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ASSEMBLEIAS DE OURIÇOS-DO-MAR E RELAÇÕES COM O HABITAT EM DIFERENTES RECIFES BRASILEIROS

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"By the same number doth nature divide the circle of the sea star, and in that order and number disposeth these elegant semicircles, or dental sockets and eggs in the sea hedgehog."

(Sir Thomas Browne, 1658

RESUMO

Em ambientes costeiros rasos, sabe-se que os ouriços-do-mar têm um papel ecológico importante, controlando a abundância de macroalgas e permitindo a coexistência de algas crostosas coralinas, e muitas vezes o assentamento de larvas de corais. O efeito dos ouriços sobre as algas é um fenômeno bem documentado em uma ampla variedade de habitats. O interesse sobre esse tópico iniciou na década de 70, nos Estados Unidos da América, com o trabalho de base nos mares temperados, onde aconteceu a proliferação de ouriços que causou a depleção nas zonas de macro algas, transformando-as em áreas dominadas por algas calcarias Sabe-se também que a estrutura física do habitat e outros fatores bióticos e abióticos podem influenciar a distribuição dos ouriços, devido à intensa relação que esses organismos têm com o substrato, como alimentação e locomoção. Poucos estudos foram realizados no Atlântico tropical sudoeste avaliando as assembleias de ouriços em substratos consolidados. Cinco espécies de equinóides são conhecidas para os estados de Santa Catarina e Bahia do Brasil, não existindo para elas dados de densidade e distribuição com relação aos habitats. O objetivo geral desse estudo foi avaliar os padrões de ocorrência e abundância de ouriços em função das características do micro-habitat em recifes coralíneos e rochosos do Atlântico Sul ocidental. Para isso verificamos: (1) a abundância e diversidade dos ouriços e (2) as relações dos ouriços com o habitat em diferentes tipos de recifes. Particularmente, buscamos avaliar a abundância em três recifes rochosos (SC) e um recife de coral (BA) para entender a relação das assembleias de ouriços com a estrutura do habitat: complexidade, profundidade, porcentagem de cobertura de bentos. Foi quantificada a riqueza e abundância dos ouriços-do-mar e foram avaliadas variáveis bióticas e abióticas do habitat. As amostragens foram realizadas através de mergulho autônomo, e os parâmetros bióticos e abióticos foram avaliados *in situ* através de contagens de organismos e classificação dos microhabitats em quadrados de 0.5mX0.5m. Seis espécies foram encontradas para SC, incluindo um novo registro da espécie *Tripneustes ventricosus*. No recife coralíneo (Recife de Fora, BA), encontramos quatro espécies mas *E. lucunter* foi a espécie dominante com média de 12,7 ±1,1 ind.m^{-2}. Nos recifes rochosos de Santa Catarina, a densidade média de *E. lucunter* na faixa rasa (1-5 m) foi de 5,12 ± 2,1 ind.m^{-2}. Outras espécies, apesar de terem densidades mais baixas, também foram representativas (e.g. *Arbacia lixula* 1,67 ind.m^{-2}; *Paracentrotus gaimardi* 1,34 ind.m^{-2}). Em relação ao habitat, na escala do microhabitat, a composição de ouriços de Santa Catarina foi melhor explicada pela seguinte variável: a complexidade de habitat (BIOENV; p_{w}=0,22). No Recife de Fora (BA), a abundância de ouriços foi melhor explicada pela cobertura de buracos (BIOENV; p_{w}= 0,217), que também é resultado do ouriço escavando o recife, e assim criando uma maior complexidade do habitat. No mesmo recife, a densidade de *E. lucunter* também teve relação com esse mesmo fator abiótico (r=0,37; P<0,0001). Os resultados do ambiente rochoso em Santa Catarina nos levam a concluir que o efeito de habitat na comunidade de ouriços é espécie-específico. Para o recife coralíneo amostrado na Bahia, sugerimos uma menor redundância funcional de ouriços herbívoros no sistema (quando comparado ao recife rochoso). Esse resultado pode ser importante em termos de resiliência do sistema. Mais estudos sobre os ouriços devem ser considerados para ajudar entender seu papel em sistemas recifais em mudança e para subsidiar ações que promovam a manutenção da resiliência de sistemas recifais.

Palavras-chave: abundância, habitat, ouriços-do-mar, recifes brasileiros

ABSTRACT

Sea urchins have important roles in marine shallow coastal environments by controlling the abundance of macroalgae, favouring the growth of crustose coralline algae, and often enabling coral spat settlement. The phenomemon of urchin effects on algae has been documented in various types of habitat. Interest in this topic began in the mid 70s in the United States in temperate reefs when a sea urchin proliferation event occured, causing a depletion of macroalgal zones and transforming them into calcareous algae zones. Sea urchins exhibit close linkages with the substrate, derived from their life habits like locomotion and feeding. Therefore, their distribution is influenced by the physical structure of the habitat as well as biotic and abiotic factors. Few studies have assessed the urchin assemblages in marine hard substratum communities of the South Atlantic. Five urchin species are known to occur in the state of Santa Catarina and Bahia in Brazil, those of which have no distribution data. The main objectives of this study were to evalute the distribution and abundance patterns of urchins and their relationships with habitat characteristics at the microhabitat scale. We determined (1) urchin abundance and diversity, and (2) their relationships with habitat variables in two different reefs. Specifically, we performed this study at three rocky reefs of Santa Catarina (SC) and one coral reef of Bahia (Recife de Fora-BA) to understand the urchin assemblages and their relation to habitat structure: habitat complexity, depth, and percent cover of substrate groups. We sampled for richness and abundance data as well as biotic and abiotic habitat variables. *In situ* sampling was performed during scuba diving by quadrat counts and classification of percent cover of the microhabitat variables using 0.5mx0.5m quadrats. Six species of urchins were found for SC, including one new species register of *Tripneustes ventricosus*. At the coral reef (Recife de Fora, Bahia), four species were found but *E. lucunter* was the main species with a mean density of 12.7 ± 1.1 ind.m^{-2}. At the rocky reefs of SC, their mean density in the shallow strata was 5.12 ± 2.1 ind.m^{-2}. Other species, despite presenting lower densities, were also representative (e.g. *Arbacia lixula* 1.67 ind.m^{-2}; *Paracentrotus gaimardi* 1.34 ind.m^{-2}). In relation to habitat at the micro-scale, the urchin composition of SC was best explained by the following variable: habitat complexity (BIOENV; p_w=0.22). At Recife de Fora, the biotic compostion was best explained by percent cover of holes (BIOENV; p_w= 0.217), which is also a result of the urchin excavating the reef thus creating a greater habitat complexity. In the same reef, *E. lucunter* density also correlated with the same variable (r =0.37; P<0.0001). Our results suggest that for the rocky reefs of Santa

Catarina, the effect of habitat on sea urchin assemblage is species-specific. For the studied coral reef of Bahia, we suggest a lack of funcional redundancy of urchin herbivores (when compared to the rocky reefs). This result may be important in terms of reef resilience. Future urchin studies should be considered in order to better understand their roles in changing reef systems and to aid in promoting management of reef resilience.

Key words: abundance, habitat, sea urchins, Brazilian reefs

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SUMMARY

INTRODUÇÃO

Na ecologia, a elucidação dos processos que determinam a distribuição e abundância dos organismos constitui um problema fundamental (Ricklefs 1979). Em um mundo hipotético, uma possível solução seria examinar a história natural de todos os organismos que formam uma determinada comunidade. Na prática, mesmo sendo o exame de todos os organismos impossível, o estudo de espécies que possam exercer uma influência presumivelmente dominante na estrutura de uma comunidade oferece, muitas vezes, resposta bastante satisfatória, proporcionando importantes subsídios para ajudar a resolver o problema de elucidar os processos que determinam a distribuição e abundância de espécies (Giordano 1986).

Em se tratando de ecologia marinha, os ouriços representam animais chaves na estrutura de uma comunidade e muitas vezes são responsáveis por alterar substancialmente a composição florística, reduzindo a cobertura vegetal (Lewis 1958; Paine & Vadas 1969; Ogden et al. 1973; Sammarco et al. 1974; Giordano 1986; Johansson et al. 2010). O efeito dos ouriços sobre as algas é um fenômeno bem documentado em uma ampla variedade de habitats (Lawrence 1975; Schiel & Foster 1986; Andrew 1993), e o estudo desse fenômeno é uma das linhas de pesquisa clássicas na ecologia (revisões: Lawrence 1975, Lawrence & Sammarco 1975, Schiel & Foster 1986, Sala *et al.* 1998, Pinnegar *et al.* 2000; Bernat 2004). O interesse sobre esse tópico iniciou na década de 70, nos Estados Unidos da América, através de um estudo realizado nos mares temperados. Este demonstrou que a proliferação de ouriços seria a causa da redução na abundância e cobertura de macroalgas não calcificadas, para que fez com que estas áreas viessem a ser dominadas por algas calcárias (Lawrence 1975). Não muito tempo depois, no Caribe, entre 1983 e 1984, houve uma alta mortalidade de ouriços *Diadema antillarum* (Lessios et al. 1984) e a ausência desse herbívoro foi considerada como a causa de um significativo aumento na dominância de macroalgas (Hughes et al. 1985; Carpenter 1990a). A cobertura de macroalgas e a densidade de ouriços passam a ser considerados, portanto, bioindicadores de degradação recifal amplamente conhecidos (Hughes 1994; McClanahan & Mutere 1994; Jackson et al. 2001; McManus & Polsenberg 2004).

