Introduction

Rocky marine substrates are characterized by the presence of clonal sessile invertebrates, such as sponges, corals and ascidians (Jackson 1977, Buss 1979, McKinney 1992). In these habitats, competition for space and predation act as major biotic determinants of sessile invertebrate’s distribution (Connell 1961, 1973, Sutherland 1976, Jackson 1977, Buss 1980). Competition for space is particularly strong in taxa that grow horizontally along the substrate, since the fitness of these organisms is often related to their size (Jackson 1977, Buss 1990).

In shallow hard substratum communities, competition with algae seems to negatively affect sessile invertebrate distribution by settlement, growth inhibition or overgrowth (Sammarco 1980, Sammarco 1982, Jernakoff 1985, Jompa and McCook 2002). Algae, for example, can inhibit invertebrate larvae settlement by chemical or physical means (Sammarco 1980, Jernakoff 1985, Jompa and McCook 2002). Additionally, algae have greater advantage over invertebrates by their extremely fast growth rates at shallower depths (Lobban and Harison 1994), which allow them to overgrow most benthic invertebrates (McCook et al. 2001). This negative effect has been demonstrated, for example, by Jompa and McCook (2002), where the presence and consequent overgrowth of the red algae *Lobophora variegata* (Lamouroux) Womersley ex. Oliveira 1977 caused significant colony tissue mortality on the coral *Porites cylindrica* Dana, 1846.

Herbivores, such as sea urchins and many fishes, are known to control algal populations leading to an increase in substrate accessibility for many organisms, thus having a fundamental role in the maintenance of diversity in those habitats. *Darwinella* sp. is a common sponge at several sites in Arraial do Cabo, Rio de Janeiro State, Brazil, but factors determining its distributional patterns are still unknown. The goal of this study was to establish the relationship among *Echinometra lucunter* density, algal and *Darwinella* sp. cover. The study was conducted at Saco do Cherne (SC) and Porcos Island (PI), Arraial do Cabo. At both sites, the density of *E. lucunter* and the percent cover of *Darwinella* sp. and algae were quantified. Additionally, *Darwinella* sp. percent cover was compared between portions of high and low *E. lucunter*’s density. Spearman Rank correlation analyses were performed between *E. lucunter* density and algae cover, *E. lucunter* density and *Darwinella* sp. cover, and between *Darwinella* sp. and algae cover. Results show that areas with high urchin density support a significantly higher cover of *Darwinella* sp. compared to areas with low density of urchins. Correlation analyses demonstrate that, in general, algae percent cover was negatively related to the density of *E. lucunter*. The same pattern was found between algae and *Darwinella* sp. percent covers. On the other hand, the relationship between *E. lucunter* density and *Darwinella* sp. cover was weakly positive. The results from this study suggest that algae is possibly competing with *Darwinella* sp. for space, but the presence of *E. lucunter* is probably mediating this interaction by decreasing the percent cover of algae. However, the weak relationship observed between *E. lucunter*’s density and *Darwinella* sp. cover suggests that other factors besides competition with algae are affecting the percent cover and distribution of the sponge *Darwinella* sp. at the studied sites.

Keywords: Algae, herbivory, sea urchin, sponge, competition
in the maintenance of diversity in marine hard substratum communities (Paine and Vadas 1969, Carpenter 1986, Jompa and McCook 2002). One remarkable example of a herbivore impact in a marine community was the mass mortality of the sea urchin Diadema antillarum Philippi, 1845 around the Caribbean region in 1983/1984 (Carpenter 1990). The decrease in 95-99% of D. antillarum population in Caribbean reefs had a large negative impact on scleractinian coral cover, changing entire reef systems from coral to algal dominated communities (Hughes 1994). Only with the slow increase in D. antillarum densities algal cover began to decrease and coral cover consequently increase (Edmunds and Carpenter 2001). Therefore, it is clear that the presence of sea urchins have a positive effect on marine hard substratum communities by the reduction of algal cover and, consequently, a greater diversity of invertebrate fauna.

