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Ecology of a key ecosystem engineer on hard coastal infrastructure and natural rocky shores

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ABSTRACT

The numbers of hard coastal artificial structures is increasing worldwide and there is now cumulative evidence that they support assemblages that are less diverse than natural shores. Here we investigated patterns of distribution and demography of the native barnacle *Chthamalus stellatus* on hard coastal structures and on natural rocky shores. Barnacles were 35% less abundant on hard structures regardless of substratum type (concrete or basalt). On a subset of sites we found that temporal population stability, growth and mortality were similar on natural rocky shores and hard structures. In contrast, barnacles were significantly larger and recruited more onto natural rocky shores. These results emphasise the important role of recruitment in determining the abundance of a key space occupier on hard coastal structures. Experimental work building on these results may generate insights that can be used as guidelines for the management of urbanised coastal areas.

1. Introduction

Concentration of human population centres in coastal regions is leading to the construction of an increasing number of hard structures (e.g. seawalls, breakwaters) in order to protect coastal urbanisation from risks of sea level rise and increased storminess (Thompson et al., 2002; Firth et al., 2013a; Wong et al., 2014). While these hard artificial coastal defence structures (hard structures or artificial structures hereafter) provide habitat for a variety of rocky intertidal organisms, there is now mounting evidence that they support intertidal assemblages that differ from natural habitats, and are generally considered poor surrogates for the habitats they replace (Chapman, 2003; Bulleri and Chapman, 2004, 2010; Moschella et al., 2005; Firth et al., 2014; Aguilera et al., 2014; Evans et al., 2015). For instance, Chapman (2003) found that within the Sydney Harbour, approximately 50% of the mobile taxa found on rocky shores were absent from seawalls.

Hard structures are often built from materials (e.g. concrete) that lack the topographic complexity (e.g. rockpools, pits, cracks, grooves) that characterises natural rocky shores, where it has an important role in the distribution of intertidal organisms (e.g. Chapman and Bulleri, 2003; Underwood, 2004; Moreira et al., 2007). In fact, studies have now shown that the experimental increase of topographic complexity of hard structures, such as the inclusion of water-retaining features and pits, can lead to local increases in diversity (Chapman and Blockley, 2009; Chapman and Underwood, 2011; Firth et al., 2013b, 2104) and abundance of important species (Martins et al., 2010; Coombes et al., 2015). Importantly, the effects of such modifications can be long-lasting (Martins et al., 2015). Although the number of studies investigating the impact of coastal urbanisation on intertidal organisms is growing, the truth is that we still know very little about the ecology of many organisms on hard structures and how these structures modify population and community dynamics (but see Bulleri, 2005; Iveša et al., 2010; Ido and Shimrit, 2015; Ponti et al., 2015).

Barnacles are common and abundant organisms on most of the world's rocky shores. The sessile nature of adult populations, small size and abundance make intertidal barnacles good and tractable

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model species and they have been used for decades to test several ecological questions. There is now extensive literature on most aspects of barnacle biology and ecology including life-history (Southward, 1987), competition and predation (Connell, 1961a,b), dispersal and recruitment (Gaines and Roughgarden, 1985; Jenkins, 2005) and demography (Roughgarden et al., 1985; Benedetti-Cecchi et al., 2000). Acorn barnacles are physical ecosystem modifiers affecting the abundance and activities of other species (Hawkins, 1981; Thompson et al., 1996; Harley, 2006). Unlike on natural rocky shores, where barnacles are often key space occupiers of mid-to-upper intertidal shore levels, the abundance of barnacles is often reduced on hard structures (e.g. Australia – Bulleri, 2005 and UK – Coombes et al., 2015). Here, we explore the population dynamics of barnacles on both hard structures and on natural rocky shores as a mean to provide clues about the processes that may be negatively influencing their abundance on such structures.

The intertidal barnacle *Chthamalus stellatus* (Poli) has a broad geographic distribution in European coastlines from N. Scotland to N. Africa, including the Mediterranean and Black Sea (Crisp et al., 1981). In the Atlantic, *C. stellatus* often occurs together with *Chthamalus montagui*, although in the Azores the latter is absent. *C. stellatus* is predominantly found on wave-beaten coasts (Jenkins, 2005) and is the most common native sessile invertebrate in the rocky intertidal shores of the Azores. It occurs at various tidal heights, but is especially abundant towards upper levels on the shore, where it often co-occurs with two littorinid species: *Tectarius striatus* (King) and *Melarhaphe neritoides* (Linnaeus) (Martins et al., 2008). *C. stellatus* recruits primarily during the warmer periods of the year, although the exact timing of recruitment is geographically variable (O'Riordan et al., 2004). A former study showed that *C. stellatus* can be found on hard structures, although these structures generally supported reduced population densities compared to natural shores (Cacabelos et al., in press). We have first done a broad-scale survey and tested the hypothesis that there is, generally, a lower abundance of barnacles on hard structures compared to natural shores. On a smaller subset of sites, we then tested predictions of a number of models that could explain the observed patterns: (1) populations of barnacles on hard structures are temporally less stable, (2) less amenable environmental conditions on hard structures lead to increased barnacle mortality, reduced size and growth, and (3) barnacles are less abundant on hard structures because recruitment is intrinsically lower.