O aumento da quantidade de equinóides é consequência direita da sobrepesca dos predadores de ouriços (Hay 1984; McClanahan 1995), o que potencialmente aumenta a densidade destes herbívoros até que esta atinja níveis críticos ou deletérios (Johansson et al. 2010). Sabe-se que os recifes de corais hoje estão em crise (Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004; Graham et al. 2007) e que a pressão originária da exploração humana e das mudanças climáticas nestes sistemas os estão transformando, com consequências imprevisíveis em relação ao funcionamento do ecosistema.

Em certos recifes do Caribe como na Jamaica e Bahamas, a redução na abundância, ou mesmo a remoção de todos os herbívoros, peixes e ouriços, resultou em uma mudança na cobertura bentônica, na qual o recife, antes dominado por corais, passou a ser dominado por algas foliosas (Hughes 1994; Wright et al. 2005). Da mesma forma, nos recifes rochosos temperados da Califórnia, a ocorrência de altas densidades agregadas de ouriços pastejadores resultou em uma mudança de estado de uma comunidade dominada por algas foliosas para um estado dominado por algas incrustantes, chamado "urchin barrens" – *manchas de ouriços em rochas quase nuas* (Dean et al. 1984; Ebeling et al. 1985; Andrew 1993; Benedetti-Cecchi et al. 1998; Shears & Babcock 2002; Wright et al. 2005). No contexto da resiliência de um recife, é importante ainda salientar a relevância da diversidade de diferentes espécies no sistema (Bellwood 2004, 2006) configurando, assim, o papel ecológico fudamental do ouriço, junto com outros herbívoros, fundamental para a manutenção da mesma.

A estrutura física do habitat e outros fatores bióticos e abióticos também podem influenciar a distribuição dos ouriços, sendo atributos importantes a serem considerados para a compreensão do funcionamento do sistema. Estudos quantitativos sobre a relação entre espécies/habitat iniciaram na década de 70 (e.g. Salvat et al. 1972; Luckhurst and Luckhurst 1978; Sale 1978, 1980) e estudos mais recentes mostram que a relação dos ouriços com o habitat tende a ser espécie-específica e altamente dependente da escala amostrada (Andrew 2003; Dumas et al. 2007; Entrambasaguas et al. 2008). Mesmo assim, trabalhos recentes têm demonstrado que determinados fatores ambientais relativos ao substrato e à coluna d'água influenciam a distribuição espacial dos organismos associados ao recife (McClanahan 1992; Lecchini et al. 1997; Cleary et al. 2005; Dumas et al. 2007). Sabe–se que para ouriços, as espécies possuem uma relação forte com o substrato, derivada das estratégias de vida como movimento e alimentação, e as padrões de distribuição geralmente refletem essa relaçào (Lawrence 2001; Dumas et al. 2007). No entanto, alguns estudos apontam que os padrões de distribuição dos ouriços são complexos e difíceis de relacionar com os fatores ambientais (Adjeroud 1997; Dumas et al. 2007).

No Brasil, o primeiro estudo citando a importância de ouriços dentro da comunidade foi realizado por Rathbun, em 1879. O autor fala sobre *Echinometra lucunter* como um ouriço comestível, escavador de rochas que ocorre desde Pernambuco, no nordeste, até Santa Catarina, no sul do país. (Giordano 1986). Segundo Tommasi (1964), havia poucos estudos ecológicos em Biologia Marinha no Brasil até meados dos anos 60, ao contrário do que ocorria em outros países. Os estudos mais aprofundados sobre ouriços até hoje são realizados na área da fisiologia. Assim, estudos ecológicos que auxiliem a compreender o papel desse importante herbívoro nos recifes brasileiros ainda são necessários e até mesmo urgentes, frente às mudanças pelas quais os ambientes marinhos vêm passando.

O presente estudo teve como objetivo avaliar a composição e abundância das assembleias de ouriços do mar em dois tipos de recifes (rochoso e coralíneo) e investigar as relações com o habitat. Mais especificamente, para os recifes rochosos, os objetivos foram de (1) avaliar as densidades dos ouriços em três ilhas rochosas de Santa Catarina, de (2) descrever as características do habitat e comparar entre os locais amostrados, e (3) investigar se determinadas variáveis ambientais explicam os padrões observados para as assembléias de ouriços na escala do microhabitat. Para o recife de coral, foram avaliadas assembleias de ouriços em cinco pontos do Recife de Fora (Bahia), a fim de (1) avaliar as densidades dos ouriços no local, (2) descrever as características do habitat e comparar entre os locais amostrados, (3) avaliar na escala do microhabitat se determinadas variáveis ambientais explicam os padrões observados das assembleias de ouriços e (4) se há relação entre a riqueza e abundância de corais e as densidades de ouriços. Adicionalmente, o presente estudo teve como objetivo final fornecer algumas das bases necessárias para facilitar futuros estudos de comparação entre recifes ao longo da costa brasileira no que se refere ao padrão de abundânica relativa dos referidos herbívoros.

CHAPTER 1
MATCHING ABUNDANCE OF SEA URCHINS AND HABITAT VARIABLES IN SUBTIDAL ROCKY REEF BRAZILIAN COMMUNITIES

FORMATTED FOR MARINE ECOLOGY

MATCHING ABUNDANCE OF SEA URCHINS AND HABITAT VARIABLES IN SUBTIDAL ROCKY REEF BRAZILIAN COMMUNITIES

Abstract: Sea urchins are key herbivores in reef systems as they exhibit close linkages with marine hard substraum communities by the reduction of algal cover. Both biotic and abiotic factors influence sea urchin distributions and assemblages in a complex and inter-related manner. The present study aimed to assess the relationships between sea urchins and rocky reef habitat of the Southwestern Atlantic. Species abundance and composition were determined in three nearshore rocky reefs to investigate the relationships with habitat. Twelve quadrats of 0.5m X 0.5m were sampled along transects at each site to assess the urchin composition and density, and the percent cover of habitat variables. Five urchin species were identified in three rocky reefs, and a new record of *Tripneustes ventricosus* was reported for the first time in south Brazil. The urchin assemblages grouped according to site (R=0.29, P <0.05) and species densities varied significantly among sites. The multivariate analysis identified one habitat variable that best explained the urchin assemblage: habitat complexity (BIOENV; p_w=0.22). The CCA analysis indicated species-specific habitat relationships and explained 76.9 % of the total variability (Axis 1= 50.7%; Axis 2=20.5%, P<0.05). Our results suggest only minor urchin-habitat correlations, thus, unexplained variation is left to stochastic events. Further long-term studies are needed to assess these urchin relationships at larger spatial and temporal scales. The rocky reefs of Southeast Brazil deserve particular attention since this region suffers consequences of overfishing and strong influences from the South Atlantic Anti-cyclonic high-pressure center.

Key words; sea urchins, abundance, habitat, rocky reefs

Problem

The community structure of the benthos of hard substrata in the tropical southwest Atlantic is poorly known (Oigman-pszczol *et al.* 2004). Despite the important functional role of sea urchins in reef systems as herbivores (Hughes *et al.* 1994; McClanahan *et al.* 1994; Young & Bellwood 2012), little is known regarding their abundance and habitat relationships in this region. In other studied systems, sea urchins have been shown to cause drastic phase-shifts due to a change in their role in the system, caused by top-down effects (predators) and extreme events. The earliest evidence of this occured in the temperate seas of California, where the collapse of the sea otter predator population led to proliferations of sea urchins that denuded large extensions of macroalgal meadows and transformed them into communities dominated by encrusting calcareous algae (Lawrence 1975; Bernstein *et al.* 1981; Fina 2004). Later in Jamaican coral reefs, the 1983-1984 mass mortality from an unknown disease depleted the population of the urchin *Diadema antillarum*, resulting in a shift from a coral dominated reef to a macro-algal dominated community (Lessios 1988; Edmunds & Carpenter 2001). In today's reefs, two widely recognized indicators (many other degradation responses also exist) responsible for coral reef decline have been identified: macroalgal cover and sea urchin density (Hughes 1994; Jackson *et al.* 2001; McManus & Polsenberg 2004; Johansson *et al.* 2010). Therefore, sea urchin studies regarding abundances and inferences on habitat relationships are required in order to understand the mechanisms that keep urchin populations at "healthy" levels. Attempts to fill this gap have begun, as it can be seen in a study that sampled Echinoderms in 76 globally-distributed rocky reef sites within 12 ecoregions, following the standardized sampling protocol of the Census of Marine Life NaGISA project (Iken *et al.* 2010) This study did not detect any latitudinal trends for echinoderm assemblages and concluded that such trends are superseded by regional diversity hotspots. As well, the same study identified a set of environmental variables as potential drivers of echinoderm assemblages by ecoregions. It was concluded that nearshore echinoderm assemblages appear to be shaped by a network of environmental and ecological processes (Iken *et al.* 2010). However, the Brazilian coast, responsible for almost the entire Southwestern Atlantic, was not included in this study, stressing the lack of available information of sea urchin assemblages in this region.