Sponges are often competitively superior to most benthic invertebrates (Jackson and Winston 1982, Bell and Barnes 2003). However, algae might be competitively superior to sponges as demonstrated in a study of competition between a coralline algae (Corallina vancouveriensis Yendo, 1901) and the sponge Halichondria panicea (Pallas, 1766) in temperate seas (Palumbi 1985). If sponges are inferior competitors to algae, their distribution in rock bottom communities may be negatively affected by algal competition, particularly in the absence of an effective herbivore (Bell and Barnes 2003). The negative association between sponges and macroalgae in temperate rocky subtidal communities has been suggested to be caused by competition between these two groups of organisms (Witman and Sebens 1990, Bell 2002). Conversely, it has been argued that the observed macroalgal and sponge distribution in those habitats might be, instead, the result of abiotic factors, such as depth and substratum inclination (Pecado and Maldonado 2005). What remains unknown is whether in habitats with similar abiotic factors competition with algae has a negative effect on sponge distribution. Wulff (2005) has argued that in the absence of abiotic factors, that could prevent a species from occurring in a particular habitat, biotic factors, such as competition, can have a large effect on sponge distribution. Consequently, if sponges are outcompeted by algae, the presence of an efficient herbivore is important to mediate these interactions and avoid the competitive exclusion of sponges in a particular habitat (Palumbi 1985).

Darwinella sp. is a demosponge that fifteen years ago was rarely seen around the Arraial do Cabo region (Rio de Janeiro State, Brazil) (Muricy et al. 1991). Currently though, Darwinella sp. can be commonly seen at some localities around Arraial do Cabo (ENC, personal observation). Although frequent, Darwinella sp. distribution in a scale of meters to kilometers seems patchy at shallower depths (0-8 m; ENC, personal observation), however, the factors affecting the distribution of this species remains unknown. In Arraial do Cabo, the sea urchin Echinometra lucunter (Linnaeus, 1758) is the most conspicuous benthic herbivore in shallow waters (Castro et al. 1995), although herbivore fishes in the area are also common (Ferreira et al. 1998). It has been shown that 98% of E. lucunter’s diet is constituted by algae, while the remaining 2% is composed of invertebrates that are probably ingested accidentally (Oliveira 1991). Therefore, one possible biotic factor determining the distribution of Darwinella sp. around Arraial do Cabo might be the relative abundance of algae, which should be regulated by E. lucunter. The goal of the present study was to evaluate the relationship among E. lucunter density, algal and Darwinella sp. cover in Arraial do Cabo, Rio de Janeiro State, Brazil.

Materials and methods

Study area

The study was conducted at Porcos Island (PI) and Saco do Cherne (SC), in Arraial do Cabo, RJ, Brazil (Fig. 1). PI is characterized by low wave action, sheltered from the northeastern winds that are predominant in the area. The substratum morphology is characterized by rocky walls with variable inclination interspaced by small portions of vertical walls. SC is a small inlet, characterized by high wave action, exposed to the predominant northeastern winds. Substratum morphology is characterized by a single rocky wall predominantly vertical. On both sites PI and SC, the interface between the rocky wall and the bottom happens abruptly in approximately 90° angle.

Sampling

Eight 5 m portions of the rocky substrate were haphazardly chosen at PI and four at SC, where every portion was located at the interface between the bottom and the vertical wall (4-6 m depth), where the urchin E. lucunter was most abundant. Within each portion, five to six vertical rectangles (60 x 40 m depth), where the urchin E. lucunter was most abundant. Within each portion, five to six vertical rectangles (60 x 40
cm) were randomly chosen and photographed (Fig. 2) using a digital camera (SONY Cyber-Shot DSC-P41). To estimate the percentage cover of *Darwinella* sp., algae, and other sessile invertebrates within each portion of the rocky substrate, all digital images were analyzed with the CPCe V.3.3 software (National Coral Reef Institute/New Southeastern University) using a 60 point grid system. Preliminary tests showed no difference in percent cover when estimated with a 60 or 100 point system. Density of *E. lucunter* was quantified by counting all sea urchins that had some portion of its body within each sampled rectangle. In the present study algae was defined by the combination of algal turfs (represented primarily by coralline filamentous algae: Steneck and Dethier 1994) and a few other macroalgae, such as *Codium* Stackh, 1797, *Sargassum furcatum* Kützing 1843 and *Dictyota* spp. Lamouroux 1809, that occur in lower densities but in conjunction with the predominant algal turfs (Yoneshigue and Valentin 1988).

**Data analyses**

Percent covers were arcsin transformed prior to all statistical analyses (Sokal and Rohlf 1995). Nonparametric tests were performed when data did not conform to assumptions of normality and homoscedasticity (Sokal and Rohlf 1995).