2. Materials and methods

2.1. Study sites

For the broad-scale study we selected a total of thirteen hard structures (seven made of basalt and six made of concrete) around the island of São Miguel, Azores (see Fig. S1, supplementary online material). In addition, we also selected eight natural shores (basalt *sensu latum*) interspersed around the hard structures (see Fig. S1). All locations were exposed to the ocean swell and, except for differences in substratum type and slope, were similar otherwise. All locations supported assemblages of animals and algae that were characteristic of Azorean shores (Martins et al., 2008). The upper eulittoral assemblages, where barnacles are most abundant, were dominated either by barnacles, limpets and bare-rock or, where barnacles were less abundant, by turf-forming algae (e.g. *Gelidium microdon*, *Caulacanthus ustulatus*).

The more detailed demographic study of *C. stellatus* was done on a subset of sites at one location, São Roque (see Fig. S1 inset). Here, about 1 km of seawall made of large basaltic blocks was built >10 years ago. In this location, despite the presence of the seawall, there are still a few sites of the original rocky shore that have remained preserved and which were used as natural shores. These stretches of natural rocky shore are interspersed and break down the seawall so that they effectively are separate sites. We selected a total of six sites: three interspersed stretches (30–50 m) of either the natural rocky shore or of the seawall. These sites supported assemblages as those described above. Barnacles spread over a larger vertical range on the natural gentle sloping shores (between 1.50 and 2.5 m above the lowest astronomical tide (LAT)) than on the sloping (ca. 45°) seawall (between 1.30 and 1.90 m above LAT). To ensure comparability, the study was done at similar shore heights in both habitats (1.60–1.80 m above LAT), which often corresponded to the shore height where barnacles were locally most abundant.

2.2. Sampling design

2.2.1. Patterns of distribution of barnacles

A broad-scale survey of barnacle density on natural shores and hard structures was done around the island of São Miguel between the 17June and 16September 2013. In each of the 21 locations, between five and ten 10 × 10 cm quadrats randomly deployed at the tidal height of highest barnacle density were photographed, and the number of barnacles in each photograph was then counted using Image J (Abramoff et al., 2004). The abundance of predators (e.g. the muricid whelk *Stramonita haemastoma*) was extremely low (probably due to intense harvesting) in all sampled sites and unlikely to contribute to any significant difference among habitats.

2.2.2. Patterns of temporal stability, size, growth and mortality

On a subset of six sites, six random 5 × 5 cm quadrats were photographed in each one: three sites on hard structures interspersed within three sites on natural shores. This procedure was repeated thirteen times between the 30April and the 1December of 2014. On each occasion, the numbers of barnacles in each photograph were counted using Image J. Temporal stability in the numbers of barnacles was calculated as 1/coefficient of variation for each quadrat over the thirteen sampling times. This population attribute was used as a surrogate to test if processes affecting the numbers of barnacles through time (e.g. mortality, recruitment), as whole, vary among habitats.

In addition to the above, in the same six sites, six random 5 × 5 cm quadrats were additionally marked with epoxy putty in the corners but not manipulated otherwise. These quadrats were photographed twice: at the start of the experiment (30April 2014) and six months afterwards. Barnacle size was estimated on the first sampling time by measuring the opercular diameter of ten randomly chosen barnacles in each photograph. These were then averaged to provide a single value for each quadrat. Barnacle growth was estimated by comparing the difference in opercular diameter between sampling times (six-month period). For each photograph, the later was done independently for five randomly selected small (<1.5 mm: mean ± SE = 0.86 ± 0.04 mm) and large (>1.5 mm: 1.82 ± 0.05 mm) barnacles. The two barnacle sizes were selected according to the range of sizes available in our study sites. Preliminary analysis showed that growth rate was independent of initial barnacle density ($r = 0.002$, $df = 70$, $P = 0.986$) suggesting that differences in barnacle density between habitats are unlikely to affect the comparison in growth rates. In the same marked plots, we further estimated barnacle mortality by randomly selecting ten barnacles within each photograph at the starting date and assessing whether these were alive or dead in the corresponding quadrat photograph six months latter.

Analysis of barnacle size and growth was done at the scale of the quadrat by averaging sampled individuals size and growth within each quadrat. Mortality was expressed for each quadrat as percent mortality.