Concerning urchin-habitat relationships, studies have shown that the presence of sea urchins is positively correlated with marine hard substratum communities by the reduction of algal cover and consequently promoting a greater diversity of invertebrate fauna (Carpenter 1981;

Sammarco 1982a; Johson & Mann 1993; Calderon *et al.* 2007). In no-take temperate areas, with an abundance of urchin predators, the benthic physiognomy is determinated by abundant fleshy algal cover, and reduced amounts of sea urchins and crustose coralline algae (O'Leary & McClanahan 2010). Tuya *et al.* (2004) states that the strong negative relationship between the percentage of macro-algal cover and density of other echinoid species has also been described in the western Mediterranean (Sala & Bourdesque 1997), the Kenyan Coast (McClanahan *et al.* 1996), New Zealand (Andrew & Choat 1982; Babcock *et al.* 1999; Shears & Babcock 2003) and in the northwestern Atlantic (Vadas & Steneck 1995). As for Brazil, *Echinometra lucunter* is the most abundant sea urchin (Xavier 2010), but few studies have assessed their abundance patterns and habitat relationships. Similarly, classical studies of such fish-urchin-algae relationships in warm temperate reefs showed that physical complexity of the habitat, an abiotic variable, was also important in determining local patchiness of the urchin *Diadema antillarum* but not important in well-developed urchin grazed areas where a high density was previously established (Tuya *et al.* 2004). Urchin assemblages, like any other benthic fauna, are also influenced by physical factors such as water quality (Flammang *et al.* 1997; Dumas *et al.* 2007), hydrodynamics (Russo 1977; Entrambasaguas *et al.* 2008), and light intensity (Barnes & Crook 2001; Entrambasaguas *et al.* 2008).

The present study explores the relationships between sea urchins and the rocky reef habitat in the Southwestern Atlantic, a poorly studied area that is influenced by recent climate changes (Alves & Melo 2001). The variability of the South American climate (i.e., interannual and interdecadal changes) results from the superposition of several large-scale phenomena (Garreaud *et al.* 2009). Understanding the habitat relationships and sea urchin assemblages in the rocky reefs of Santa Catarina, in a transition belt between tropical and temperate regions (Bouzon *et al.* 2012), is potentially important for future management plans since over-fishing is a worldwide threat that can lead to sea urchin outbreaks at damaging levels (McClanahan & Muthiga 1989; Sala & Zabala 1996; Young & Bellwood 2012).

This study assesses sea urchin abundance and composition and its relationships with environmental habitat variables. More specifically, we aimed to determine the sea urchin species abundances in three rocky reef island sites and if they vary among sites. The null hypothesis (H_0) was that no differences in urchin abundances exist between sites. For all study sites, we also determined any existing relationships between sea urchin abundances and 10 assessed environmental habitat variables (biotic and abiotic). Here, our alternative hypothesis (H_1) was that urchin abundances would vary accordingly with variations in environmental habitat variables (for ex. habitat complexity and percent cover of substrate/benthic groups). Finally, we aimed to detect if any of these environmental habitat variable(s) best explain(s) the sea urchin assemblages at the microhabitat scale.

Material and Methods

1. Study Area

This study was conducted the summer-spring months (December 2011-April 2012), during the daytime in three island sites off the coast of Santa Catarina Island, Brazil, in the Southwestern Atlantic Ocean: Arvoredo Island (27°17’0’S, 48°22’23’W), Xavier Island (27°60’97’S, 48°38’64’W) and Campeche Island (27°70’00’S, 48°46’78’W), located at 11, 3.8 and 1.8 km from the coast, respectively (Fig. 1). The coast of Southeastern Brazil is characterized by narrow sandy and/or gravel beaches and granitic rocky shores, made up of intrusive igneous rocks. The predominant winds come from the northeast, and the less frequent but stronger winds come from the south. The study period ran when fieldwork is most feasible due to smaller swells, enabling easier and more frequent access to the proximate islands. The average sea surface temperatures range from 17°C in the winter to 27°C in the summer (Nimer 1989), while the annual mean sea surface temperature at Santa Catarina is 22.5^{o}C (average annual temperatures from 1999-2009) (NOAA, 2013).

This region comprises an area of ressurgence of cold and rich water primarily in the summer months, due to the morphology of the continental platform and the wind regimes (Carvalho *et al.* 1998). Tide regimes are semi-diurnal and present patterns of micro-tides with maximum amplitude of 1.4 meters (Dhiel & Horn-Filho 1996). The hydrodinamism of the region during the spring and summer months is characterized by temporal variation in wave height and direction with predominant eastern swells in the spring, later balancing out with the southern swells during summer (Lanari 2007). Data from two of the three sites were collected adjacent to protected areas: the Arvoredo Marine Reserve (REBIO) was created in March of 1990 (Brazil 2000); Campeche Island was designated by the governmental Institute of National Artistic and Historical Patrimony (IPHAN) as a cultural heritage site, with a defined no-take zone managed by IPHAN.

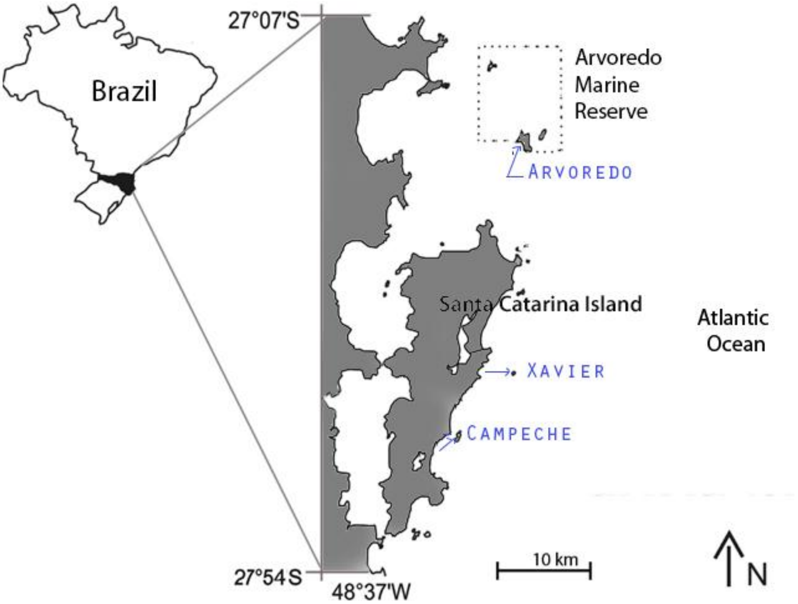

Fig. 1. Map of three study sites, adjacent to Santa Catarina Island, Southwestern Atlantic Ocean. Dotted lines define the limits of the Arvoredo Marine Reserve. Island sites studied are in blue.

2. Survey methodologies

SCUBA was used to conduct the urchin counts. The diver selected the areas to be studied based on the presence of urchin individuals (often having agregated distributions) and extended a 20x1m belt transect along the reef substrate to help guide the placement of quadrats. Along the transect, a 0.5x0.5m PVC quadrat was placed at alternating sides at every meter for a total of 12 quadrats in each transect. Depth of each transect was recorded. Transects were laid out between depths of 3−7m, according to the reef topology and presence of sea urchins. At each island, 10 transects (replicas) were performed, except for Campeche with 6 transects, due to its smaller depth range, and more compact reef area. In each quadrat, the urchins, if any, were identified *in situ* to the species level and their abundances were recorded. Also in each quadrat, we assessed the percent cover of substrate/benthic organism groups (environmental habitat variables) along with a semi-quantitative evaluation of habitat complexity.

For easy and quick classification in the field, a value from 1−5 was attributed to each group ranking its percent cover in each quadrat where 1) ≤5% 2) 6-25% 3) 26-50% 4) 51-75% 5) >75%. These groups were: Epilithic algal matrix (EAM), Crustose corralline algae (CA), and Foliose algae (groups were defined based on functional groups commonly used in other studies: see Ebeling *et al*. 1985, Benedetti-Cecchi *et al*. 1998, Konar & Estes 2003; Wright *et al*. 2005). Among the other groups were: Sand, Crevice, Bare Rock, Porifera, Ascidia, and Anemone.

Habitat complexity, another variable, was evaluated in a semi-quantitative manner adapted from Silveira (2010), where complexity was rated in each quadrat from one to three: (1) Low complexity: rocks of ≤0.5m in diameter placed along a sandy bottom, or a larger flat rock with no crevices; (2) Medium complexity: rocks of ≤1m in diameter with little or no sandy bottom, few crevices present; (3) High complexity: rocks >1m in diameter with crevices and vertical inclinations present.

3. Data Analysis

Mean urchin density in each transect was calculated by summing up the total abundance from 12 quadrat counts and then dividing by the total area (3 m^2). Urchin density data did not show a normal distribution. Therefore, differences in urchin abundances among sites were assessed using non-parametric tests. Kruskal–Wallis was used to compare data (percent cover of substrate and urchin species density as variables) between sites (factor). Multiple comparisons of mean rank for all groups were perfomed to identify differences. A Bray-Curtis dissimilarity matrix (Ward Method) was performed using the mean urchin abundances of each transect for all three sites in the Cluster analysis, and the corresponding MDS was plotted. An analysis of similarities was performed using the mean abundances from the 26 transects to test for differences between sites (ANOSIM, Monte Carlo test, 999 permutations). To select a combination of the assessed variables that best matched the urchin assemblages, a similarity matrix with the quadrat data of environmental variables based on Euclidean distances was linked to the biotic dissimilarity matrix using the BIOENV routine (Primer v6 Software). Environmental variables with mean rank values lower than 1 (<5% cover) were removed from the analysis (Sand, Porifera, Anemone, Ascidia, Bare Rock), thus leaving the remaining five and mean depth values in the analysis. Both resemblance matrices received the same treatment, transformation to the fourth root and normalized. A canonical correspondence analysis (CCA) was performed (using CANOCO for Windows) to explore the possible relationships between the spatial variation of urchin assemblages and the detection of environmental gradients (ter Braak & Prentice 1988). For the CCA, species abundance data were square root transformed. The relative contribution of each environmental variable was analysed with a Monte-Carlo test (Reduced model, 499 permutations).

Results

1. Urchin Assemblage

Six sea urchin species were detected during this study from which 5 were (Fig. 3) already registered for the state of Santa Catarina and one was a new record for this location (1 individual of *Tripneustes ventricosus* Lamarck, 1816, see Fig. 2).