A Mann-Whitney test compared the percent cover of *Darwinella* sp. between areas of high and low densities of *E. lucunter*. To choose areas with significant differences in sea urchin densities (i.e., high and low densities), at PI, out of the eight sampled portions of the rocky substratum, two with the highest and two with the lowest average densities of *E. lucunter* were chosen to be used in the comparison of *Darwinella*’s percent cover (Fig. 3). A one way ANOVA followed by a Tukey post hoc test, established whether there were significant differences in sea urchin’s density within and between high and low density portions. No significant differences in urchin densities were found within low (F = -2.87; df = 3, 19; P > 0.5) or high (F = 0.000; df = 3, 19; P > 0.5) urchin density portions, while portions of high density were significantly different form portions of low urchin density (F = 14.20; df = 3, 19; P < 0.005). Therefore, the two portions of low density, as well as the two of high density were pooled for the comparison of the percent cover of *Darwinella* sp.

To establish the relationship among *E. lucunter* densities, algal and *Darwinella* sp. cover, three pair-wise Spearman Rank correlation analyses were performed: 1) *E. lucunter* density and *Darwinella*’s cover; 2) *E. lucunter* density and algal cover; 3) algal cover and *Darwinella*’s cover. All three correlations were performed separately for each locality and afterwards by pooling data from both PI and SC. In all tests, the portions along the rocky bottom were pooled at each locality and the photographed rectangles were used as replicates.

**Results**

The density of *Echinometra lucunter* varied greatly among portions of the rocky bottom at each locality (Fig. 3). At PI, sea urchin density varied between 3.33 ± 1.56 and 65.28 ± 8.95 individuals/m², while density at SC varied between 6.25 ± 2.57 and 32.64 ± 4.15 individuals/m² (mean ± SD; Fig. 3). *Darwinella* sp.’s percent cover varied between 0% and 17.69 ± 7.30% at PI and 2.68 ± 3.16% and 6.47 ± 2.66% at SC.
with averages of 3.92% and 7.53% (PI and SC, respectively; Fig. 4). Algal cover was extremely high at both localities, reaching up to 90.33% at PI and 74.64% at SC (Fig. 4). All other invertebrates together reached maximum densities of 26.66% and 78.33% at PI and SC, correspondingly.

*Darwinella* sp. cover was significantly different between portions of high (62.5 ± 7.43 individuals/m$^2$) and low (9.85 ± 3.24 individuals/m$^2$; mean ± SE; Fig. 3) density of sea urchins ($U = 121.00; N = 12; P < 0.0001$; Fig. 5). The percent cover of *Darwinella* sp. was more than ten-fold higher in areas of high (11.92 ± 2.73%; mean ± SE) compared to areas with low sea urchin densities (0.08 ± 0.08%; mean ± SE; Fig. 5).

In general, algal cover was negatively related to the density of *E. lucunter* ($R = -0.807; N = 70; P < 0.0001$; Fig. 6A). A similar relationship was found between the percent cover of algae and *Darwinella* sp. ($R = -0.649; N = 70; P < 0.0001$; Fig. 6B). Conversely, the relationship between sea urchin density and *Darwinella* sp. cover, although significant, was weakly positive ($R = 0.470; N = 70; P < 0.001$; Fig. 6C). The same pattern was found when analyses were performed solely for PI (Fig. 7A, 7B, 7C). At SC, most relationships were weak (Fig. 7D, 7E, 7F), with the strongest relationship being between *E. lucunter’s* density and algal cover ($R = -0.430; N = 24; P < 0.05$).

From the total number of *Darwinella*’s quantified in the present study ($N = 52$), 75% of them were in total or partial contact with algal turfs. Less than 20% were in partial contact with other invertebrates, particularly the bryozoan *Schizoporella errata* (Walters, 1878). In most partial contacts between *Darwinella* sp. and other invertebrates, only 10% of the sponge surface was actually in contact with the invertebrate.

**Discussion**

The present study demonstrates that areas with high density of the sea urchin *Echinometra lucunter* have a significantly higher cover of the sponge *Darwinella* sp. than areas with low sea urchin density. This observation, in addition with the negative correlations found between *E. lucunter’s* density and algal cover, and also between *Darwinella* sp. and algal cover suggest that *Darwinella* sp. and algae are...
possibly competing for space and that the sea urchin might be controlling algal population. This result is corroborated by the frequent observation of contacts between Darwinella sp. and algae, however, manipulative experiments would be required to confirm this hypothesis. On the other hand, the weak relationship found between E. lucunter’s density and Darwinella sp. cover also suggests that there might be other factors besides competition with algae that is affecting the density and distribution of Darwinella sp. in Arraial do Cabo.

