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Factors limiting the establishment of canopy-forming algae on artificial structures

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ABSTRACT

Macroalgal canopies are important ecosystem engineers, contributing to coastal productivity and supporting a rich assemblage of associated flora and fauna. However, they are often absent from infrastructures such as coastal defences and there has been a worldwide decline in their distribution in urbanised coastal areas. The macroalga *Fucus spiralis* is the only high-shore canopy forming species present in the Azores. It is widely distributed in the archipelago but is never found on coastal infrastructures. Here we evaluate factors that may potentially limit its establishment on artificial structures. A number of observational and manipulative experiments were used to test the hypotheses that: (i) limited-dispersal ability limits the colonisation of new plants onto artificial structures, (ii) vertical substratum slope negatively influences the survivorship of recruits, and (iii) vertical substratum slope also negatively influences the survivorship and fitness of adults. Results showed that the limited dispersal from adult plants may be a more important factor than slope in limiting the species ability to colonise coastal infrastructures, since the vertical substratum slope does not affect its fitness or survivorship.

1. Introduction

Canopy-forming algae are key species on intertidal rocky shores (Jonsson et al., 2006) as they can provide shelter from environmental stressors (e.g. desiccation or ultraviolet radiation) for a diverse range of flora and fauna. By doing this, they play an important role in regulating community structure, nutrient cycling and primary production and therefore their conservation should be considered a priority (Bertocci et al., 2011; Perkol-Finkel and Airoldi, 2010; Perkol-Finkel et al., 2012). Despite their importance, marine canopy-forming algae have declined over the past decades (Perkol-Finkel and Airoldi, 2010; Strain et al., 2015), with major implications for the biodiversity and rocky reefs ecosystem goods and services (Airoldi and Beck, 2007; Smale et al., 2013; Voerman et al., 2013). There is thus a clear need to understand the drivers underlying their loss (Perkol-Finkel and Airoldi, 2010), the mechanisms that confer them stress tolerance (but see Martinez et al., 2012), and how the relative balance of physical (e.g. wave action) and biological factors (e.g. grazing) control their establishment and persistence (Davison and Pearson, 1996; Jonsson et al., 2006). Evidence worldwide has demonstrated that stressors such as climate change, eutrophication or urbanisation strongly affect marine canopies (e.g. Mangialajo et al., 2008). However, both direct and indirect human-induced modifications on physical habitat, acting as drivers for the decline of canopy-forming algae, have been usually overlooked (Perkol-Finkel and Airoldi, 2010).

Many coasts are becoming increasingly urbanised worldwide which can result in extensive modification of natural shores, altering habitat heterogeneity, complexity, slope and available area for benthic biota. This affects natural processes e.g. recruitment, colonisation, survival, population densities and connectivity, fecundity or/and species interaction (Bulleri et al., 2004; Bulleri, 2005; Chapman and Bulleri, 2003; Moreira et al., 2006; Perkol-Finkel and Airoldi, 2010). Several studies have investigated the patterns of distribution of benthic communities supported by

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artificial coastal defence structures and showed they are generally poor surrogates for the habitats they replace (e.g. Moschella et al., 2005). Although a variety of factors differ between artificial structures and the adjacent rocky shores, substratum slope is often fundamentally different. This modified slope has been shown to be a major determinant influencing the structure of intertidal assemblages (Bulleri and Chapman, 2004; Glasby and Connell, 2001). The differences in assemblages generated and maintained by a combination of differential recruitment and post-recruitment processes (Vaselli et al., 2008), result in considerable changes to coastal ecology. Canopy-forming algae are strongly affected by urbanisation (Airoldi and Beck, 2007; Benedetti-Cecchi et al., 2001), and little is known about the consequences of changes in the habitat related characteristics of the shore for their functional properties, like productivity and resilience (i.e. the ability of organisms to recover after events of disturbance, Grimm and Wissel, 1997). Changes have already been showed in demographic parameters such as growth or mortality of populations submitted to disturbance (Araújo et al., 2011), or in morphological parameters such as thalli thickness against desiccation stress or thalli size against wave exposure (Blanchette, 1997; Jorve, 2008). The steep slope of artificial structures could alter the physical stress to which plants are submitted, e.g. different desiccation regimes, and therefore change life-history traits, namely differentiation of populations via phenotypic plasticity (Blanchette, 1997). Moreover, although dispersal via drifting algal rafts has been cited as a mechanism to increase its gene flow (Coleman and Brawley, 2005), gamete dispersal is limited in fucoids (Coyer et al., 2011). This can limit its ability to colonise the 'newer' habitats. Understanding the processes that maintain differences in canopy-forming algae recruitment, growth and survival among different substrata, and identifying the factors that promote the loss of canopy-forming species, is thus of great importance in order to evaluate the consequences of coastal urbanisation worldwide and effectively manage and preserve marine coastlines (Coleman et al., 2008; Perkol-Finkel et al., 2012). But although potential explanations have been suggested, experimental tests of causal effects are not common and have usually focused on artificial substrata (Glasby, 2000).