Fig. 2. First report of *Tripneustes ventricosus* at 4 m depth at Deserta Island, located inside REBIO Reserva Biológica Marinha do Arvoredo, Santa Catarina. Date: May 5th, 2012 (Photo: Anderson Batista)

A total of 695 sea urchins comprising the five species were counted from all three sites, where Arvoredo presented a 4-fold magnitude difference in mean density (Fig. 3). Of the 695 urchins, 485 urchins were counted at Avoredo, 130 individuals at Xavier and 80 at Campeche. Density of *Echinometra lucunter* was highest at Arvoredo (12.1±2.1 ind.m^{-2}). *Arbacia lixula* presented the highest mean density at Xavier (3.04±0.5 ind.m^{-2}). Significant differences were observed between mean densities amongst sites for all urchin species, except for *Eucidaris tribuloides* (ANOVA Kruskal-Wallis H (2, N=26): $P<0.001$, $P_{Eu.t} = 0.9$). Relative frequencies of urchin species abundance per site are shown in Table 1.

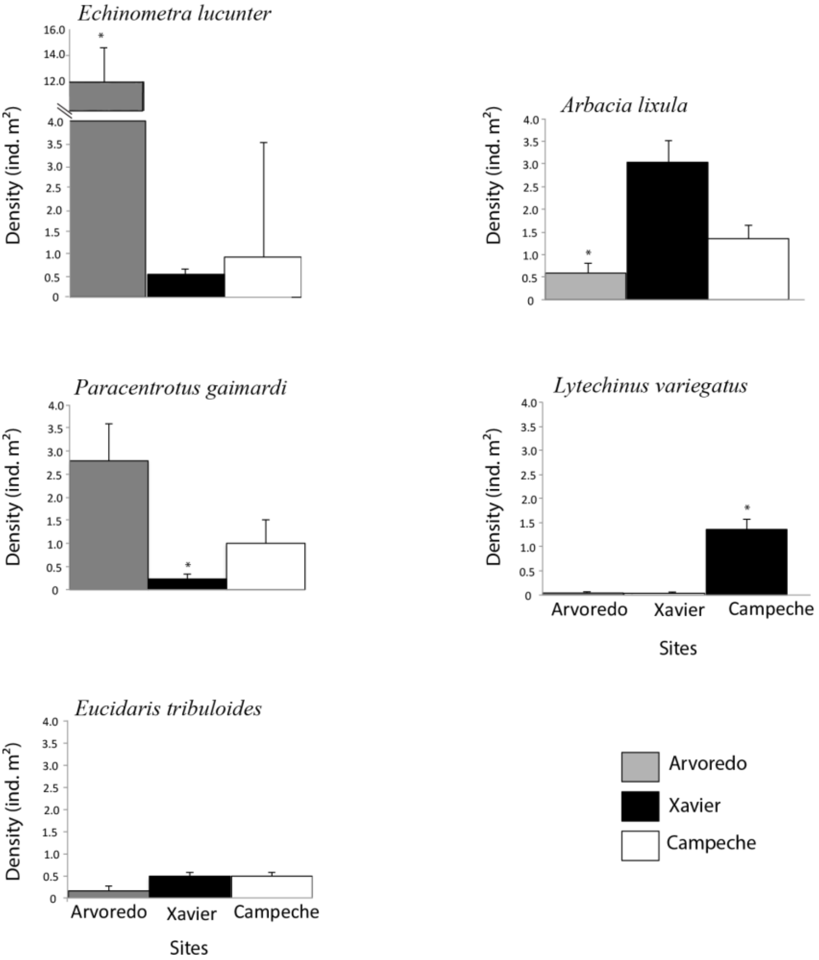

Fig. 3. Mean species density in three rocky reef island sites of Santa Catarina collected from transects (n=26 transects). Arvoredo (n=10); Xavier (n=10); Campeche (n=6), * = significant differences of species densities among sites (*p* <0.05).

Table 1. Relative frequency of abudance (%) of each species at Arvoredo, Xavier and Campeche sites (n=10, 10, 6 transects), respectively.

Species /Site	***E. lucunter***	***A. lixula***	***P. gaimardi***	***L. variegatus***	***E. tribuloides***
Arvoredo	77.0	3.9	18.0	0.2	1.0
Xavier	11.0	70.0	5.0	7.6	1.3
Campeche	20.0	29.0	21.0	29.0	1.2

The Bray Curtis Dissimilarity Cluster grouped the urchin assemblages using the *log*-transformed mean abundances for all 5 species according to site from all transects (Fig. 4). Arvoredo Island was the most different of the three islands, seperating with approximately 40% dissimilarity. The second knot formed a sub-group of transects from Xavier and Campeche with approximately 20% dissimilarity in their composition. Within this sub-group, Campeche samples formed a mini-group with just one sample from Arvoredo. Xavier's samples formed the remaining group with some samples from Campeche. As illustrated in Figure 4, the seperation of sea urchin assemblages between sites was small but significant (1-way ANOSIM, Global R=0.29, *P*=0.003). The MDS analysis grouped the urchin abundances with a low stress of 0.12 (Bray-Curtis Similarity).

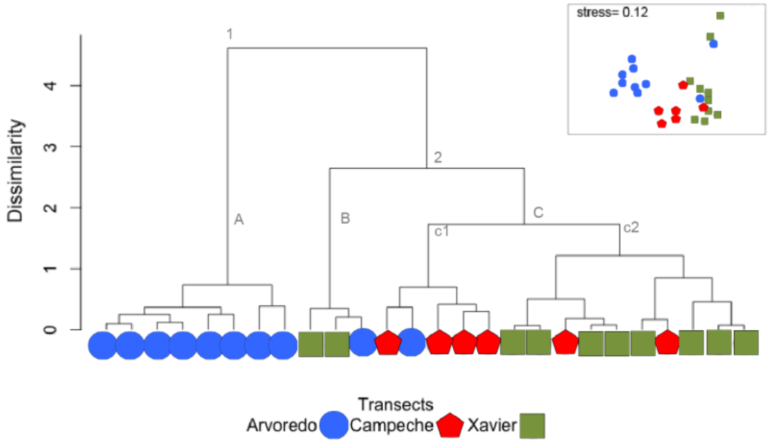

Fig. 4. Bray Curtis Dissimilarity (Ward Method) Cluster for mean *log*-transformed abundances of all 5 sea urchin species sampled from 26 transects in three study sites and corresponding MDS (stress= 0.12). Numbers and letters represent division of transects into groups in order: 1 making group A; and 2 followed by seperations at B, C and a final division at c1 and c2.

2. Environmental Habitat Variables

When analyzing environmental habitat variables among sites, significant differences in the mean ranks of percent cover were observed (values from 1−5) for all algal groups: Crustose coralline algae, EAM (Epilithic Algal Matrix), and Foliose algae (Kruskal–Wallis ANOVA by ranks H (2, N=312; $P<0.05$) (Fig. 5).

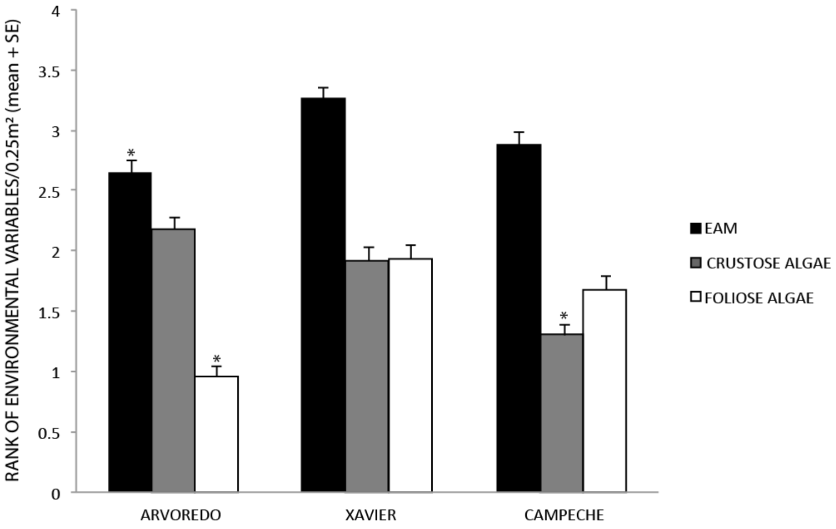

Fig. 5. Mean ranks of benthic variables assessed per quadrat ($0.25m^2$) (+ SE) at each study site. Values represent the mean rank of percent cover where (1) ≤5%, (2) 6-25%, (3) 26-50%, (4) 51-75%, (5) >75%. *, Indicate significant differences formed, EAM= epillithic algal matrix.

As for the algal composition in the three islands, significant differences were encountered at Arvoredo Island with the lowest EAM cover and Foliose cover. Campeche Island presented the lowest cover of crustose algae (CCA). Xavier Island comprised of intermediate values of Foliose and Crustose cover but presented higher EAM cover. As for the remaining variables, Crevice cover was found highest at Xavier and lowest at Arvoredo. The semi-quantitive variable, Habitat Complexity, was found similar across all sites (Table 2). Campeche Island presented a shallower mean depth due to a more compact reef area. Ascidian cover was highest and significant at Campeche, while Porifera and Sand were higher at Xavier and Campeche than Arvoredo. Anemone cover was slightly higher at Arvoredo than the other sites. Percent cover of Bare Rock and number of invertebrates (gastropods, sea stars) were excluded from the analysis due to their low occurences.