Species of the genus Echinometra usually possess strong homing behavior and are often distributed in an aggregated pattern (McClanahan and Murtiga 2001). In the present study, the large variation in sea urchin density found among portions of the rocky substratum at both localities suggests that E. lucunter is distributed in an aggregated manner (in a scale of less than 0.5 meters), as observed in other species of this genus (McClanahan and Kurtis 1991). Therefore, it is expected that areas of high sea urchin density will support a low algal cover and vice versa, since this urchin’s diet is mainly composed of algae (Oliveira 1991). The negative correlation between sea urchin density and algal cover, in the present study, supports Oliveira’s (1991) findings that algae is E. lucunter’s main diet. However, it has been argued that in the absence of algae, E. lucunter can also feed on benthic invertebrates, such as sponges and cnidarians (McClintock et al. 1982, Oliveira 1991, McClanahan and Murtiga 2001). During the course of this study it was observed that Darwinella sp. that was found close to sea urchin aggregations presented irregular shapes that visually appeared to be caused by sea urchin removal (e.g., predation or abrasion). Thus, the weak relationship found between urchin density and Darwinella sp. cover could be due to the sea urchin’s grazing activity (predation) or by the accidental removal of sponge tissue (abrasion) when sea urchins move along the substratum.

Although few studies have focused on sponge/algae competitive interactions (but see Palumbi 1985), studies on the negative effect of algae on the distribution of
other invertebrates are abundant (Quinn 1982, Jemakoff 1985, McCook et al. 2001). Algae are often the dominant competitive organism owing to their relative fast growth rates and the presence of secondary metabolites (Duffy and Hay 1990), although, sponges are also known to produce large quantities of chemical compounds (Thacker et al. 1998). The negative correlation between algae and Darwinella sp. cover in the present study suggests that, if competition is occurring, algae are competitively superior to sponges. If that is the case then, it would be interesting to determine what factors make algae competitively superior to sponges, and how general is this phenomenon.

In general, the relationships among sea urchin density, Darwinella sp. and algal cover were similar at both localities, although they were weaker at SC compared to PI. The weak relationships at SC might be due to a lower sample size compared to PI, or it can possibly be due to site differences, such as fauna and flora composition or abiotic factors. At SC there was a higher abundance of benthic invertebrates, other than Darwinella sp., when compared to PI (Fig. 4). The high cover of other invertebrates at SC could have a negative effect on the distribution of Darwinella sp., through competition, which could have led to the observed weak relationship between algae and Darwinella sp. and also between Darwinella sp. and E. lucunter. The algal composition was also different between localities, with PI being dominated primarily by algal turfs, while SC had a larger abundance of macroalgae such as Codium sp. and Dictyota spp. (ENC, personal observation). Besides their greater palatability, macroalgae have a relatively higher biomass than algal turfs (Duffy and Hay 1990). Therefore, sea urchins at SC might have smaller grazing patches than at PI, since it has been demonstrated that patch size and grazing patterns are dependent on food availability (Russo 1977, McClanahan and Murtiga 2001).

Many authors in the past have suggested that sponge distribution was intimately related to competition (reviewed by Wulff 2006). However, recent studies have pointed out the importance of abiotic factors as determinants of sponge distribution (Preciado and Maldonado 2005). What has recently been argued is that abiotic factors could actually exclude species from a locality (Alcolado 1994, Wulff 2005), but if a species is not inhibited by these factors, competitive interactions may greatly affect species distribution (Wulff 2005). In the present study, abiotic factors such as substratum inclination and depth were similar; however, water flow regimes were different with SC being an exposed site and PI a sheltered one (Fig. 1). This difference in water flow regimes might affect the distribution of Darwinella sp. and its relationship with algae and other invertebrates.

To conclude, the results of this study point to a possible competition for space between algae and Darwinella sp., which is probably mediated by the sea urchin E. lucunter. Nevertheless, manipulative studies are needed in order to confirm the negative effect of algal cover on the cover of Darwinella sp. and the positive impact of the sea urchin on Darwinella sp. distribution.

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References

Duffy JE, Hay ME (1990) Seaweed adaptations to herbivory: chemical, structural, and morphological defenses are often adjusted to spatial or temporal patterns of attack. BioScience 40(5): 368-375