the edge: co-occurrence distribution patterns in *Scurria* limpets. Mar. Ecol. Prog. Ser. 483, 185–198.

Airoldi, L., Abbiati, M., Beck, M.W., Hawkins, S.J., Jonsson, P.R., Martin, D., Moschella, P.S., Sundelöf, A., Thompson, R.C., Åberg, P., 2005. An ecological perspective on the deployment and design of low crested and other coastal defences. Coast. Eng. 52, 1073–1087.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Beck, M.W., 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Mar. Ecol. Prog. Ser. 169, 165–178.

Beck, M.W., 2006. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. Mar. Ecol. Prog. Ser. 249, 29–49.

Browne, M.A., Chapman, M.G., 2011. Ecologically informed engineering reduces loss of intertidal biodiversity on artificial shorelines. Environ. Sci. Technol. 45, 8204–8207.

Bulleri, F., 2006. Is it time for urban ecology to include the marine realm? Trends Ecol. Evol. 21, 658–659.

Bulleri, F., Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. J. Appl. Ecol. 42, 1063–1072.

Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47, 26–35.

Burt, J., Bartholomew, A., Usseglio, P., Bauman, A., Sale, P.F., 2009. Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? Coral Reefs 28, 663–675.

Burt, J., Sale, P.F., Bartholomew, A., 2011. Benthic development on large-scale engineered reefs: a comparison of communities among breakwaters of different age and natural reefs. Ecol. Eng. 37, 191–198.

Burt, J.A., Feary, D.A., Cavalcante, G., Bauman, A.G., Usseglio, P., 2012. Urban breakwaters as reef fish habitat in the Persian Gulf. Mar. Pollut. Bull. 72, 342–350.

Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Elizabeth, P., 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102, 189–201.

Carl, C., Poole, A.J., Sexton, B.A., Glenn, F.L., Vucko, M.J., Williams, M.R., Whalan, S., de Nys, R., 2012. Enhancing the settlement and attachment strength of pediveligers of *Mytilus galloprovincialis* by changing surface wettability and microtopography. Biofouling 28, 175–186.

Chapman, M.G., 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Mar. Ecol. Prog. Ser. 264, 21–29.

Chapman, M.G., 2006. Intertidal seawalls as habitats for molluscs. J. Mollus. Stud. 72, 247–257.

Chapman, M.G., Blockley, D.J., 2009. Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. Oecologia 161, 625–635.

Chapman, M.G., Bulleri, F., 2003. Intertidal seawalls—new features of landscape in intertidal environments. Landscape Urban Plan. 62, 159–172.

Chapman, M.G., Underwood, A.J., 2008. Scales of variation of gastropod densities over multiple spatial scales: comparison of common and rare species. Mar. Ecol. Prog. Ser. 354, 147–160.

Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. J. Exp. Mar. Biol. Ecol. 400, 302–313.

Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clynick, B.G., Chapman, M.G., Underwood, A.J., 2008. Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecol. 33, 140–150.

Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J., Castro, J., Hartnoll, R.G., Jenkins, S.R., Paula, J., Della Santina, P., Hawkins, S.J., 2006. A continental scale evaluation of the role of limpet grazing on rocky shores. Oecologia 147, 556–564.

Connell, S.D., Glasby, T.M., 1999. Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. Mar. Environ. Res. 47, 373–387.

Dutilleul, P., 1993. Spatial heterogeneity and the design of ecological field experiments. Ecology 74, 1646–1658.

Erlandsson, J., McQuaid, C.D., Kostylev, V.E., 2005. Contrasting spatial heterogeneity of sessile organisms within mussel (*Perna perna* L.) beds in relation to topographic variability. J. Exp. Mar. Biol. Ecol. 314, 79–97.

Espoz, C., Lindberg, D.R., Castilla, J.C., Simison, W.B., 2004. Los patelogastrópodos intermareales de Chile y Perú. Rev. Chil. de Historia Nat. 77, 257–283.

Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M., Hawkins, S.J., 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Divers. Distrib. 19, 1275–1283.

Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J., Hawkins, S.J., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. Coast. Eng. 87, 122–135.

Fortin, M.-J., Dale, M.R.T., 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press, Cambridge, UK.

Foster, M.S., Harrold, C., Hardin, D.D., 1991. Point vs. photo quadrat estimates of the cover of sessile marine organisms. J. Exp. Mar. Biol. Ecol. 146, 193–203.

Garrity, S.D., 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. Ecology 65, 559–574.

Harper, K.D., Williams, G.A., 2001. Variation in abundance and distribution of the chiton *Acanthopleura japonica* and associated molluscs on a seasonal, tropical, rocky shore. J. Zool. 253, 293–300.

Jenkins, S., Arenas, F., Arrontes, J., Bussell, J., Castro, J., Coleman, R., Hawkins, S., Kay, S., Martínez, B., Oliveros, J., Roberts, M., Sousa, S., Thompson, R., Hartnoll, R., 2001. European-scale analysis of seasonal variability in limpet grazing activity and microalgal abundance. Mar. Ecol. Prog. Ser. 211, 193–203.

Jones, K.M.M., Boulding, E.G., 1999. State-dependent habitat selection by an intertidal snail: the costs of selecting a physically stressful microhabitat. J. Exp. Mar. Biol. Ecol. 242, 149–177.