Table 2. Mean depth (m) and mean ranks of the variables of assessed in three study sites: Arvoredo, Xavier, and Campeche (mean ± SE). Letters a, b, and c indicate significant differences between multiple comparisons of mean rank for all groups following Kruskal-Wallis ANOVA by ranks values H (2, N=312); *$P<0.01$*.

Sites/ Variables	**Arvoredo (n=120)**	**Xavier (n=120)**	**Campeche (n=72)**
Mean Depth (m)	5.4	6	3.6
H.complexity	2.02 (±0.1)	2.17 (±0.1)	2.06 (±0.1)
Sand	0.25 (±0.7)	0.63 (±0.1)	0.75 (±0.2)
Crevice	**0.65 (±0.1)** ^{a}	**1.44 (±0.1)** ^{b}	**1.06 (±0.1)** ^{c}
Porifera	0.28 (±0.05)	0.39 (±0.05)	0.36 (±0.1)
Anemone	0.25 (±0.04)	0.20 (±0.04)	0.08 (±0.03)
Ascidia	**0.09 (±0.03)**^{a}	**0.01 (±0.01)**^{a}	**0.27 (±0.1)**^{b}

Correlation of the matrices of environmental and biological variables (BIOENV) indicated that the variables “best explaining” the patterns of urchin abundances, based on their biological information were: Habitat Complexity (p_w= 0.22), followed by a combination of Habitat Complexity and Depth (p_w= 0.19) (Table 3)

Table 3. BIOENV results showing the environmental variable combinations that best match the biotic similarity matrices using the weighted Spearman rank correlation (p_w) and D1 Euclidean distance.

Number of Variables considered	**Correlation p_w**	**Selections**
1	0.22	Habitat Complexity
2	0.19	Habitat Complexity +Depth

Axes 1 and 2 of the CCA performed on sea urchin abundances cumutatively accounted for 76.9% of total variance in abundance data and were significant (Axis 1; 50.7% and Axis 2; 21.5%, P=0.004) (Fig. 6). The Monte-Carlo permutation procedure on the CCA showed that both ordination axes were determined by habitat and benthic structure, the first positively correlated with Foliose algae and negatively with Anemone and crustose algae cover. The second axis was positively associated with Depth and Sand, and to a lesser extent (and negatively) with Ascidia cover. *A. lixula* was both associated to Xavier's and Campeche's samples with Foliose cover, while *L. variegatus* was site-attached at Campeche Island and associated with Ascidia. *E. lucunter* was also site-attached at Arvoredo Island and associated with Anemone cover. *P. gaimardi* was not associated to any assessed environmental habitat variable. *Eucidaris tribuloides*, located in upper right quadrant, presented a low abundance in all study sites and associated with Xavier's samples with with Depth and Sand.

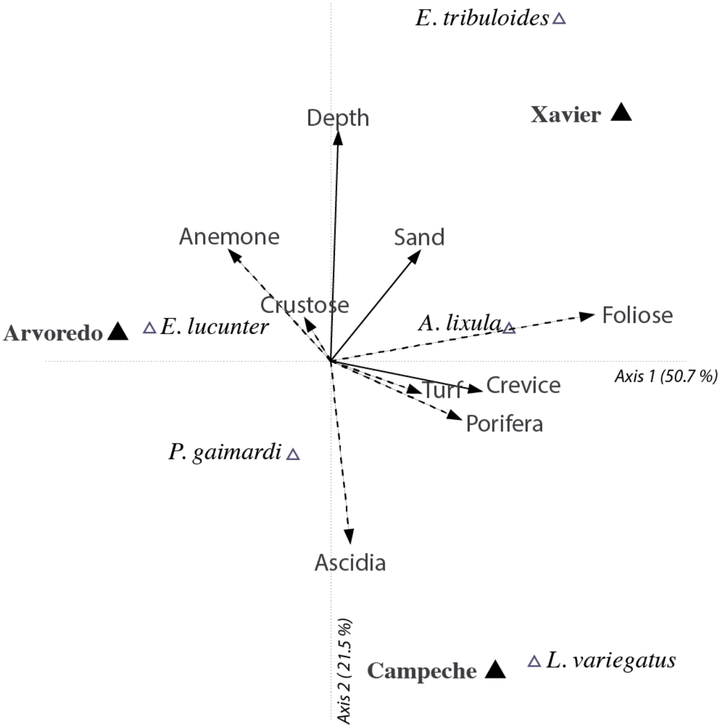

Fig. 6. Canonical correspondence analysis (CCA) bi-plot ordination diagram for species and nine environmental habitat variables; solid lines abiotic and dashed lines biotic variables. Species are represented in italics and open triangles, and sites in filled black triangles.

Discussion

Urchin assemblage

In general, the urchin assemblage varied significantly among sites as did species density. *Echinometra lucunter* was the most abundant urchin in our study, as it is the most abundant sea urchin in Brazil (Xavier 2010). When comparing their density to other studies in Brazilian rocky reefs, we find similarities in density and variability. Higher densities than ours have been recorded in a rocky reef of Rio de Janeiro (Porcos Island), ranging from 3.33 ± 1.56 ind. m^{-2} to 65.28 ± 8.95 ind.m^{-2} (Calderon *et al.* 2007) Another study conducted in Santa Catarina presented densities of 4 ind.m^{-2} at the 3 m strata (Dalben & Floeter 2012). McClanahan and Muthiga (2001) assessed distribution patterns of *Echinometra lucunter* and *Diadema antillarum* and observed variations of urchin densities over short distances within and between sites, and spatial variability of *Echinometra* from less than 50% within reef sites to more than 150% between reefs. The same authors also state that species of the genus *Echinometra* usually possess strong homing behavior and are often distributed in an aggregated pattern. Moreover, Arvoredo was the only site that presented a large porportion of *Echinometra lucunter* juvenile individuals (Fig. 3, pg. 22). We also suggest that the higher urchin abundances at Arvoredo could be result of other abiotic factors playing a role, for example, anthropogenic effects and degree of wave exposure. Anthropogenic disturbance presents differences among islands, using the distance from the nearest coast and protection level of study site where (1) the Arvoredo site is situated approximately 200 m from the reserve and is also situated farthest from the coast (11 km from Santa Catarina Island); (2) Xavier Island is at an intermediate distance (3.7 km) with no protection level; and lastly (3) Campeche Island is located closest to the coast (1.77 km) but comprises a small no-take area. Another possible factor that differs among sites is wave exposure, potentially influencing the sea urchin assemblages at these three sites. According to Segatto's (2011) wave exposure indices, a indice that is calculated using the direction, frequency and intensity of wind (adapted from Thomas 1985), the western side of Arvoredo, where our study was conducted, presents a lower wave index value, followed by Campeche with an intermediate index, and Xavier the highest. At Arvoredo, these calmer waters can be potentially maintaining high *Echinometra lucunter* populations, and faciliting juvenile survivorship. In areas exposed to strong wave action, sea urchins may be dislodged from the substratum by sporadic severe waves (Denny & Gaylord 1996; Kawamata *et al.* 2011), possibly resulting in lower urchin abundances of *Echinometra lucunter* in higher wave action sites like Campeche and Xavier.

Many studies have described distribution patterns of the five urchin species observed in this study already registered in the south-southeastern region of Brazil (Giordano 1986; Tomassi 1964; Castro et al. 1995; Tavares 2004), although only generalizations are made regarding urchin abundance or frequency. Few studies provide comparative quantitative information for such species in consolidated hard substrate along the Brazilian coast (Tavares 2004*)*. In the Meditteranean, *Arbacia lixula* is one of the most abundant echinoids in shallow rocky habitats (Wangensteen *et al.* 2012), inhabits high wave action sites, and is often found in vacant holes that were previously inhabited by *E. lucunter* (Giordano 1986). The ecology of *A. lixula* is well described in other seas, but a phylogeographic study found the Brazilian populations to be different from the Eastern Atlantic and Meditteranean populations (Wangensteen *et al.* 2012). Although this study only studied the COI gene from 35 individuals, highlighting the need for further studies on this species ecology. One study in Paraná, southeastern Brazil, has detected similar densities ranging from 0 to 7 ind.m^{-2} in a rocky reef island (Tavares 2004). In our study, *P. gaimardi* was often found nearby *A.lixula* at both Campeche and Xavier. Studies have shown that its sister species, *P. lividus* (Lamarck, 1816), often overlap habitats with *A. lixula* and are traditionally thought to have the ability to trigger the development of subtidal barren zones of reduced benthic productivity and diversity (Verlaque 1987; Bulleri *et al.* 2002; Privitera *et al.* 2008). *Eucidaris tribuloides*, known to be solitary and widely distributed (Kier & Grant 1965), was detected at very low numbers in all sites. *L. variegatus* was also observed at low densities, similar to the findings from Junqueira *et al.* (1997), which varied between 0.57±0.10 and 0.06± 0.05 ind.m^{-2} in a sea grass flat in Rio de Janeiro, Brazil. Finally, during our sampling season inside the REBIO reserve near Arvoredo, we recorded one *Tripneustes ventricosus* specimen on a sandy bottom at 4 m depth. This is the first record of this species for South Brazil. The specimen was identified using photo-identification. This species is a tropical species, with a distribution ranging from Bermuda (Caribbean) and Southern Florida (USA) down to Rio de Janeiro State in Brazil (Tommasi 1972; Lawrence 2007). *T. ventricosus* has also been observed in Fernando de Noronha, Atol das Rocas, Trindade (Brazil), Ascencion Island (UK) and in the Western Atlantic African coast from Gulf of Guinea to Walfish Bay in Namibia (Lawrence 2007). The presence of this species in Santa Catarina exemplifies the lack of knowledge of benthic communities.