In the Northeast Atlantic midshore there is generally a dynamic balance between fucoids, barnacles and limpets on the shore (Hawkins and Hartnoll, 1983; Hawkins et al., 1992; Thompson et al., 1996), although fucoids become less predominant at lower latitudes (Ballantine, 1961). The upper eulittoral in the Azores oceanic archipelago (located between 37 and 40°N and 25–31°W) is often dominated by two perennial macroalgae species, the Ochrophyta *Fucus spiralis* Linnaeus and the Rodophyta *Gelidium microdon* Kützing, 1849. The desiccation-resistant *F. spiralis* is the unique species of the genus found in Azores, where it forms scattered populations. It appears on exposed shores, in areas that are partially sheltered and not directly exposed to the full force of the incoming waves (Neto, 2000), and although it can appear on a variety of slopes, their abundance generally increase with decreasing slope (pers. observ). In Azorean coasts, formed by steep cliffs and volcanic rubbles, most artificial structures are used to protect nearby towns from high sea levels during winter storms. Coastal defences are mostly built by deploying piles of locally quarried rock or concrete boulders upon natural rocky shores, resulting in artificial structures with steeper inclination than natural shores. Although epibenthic assemblage composition differ (Cacabelos et al., 2016), qualitative similarities were found on both natural habitats and coastal defences. However, *F. spiralis* is conspicuously absent from these coastal defences, even though it can occur in the adjacent rocky intertidal.

Here we investigate factors that could potentially limit the ability of *F. spiralis* from establishing onto artificial structures. Specifically, we investigate the effects of substratum slope (vertical vs horizontal) on the growth and the level of desiccation of adult *F. spiralis*, and on the survival of recruits. In addition, we measured recruitment at several distances from the nearest source of propagules (clumps of *F. spiralis*) to investigate the species ability to disperse and colonise new areas.

2. Material and methods

We tested the hypothesis that *F. spiralis* is absent from artificial structures because adult plants do not survive on vertical or nearly vertical slopes. Adult individuals were collected in the field from horizontal substrates. Plants were weighed (fully hydrated wet weight, WW) and the fronds length (L) and maximum circumference (perimeter, P) measured. Dichotomies and receptacles were counted. Plants were then attached to nets that were subsequently attached to the substratum using stainless screws. Experimental plants were placed following the same procedure in interspersed areas with nearly horizontal and nearly vertical surfaces in the natural shore. Plants transplanted to horizontal surfaces were used to control the effects of manipulation (procedural control). The entire procedure was accomplished *in situ* and as quickly as possible to minimize the disturbance effect of the manipulation. Unmanipulated individuals (on horizontal surfaces) were randomly selected and marked to be measured as above and used as controls ($n = 6$). For these, WW was estimated indirectly using WW-LC^2 regressions (Åberg, 1990). The experiment was initiated at the end of July 2014 and replicated on two natural shores of similar wave exposure (site 1, Farol; site 2, Vulcanológico). After 3 months plants were re-measured and re-weighed, and linear growth, variations in biomass and number of dichotomies and receptacles were calculated by subtracting the initial values to the final ones.

The effect of slope on desiccation was investigated by comparing loss of water from plants ($n = 6$) deployed on horizontal and vertical surfaces in mesocosm. Tissue weight (Wt) was recorded for each plant every hour for a period of 5 h, and finally, plants were dried at 60 °C for 48 h to estimate the dry weight (DW). The relative water content (RWC) of each plant was calculated according to the formula $RWC = (Wt - DW)/(WW - DW)$ (DW, dry weight; Shafer et al., 2007). RWC of each plant was plotted against elapsed time, and exponential curves were fitted to each plot by using the formula $I_t = I_0e^{-kt}$ (I_t, RWC at time t; I_0, RWC at initial time; k, desiccation coefficient; Tanaka and Nakaoka, 2004).

To test the hypothesis that surface slope affects the early survivorship of recently recruited plants, fertile receptacles of *F. spiralis* were collected from the field early April 2015 to be used as source of zygotes. Receptacles were taken to the laboratory inside plastic bags in an ice-chest and kept in darkness. Receptacles were then washed in cold seawater, wiped with paper towels and placed on dry tissue paper at room temperature for zygotes release, following the protocol of McLachlan et al. (1971). The partially dehydrated receptacles were then placed inside dry grass covered Petri dishes and kept inside a culture chamber at 8 °C in the dark overnight. When zygotes started to release, receptacles were covered with cold sterile seawater until zygotes complete release and sunk to the bottom of the dish. Zygotes were then isolated from conspicuous mucilage, translated to aquaria with sterile seawater where the bottom was covered with recruitment plates (6 × 6 cm), and allowed to settle. Plates were incubated at room temperature, changing half of the water every 3 days. After 10 days, the initial concentration of recruits in plates was counted in 6 fixed subquadrats 1.5 × 1.5 cm under binocular lens. Plates were then transported to the field and randomly attached onto horizontal and vertical surfaces ($n = 8$) using stainless screws. After a period of