Jones, C.G., Lawton, J., Shachak, M., 1994. Organisms as ecosystems engineers. Oikos 69, 373–386.

Kelaher, B.P., Castilla, J.C., Prado, L., 2007. Is there redundancy in bioengineering for molluscan assemblages on the rocky shores of central Chile? Rev. Chil. de Historia Nat. 80, 173–186.

Klein, J.C., Underwood, A.J., Chapman, M.G., 2011. Urban structures provide new insights into interactions among grazers and habitat. Ecol. Appl. 21, 427–438.

Kostylev, V.E., Erlandsson, J., Ming, M.Y., Williams, G.A., 2005. The relative importance of habitat complexity and surface area in assessing biodiversity: fractal application on rocky shores. Ecol. Complex. 2, 272–286.

Legendre, P., Fortin, M., 1989. Spatial pattern and ecological analysis. Vegetatio 80, 107–138.

Manly, B., 1997. Randomization, Bootstrap and MonteCarlo Methods in Biology. Chapman & Hall.

Martins, G.M., Thompson, R.C., Neto, A.I., Hawkins, S.J., Jenkins, S.R., 2010. Enhancing stocks of the exploited limpet *Patella candei* d'Orbigny via modifications in coastal engineering. Biol. Conserv. 143, 203–211.

McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. In: McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Springer, pp. 3–27.

McGuinness, K.A., Underwood, A.J., 1986. Habitat structure and the nature of communities on intertidal boulders. J. Exp. Mar. Biol. Ecol. 104, 97–123.

Meager, J., Schlacher, T., Green, M., 2011. Topographic complexity and landscape temperature patterns create a dynamic habitat structure on a rocky intertidal shore. Mar. Ecol. Prog. Ser. 428, 1–12.

Moreira, J., Chapman, M.G., Underwood, A.J., 2007. Maintenance of chitons on seawalls using crevices on sandstone blocks as habitat in Sydney Harbour, Australia. J. Exp. Mar. Biol. Ecol. 347, 134–143.

Moschella, P.S., Abbiati, M., Åberg, P., Airoldi, L., Anderson, J.M., Bacchiocchi, F., Bulleri, F., Dinesen, G.E., M. Frost, F., Gaciag, E., Granhag, L., Jonsson, P.R., Satta, M.P., Sundelöf, A., Thompson, R.C., Hawkins, S.J., 2005. Low-crested coastal defence structures as artificial habitats for marine life: Using ecological criteria in design. Coast. Eng. 52, 1053–1071.

Navarrete, S.A., Castilla, J.C., 2003. Experimental determination of predation intensity in an intertidal predator guild: dominant versus subordinate prey. Oikos 2, 251–262.

Pech, D., Condal, A.R., Bourget, E., Ardisson, P.-L., 2004. Abundance estimation of rocky shore invertebrates at small spatial scale by high-resolution digital photography and digital image analysis. J. Exp. Mar. Biol. Ecol. 299, 185–199.

Perkol-Finkel, S., Ferrario, F., Nicotera, V., Airoldi, L., 2012. Conservation challenges in urban seascapes: promoting the growth of threatened species on coastal infrastructures. J. Appl. Ecol. 49, 1457–1466.

Pister, B., 2009. Urban marine ecology in southern California: the ability of riprap structures to serve as rocky intertidal habitat. Mar. Biol. 56, 861–873.

Prado, L., Castilla, J.C., 2006. The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: biodiversity, habitat structural complexity and environmental heterogeneity. J. Mar. Biol. Assoc. U.K. 86, 417–421.

Rossi, R.E., Mulla, D.J., Journel, A.J., Franz, E.H., 1992. Geostatistical tools for modelling and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277–314.

Santelices, B., 1990. Patterns of organization of intertidal and shallow subtidal vegetation in wave exposed habitats of central Chile. Hydrobiologia 192, 35–57.

Santelices, B., 1991. Littoral and Sublittoral Communities of Continental Chile. In: Mathieson, A.C., Nienhuis, P.H. (Eds.). Intertidal and Littoral Ecosystems, pp. 347–369.

Santelices, B., Martínez, E., 1988. Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. J. Exp. Mar. Biol. Ecol. 118, 281–306.

Sokal, R.R., Oden, N.L., 1978. Spatial autocorrelation in biology. Biol. J. Linn. Soc. 10, 199–228.

Thiel, M., Ulrich, N., 2002. Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bot- toms along the coast of Chile, and considerations on the functional role of mussel beds. Helgol. Mar. Res. 56, 21–30.

Underwood, A.J., Chapman, M.G., 1998. A method for analysing spatial scales of variation in composition of assemblages. Oecologia 117, 570–578.

Valdivia, N., Thiel, M., 2006. Effects of point-source nutrient addition and mussel removal on epibiotic assemblages in *Perumytilus purpuratus* beds. J. Sea Res. 56, 271–283.

Vaselli, S., Bulleri, F., Benedetti-Cecchi, L., 2008a. Hard coastal-defence structures as habitats for native and exotic rocky-bottom species. Mar. Environ. Res. 66, 395–403.

Vitousek, P., Mooney, H., Lubchenco, J., 1997. Human domination of earth ecosystems. Science 277, 494–499.

Williams, G.A., Morritt, D., 1995. Habitat pertitioning and thermal tolerance in a tropical limpet, *Cellana grata*. Mar. Ecol. Prog. Ser. 124, 89–103.