Environmental Habitat Relationships

In general, the habitat composition of three sites was quite similar. At Campeche, low urchin abundance could reflect a lack of grazing of foliose algae, hence lower crustose algae cover, or vice versa. Yet, despite the close linkages that urchins have with substrata, deriving from their life habits such as feeding strategies, locomotory behavior, and substrate relations (Dumas *et al.* 2007), we did not detect any strong correlations with any of the habitat variables. High correlations with habitat variables are often difficult to find when analzying more than one species abundance at a time. This idea is supported in other studies, observing a high variability as the result of complex interactions between habitat variables for example, depth, wave exposure, water/sediment composition and the presence/absence of reef-building or covering species (Nishira *et al.* 1991; Chiappone *et al.* 2002; Dumas *et al.* 2007).

As expected, Habitat Complexity slightly influenced the urchin assemblages at the microhabitat scale (quadrat). Another echinoderm-habitat study has found habitat complexity (described here by the numbers of boulders of different sizes) and, to a lesser extent, habitat heterogeneity descriptors (rocky substrata with greater proportions of patches of sand, coral and algal cover) to exert a significant effect on echinoderm assemblage (Entrambasaguas *et al.* 2008). Urchin abundances are correlated with habitats of high complexity that are thought to provide refuge from predators (McClanahan & Muthiga 2001). Increasing the interstitial space in a complex habitat substantially reduces foraging efficiency of predators (Bartholomew *et al.* 2000; Entrambasaguas *et al.* 2008). Also, complex habitats provide refuge from strong waves and currents, where urchins take shelter from excessive water movement (Russo 1977; Grunbaum *et al.* 1978). Moreover, complex habitats have greater amounts of anfractuosities (e.g. pits, holes, cracks or projections), which provide more available living space or surface area, and supply more abundant and/or diversified resources as a result of the increase in the number of potential habitats (Entrambasaguas *et al.* 2008). Depth also slightly influenced the urchin assemblages, probably because urchins prefer a certain depth between the sampled depth range of 1-10 m along the rocky reef. Finally, like our study, it should be noted that observed correlations detected can not establish cause and effect, however give us some insight into which habitat variables are the most influencial (Cruz-Motta *et al.* 2010).

As shown in the CCA analysis, all species, except for *P. gaimardi*, specifically associated with a certain site and/or variable(s). Also, each species has different requirements, explaining their associations with certain habitat variables. Since only weak correlations were detected when observing the entire urchin assemblage at this microhabitat scale, we suggest that the effect of habitat structure is species-specific, supporting the idea that each species possibly has different habitat and feeding preferences. Most sea urchins in this study are herbivores, except for *Arbacia lixula* and *Eucidaris tribuloides* (carnivores). Other studies report omnivorous or carnivorous behavior of *A. lixula* outside the Mediterranean (Marques 1984; Oliveira 1991; Tavares & Borzone 2005), which could be the case for Santa Catarina. *A. lixula* and *E. tribuloides* could be feeding on Porifera (sponges), explaining their negative association at Xavier Island. In the Mediterranean, where sea urchin diet preferences are well-studied, Privitera et al. (2008) demonstrates that species *A.lixula* and *P. lividus* (sister species of *P. gaimardi*) occupy different trophic niches in resource-limited (barren) areas, again in the sense that *A. lixula* feeds mainly on encrusting corallines while *P. lividus* feeds on non-encrusting macrophytes. When associating habitat variables to echinoderm assemblages, a study by Entrambasaguas *et al.* (2008) suggests the same species-specific trend, correlating with variables indicating heterogeneous (with an important proportion of algal cover and sand) and/or complex habitats (determined by small and medium-sized boulders). In our study, *Eucidaris tribuloides* was more associated with sand and lower depths at Xavier. *Eucidaris tribuloides* in the Florida Keys has been observed on seagrass and sand, and in shallow offshore reefs and deeper fore reef environments to depths up to 55 m (McPherson 1968). Also, the close association with Anemones and *E. lucunter* could be due to a specific habitat-association to Arvoredo (see Fig. 6). Moreover, species-specific habitat associations have also been observed for other echinoderms, such as sea cucumbers (Guzman & Guevara 2002; Entrambasaguas *et al.* 2008).

It should be noted that all the assessed variables are of deterministic nature, derived from a niche assembly perspective, leaving behind the unexplainable derived from a neutral point of view (eg. stochastic effects, ecological drift). For example, a random effect like recruitment, can mediate chemical signals and maintain populations (Uthicke et al. 2009), possibly explaining the barren-forming *E. lucunter* population at Arvoredo. For planktotrophic developers, like *E. lucunter*, Levitan (1991) showed that reduced individual gamete output is outweighed by an enhanced population outcome and improved fertilization rates due to close proximity of individuals (Uthicke et al. 2009) Thus, the close proximity of *E. lucunter* individuals at Arvoredo could be facilitating better fertilization rates. At these urchin barrens, greater rates of urchin settlement or recruitment, on urchin barrens compared with kelp beds, have been observed in several areas of the world (Tegner & Dayton 1981; Leinaas & Christie 1996). Real ecological communities are undoubtedly governed by both niche-assembly and dispersal-assembly rules, along with ecological drift but the important question is: What is their relative quantitative importance? (Hubbell 2001) This grand question remains untested in community ecology of marine organisms, and further studies on the explanatory variables (both niche and neutral-derived) of sea urchin assemblages could benefit from such an idea.

We must keep in mind that this study was conducted during one summer season and during the daytime only, potentially masking other important drivers, illustrating the need for a continuous monitoring program. It is also important to consider the spatial and temporal scales at which these populations naturally fluctuate. Actual causes between environmental drivers and rocky shore assemblages are further complicated due these inherent complexities (Cruz-Motta *et al.* 2010). As well, our study was limited to the microhabitat scale, evaluating the urchin-habitat relationships using quadrats and transects. This is one of the first studies addressing relationships between urchin assemblages and habitat in Brazilian warm temperate rocky reefs, and is the first study to attempt to replicate this on a larger spatial scale (at three islands). Futher urchin studies in Southwestern Atlantic rocky reefs are required. This is especially important since this region is under direct influence by a high semi-permanent South Atlantic Anti-cyclonic high pressure centre (Nobre *et al.* 1986; Nimer 1989; Garreaud *et al.* 2009), putting these reef systems at a high risk of irreversible phase-shifts.

Summary

The urchin assemblages detected in this study differed among sites. When considering each urchin species individually, density also varied significantly. *E. lucunter* was the most abundant urchin in our study, attaining a mean density of 12 ind.m^{-2} at Arvoredo Island. Considering sea urchin assemblages, the environmental habitat variables only explained a small percentage of the variance−those being habitat complexity and depth. This weak community correlation between the environmental variables and urchin abundances at the microhabitat scale supports the idea that urchin habitat relationships are species-specific. Other important non-deterministic drivers not assessed in this study can also be playing an important role in shaping the sea urchin assemblages.

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CHAPTER 2
SEA URCHIN ASSEMBLAGES AND HABITAT RELATIONSHIPS IN A COASTAL CORAL REEF OF NORTHEASTERN BRAZIL

FORMATTED FOR CORAL REEFS

Sea urchin assemblages and habitat relationships in a coastal coral reef of Northeastern Brazil

ABSTRACT

Sea urchins are important herbivores in reef systems, keeping macroalgae under control, thus preventing phase-shifts. A close linkage is observed between urchin distribution and the substrate due to their life habits like locomotion and feeding behaviour. The main objective of this study was to assess sea urchin assemblages in a coral reef at Recife de Fora (Bahia) and investigate the relationships with habitat variables at the microhabitat scale. We sampled for urchin counts and assessed percent cover of substrate groups and coral richness using 0.5mx0.5m quadrats along transects at five study sites. The main species was *Echinometra luncunter*, reaching densities up to 30 ± 1.2 ind.m^{-2} (mean ±SE). The total urchin density varied between sites ($F_{4,10}$ = 3.54, $P < 0.05$). Following the same trend, the assessed habitat variables also grouped according to site. Crevice cover was identified as the variable that best explained the urchin assemblage (p_w= 0.217). A low-moderate correlation was detected between crevice cover and *E.lucunter* density (r=0.37, P<0.05). Finally, no correlation was observed between coral richness, cover, and urchin density. Our results suggest a unique situation at Recife de Fora, where *E. lucunter* is the main urchin herbivore, and only relates to crevice cover at the microhabitat scale. We suggest a low herbivore functional redundancy at this coastal reef, which could compromise reef resilience.

KEY WORDS: coral reef, *E. lucunter* density, habitat complexity, percent cover of substrate

INTRODUCTION

Despite the diversity of responses of coral reef degradation, two widely recognized indicators of coral reef decline are macroalgal cover and sea urchin density (Hughes 1994; McClanahan and Mutere 1994; Johansson et al. 2010). Independently, these 2 taxa can increase in abundance and biomass on degrading reefs and may create undesirable alternative states (Done 1992; McClanahan and Mutere 1994; McManus and Polsenberg 2004; Bellwood et al. 2006; Mumby et al. 2006; Norström et al. 2009; Johansson et al. 2010), such as macroalgal blooms or urchin barrens. As well, intense sea urchin grazing or spine abrasion can hinder coral spat settlement, thus reducing coral abundance (McClanahan and Mutere 1994). Therefore, sea urchins play a crucial role in the phase shift dynamics of coral reefs (Lessios et al. 2001; Norström et al. 2009). Macroalgal irreversible states, one of the common outcomes in today’s reefs, have proven to be highly stable. Also, the chances of preventing and escaping this deadlock of macroalgal proliferation differ widely between reefs and are known to depend on resilience factors like the composition and diversity of key functional like herbivores (Dietzel 2011; Graham et al. 2011). Sea urchins have a love-hate relationship with reef resilience as they may compensate from herbivore losses (overfishing) but at the same time, if released completely and achieve high densities, they can also bioerode coral colonies and inflict serious damages to reefs (Eakin 1996; Dietzel 2011). Functional redundancy of key herbivores like urchins ensures proper reef resilience, which was not the case in 1983-1984 in the Carribean, when a mortality of *Diadema antillarum* completely wiped out the population (Lessios et al. 1984; Dietzel 2011). This region of the Carribean had been previously overfished, and the mass mortality of this urchin combined with the absence of herbivorous fish resulted in a complete loss of control by herbivores in the reef system, allowing for macroalgae to proliferate (Lessios et al. 1984). Yet, despite the magnitude of urchin impacts, few studies have examined the relative contributions of habitat variables to the distribution of coral reef urchins (Dumas et al. 2007).

