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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.

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