In coral reefs, studies on species-habitat associations began in the mid 70s (e.g. works of Salvat et al. 1972; Luckhurst and Luckhurst 1978; Sale 1978, 1980), yet understanding the factors that influence species composition and community structure remains a challenge (Hughes and Connell 1999; Chiappone et al. 2002; Schiel et al. 2004; Dumas et al. 2007). In comparison with fishes, available data on the factors structuring reef invertebrates are scarce (Dumas et al. 2007). Perhaps among the exisiting literature a primary focus has been a need to understand the regulation of local abundance of sea urchins and the factors that lead to large fluctuations in populations (Dayton 1985, Schiel and Foster 1986; Andrew 1993). Sea urchin species exhibit a close linkage with substrata, deriving from their life habits i.e. feeding strategies and locomotory behaviour (Lawrence 2001; Dumas et al. 2007). Moreover, structural species such as corals and algae constitute a critical dimension of habitats (Done et al. 1996) that should be encompassed in studies addressing reef urchin distribution patterns.

The present study investigates the urchin assemblage and its relation to habitat in a tropical reef of northeastern Brazil, in the Southwestern Atlantic, where the role of these herbivores remains unknown in terms of reef resilience. More specifically, we surveyed the urchin abundance and species composition in five sites of the reef from Parque Municipal Marinho do Recife de Fora, NE Brazil, to 1) investigate if any relationship exists between the habitat variables and urchin assemblages and if any, what habitat variable(s) best explain(s) the urchin assemblage at this microhabitat scale; 2) detect if any correlation exists between coral richness and abundance and urchin density at Recife de Fora.

METHODS

Study Area

This study was conducted at Parque Municipal Marinho do Recife de Fora (herein referred to as Recife de Fora), a 17.5 km^2 patch reef area that lies 5 km offshore from Porto Seguro, a major tourist destination in Bahia, Brazil (Lat 16°23’S−16°26’S, Long 039°00’W−038°58’W) (Figure 7). Recife de Fora comprises 14 out of the 16 registered scleractinian corals of Brazilian reefs (Castro and Pires 2001; Arantes 2012), including at least three coral species endemic to the South Atlantic. The reef is biogenic, composed of rounded formations that do not surpass 20 m depths (Laborel 1969; Arantes 2012). As a marine protected area since 1997, Recife de Fora provides a visitation program permitting up to 400 visitors per day mostly during spring tides (Seoane *et al.* 2012). Five sites on the reef were sampled, each from different areas encompassing the North, East, South, and West side the reef in order to obtain a more general sample of the reef characteristics and sea urchin abundances. These study sites were: Forereef-N, Forereef-S, Patchreef-W, Forereef-E and Backreef-N. The study was conducted during the spring of November 2012 when NE winds predominate (Arantes 2012; Silva et al. 2008). This region also presents semi-diurnal mesomareal tide regimes and amplitudes up to 2.5 m. High tide quadrants are 1.7 m and low tides are 0.3 m (DHN 2012).

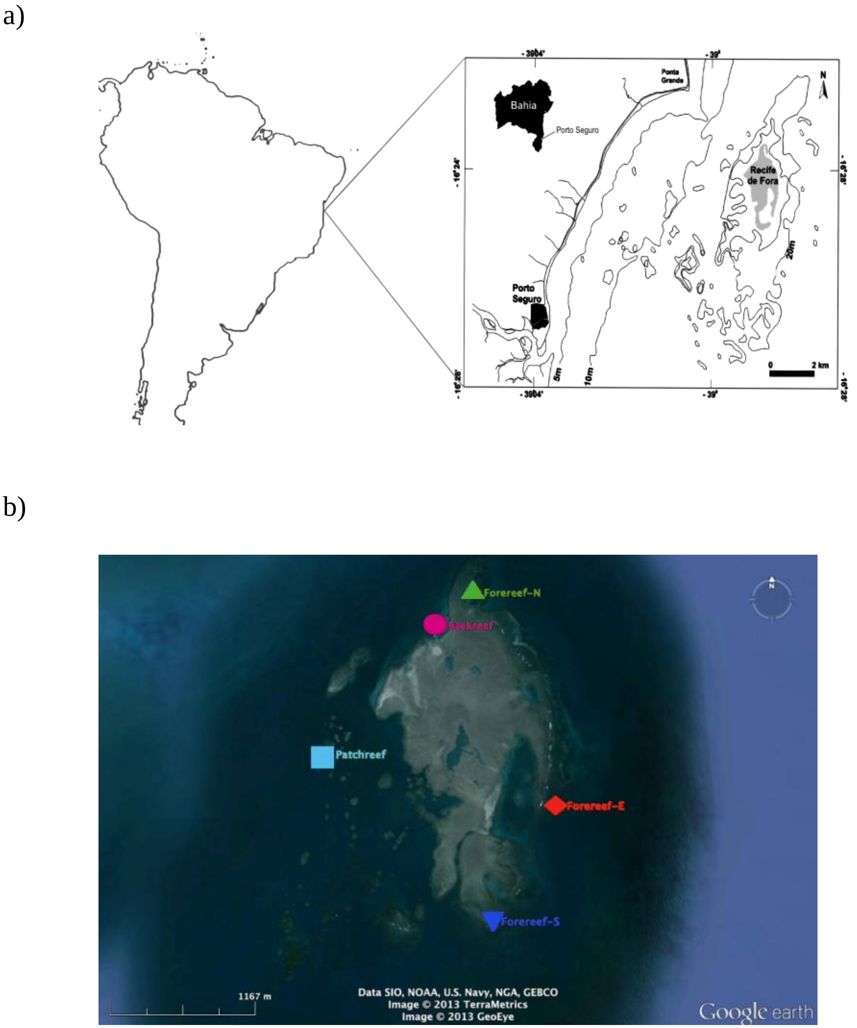

Fig. 7 Study Area a) coordinates and location and b) five study sites at Recife de Fora, Northeastern Brazil

Sampling

The data was collected with the aid of SCUBA. To assess the density of sea urchins and percent cover of habitat variables in the five study sites, 3 transects were conducted in each site, which were all placed in areas with urchin present (n= 15 transects). The depths sampled in this study varied between 1.5 m and 5 m, as the reef is mainly shallow. Depths did not vary more than 1 to 2 m within sites. To obtain data on urchin species abundance, a quadrat was placed along the transect, alternating sides at each meter, to sample for urchins and percent cover of habitat variables. A total of 12 quadrats were sampled in each transect. In each quadrat, the diver registered the sea urchin species if any, and number of individuals, exact quadrat depth, a semi-quantitative evaluation of habitat complexity, and the percent cover of substrate groups. For easy and quick sampling in the field, a value from 1 to 5 was attributed to each substrate group ranking its percent cover in each quadrat where 1; ≤5%, 2; 6-25%, 3; 26-50%, 4; 51-75%, 5; >75%. The 11 sampled substrate groups were: Sand, Epilithic algal matrix (EAM), CCA algae (crustose coralline algae), Foliose algae, Crevice, Milleporids, Gorgonians, Scleractinians, other sessile invertebrates (sponges, anemones, ascidians, bryozoans, *Palythoa* sp), the non-sessile group (feather stars, Christmas tree worms, fan worms, polychaetes, gastropods) which was counted as number of individuals, and finally Habitat Complexity. When possible, percent cover of substrate was identified to the species level. Coral species data (Scleractinians only) was used to calculate richness and abundance. Habitat complexity was defined in a semi-quantitative way, which facilitates fieldwork and generates similar results to the traditional quantitative techniques (rugosity “chain-link” method) (Luckhurst and Luckhurst 1978; Ferreira et al. 2001; Dinslaken 2012). We performed a visual assessment of reef topography and reef benthos to categorize and evaluate reef complexity (Polunin and Roberts 1993; Spalding and Jarvis 2002; Graham et al. 2003; Silveira 2010). Habitat complexity was determined according to the abundance of coral species (rank percent cover) and topographic complexity (holes and inclinations) in each quadrat, and was given a rank from 1− 5 (see table 4).

Table 4 Criteria for Ranking Habitat Complexity in each quadrat (0.5mx0.5m) adapted from Polunin and Roberts 1993; Spalding and Jarvis 2002; Graham et al. 2003.

Rank	Coral Cover	Topographic complexity
1	(0-5%)	flat surface (0 holes)
2	(5-25%)	1-2 holes, flat surface
3	(25-50%)	1-2 holes and few surface inclinations
4	(50-75%)	3-5 and different surface inclinations
5	(>75%),	>5 holes and many surface inclinations

Data Analysis

To determine differences between urchin densities and habitat variables among sites, one-way ANOVAs were performed for *E. lucunter*, and *D. antillarum* followed by Tukey HSD tests. The fixed factors were the species densities, while the random-factors were sites. To avoid overestimating density when converting quadrat density to number of individuals per m^2, mean quadrat density was calculated as the total number of individuals from 12 quadrats divided by the total area sampled (3 m^2). Before ANOVA, homogeneity of variances was tested using Levene's test, and where variances were found to be heterogenous, data was square root transformed. In the cases in which transformations did not remove heterogeneity, we performed the analysis anyway, since analysis of variance is quite robust to departures from their assumptions, especially when the design is balanced (Underwood 1997; Entrambasaguas *et al.* 2008). Cluster analysis (Euclidean Distance) was used to examine the relationships between the compositions of habitat variables (transects) using square root transformed data, in order to meet assumptions of normality (PRIMER 6 software). Correlation analysis was performed using square root transformed data after testing for normality.

To explore the correlation between the dissimilarity matrices of biotic data (urchin abundances in each transect) and the corresponding environmental data from the same transects, a multivariate analysis (BIOENV) was performed to detect a combination, if any, of the best explaining environmental variable(s) to generate a rank correlation coefficient p. The weighted Spearman correlation, p_{w}, was preferred since it places more emphasis on the small distances. Data was square root transformed and normalized for the environmental matrix. The biotic similarity matrix was also square root-transformed. Redundant variables were identified using multiple correlation analysis (i.e., draftsman plots) after square-root transformations of skewed variables, and were thus excluded from the analysis (Bare Rock, Asicidia, Anemona, Porifera). Furthermore, three environmental variables (crevice cover, scleractinian richness and abundance) were further explored using simple regressions after verifying normality and homocedasticity of the data (Kolmogorov-Smimov).

RESULTS

Urchin Densities

We counted a total of 1,349 urchins in the five study sites. Four species were observed; primarily all were *Echinometra lucunter,* followed by a few *Diadema antillarum* and only 1 of each individual of *Eucidaris tribuloides* and *Lytechinus variegatus*. Five species are known to occur at Recife de Fora (Cerqueira et al. 2000) yet only four were recorded here. *Tripneustes ventricosus*, although registered in Bahia's Echinoderm Inventory (Magalhães et al. 2005), was not observed. We also observed a low number of *D. antillarum* individuals, those often being found hiding under reef formations (personal observation). *E. lucunter* density was highest at Forereef-S, followed by Forereef-N and Backreef-N. Densities of *E. lucunter* collected in the quadrat counts varied with significantly between sites ($F_{4,10}$ = 3.54, $P < 0.05$). Urchin species densities at each site and homogenous groups formed after Post hoc Tukey tests are shown below in Table 5.

Table 5 Mean densities of sea urchins from 15 transects in five sites (±SE). Letters indicate the homogenous groups formed by Tukey's HSD tests.

Sites **Assessed variables**	**Forereef-N**	**Forereef-S**	**Patchreef-W**	**Forereef-E**	**Backreef-N**
Echinometra lucunter (ind.m^{-2})	10.6(±2.4) a,b	**30(±1.2)** **b**	4.4(±0.4) a	4.8(±0.2) a	13.9(±1.4) a,b
Diadema antillarum (ind.m^{-2})	0.3(±0.3) a	—	0.1(±0.2) a	—	—

Habitat Variables

Regarding substrate variables, sites were classified in two major groups at a separation distance of approximately 8 (80% dissimilarity) (Figure 8). The A cluster comprised the East-West group, where all transects from Patchreef-W and Forereef-E sites as well as two transects from Forereef-N grouped with less than 30% dissimilarity. The B cluster comprised the North-South group, where all transects from Forereef-S and two from Backreef-N (Northern site) and one transect from Forereef-N grouped at a distance less than 4 (40% dissimilarity). The environmental composition of Forereef-N and Backreef-N transects were not unique to either of the two groups.

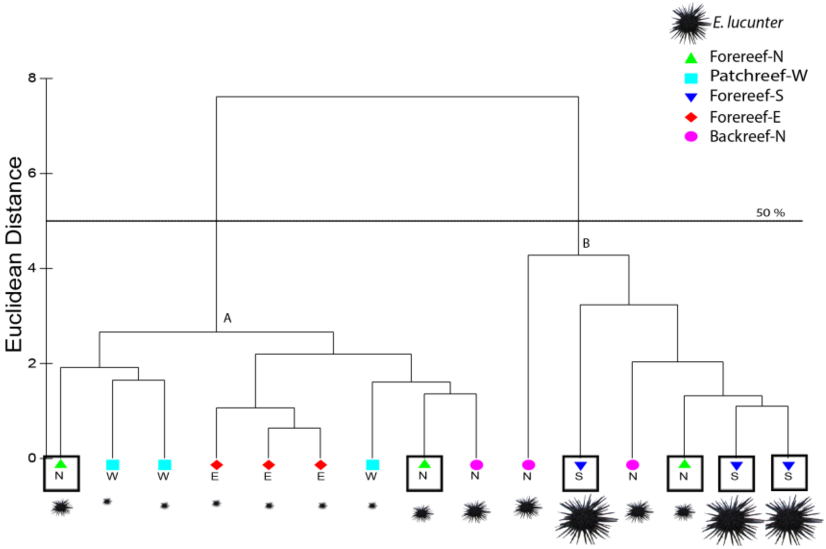

Fig. 8 Cluster analysis of from 11 environmental habitat variables (Euclidean Distance) and the 50% dissimilarity cut-off line for the 15 transects from all five sites at Recife de Fora (BA). Letters A and B identify the two knots and N, S, E and W indicate the geographic location on reef. Open black squares represent sites of high wave exposure according to Arantes (2012). Urchin size is porportional to mean *E.lucunter* density at each site.

For all sites, substrate cover was mostly composed of EAM (mean rank of 3, equivalent to the 26-50 % cover range) (Fig. 9), followed by Crevices (Table 6) and Scleractinians (mean ranks of approximately 2, equivalent to 6-25% cover) (Figure 9). The average depth sampled was 2.9±1.1 m (mean ±SE). The percent cover of habitat variables compared among sites (measured as mean ranks) presented little differences, those being significant were Foliose algae from the Algal groups, and Milleporids (mainly *Millepora alcicornis* and few *Millepora nitida)* and Gorgonian cover from the Coral groups (Fig. 9). Foliose algae was significantly lower at Forereef-S (where urchin density was highest) and higher at Backreef ($F_{4,10}$ =3.7, P <0.05). As for corals, Backreef-N presented a large significant cover of Gorgonians. Gorgonian cover was found lowest at Forereef-S and

Patchreef-W, and absent at Forereef-E ($F_{4,10} = 22.7$, $P < 0.001$). Milleporid cover was similar across all sites except for the low or absent cover at Forereef-S and Forereef-E ($F_{4,10} = 6.3$, $P < 0.01$). Among the abiotic variables that did not vary significantly between sites are: Crevice, Habitat Complexity, and Depth (Table 6). The remaining variables (non-sessile group and other sessile organisms like sponges, anemones, ascidians, bryozoans, and *Palythoa caribaeorum*−only observed at Patchreef-W) were rarely observed and therefore removed from this analysis.

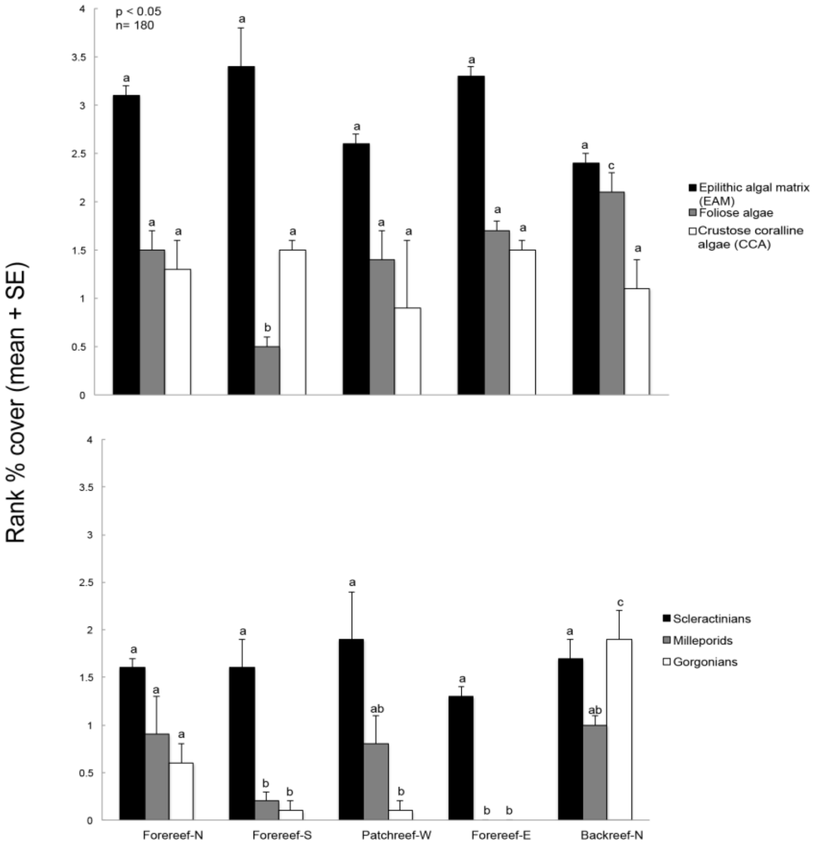

Fig. 9 Rank % cover (mean+ SE) of biotic variables for (a) coral group habitat variables and (b) algal group habitat variables in all five sites at Recife de Fora (BA). Letters represent homogenous groups identified by Tukey's HSD tests, significant with $P < 0.05$. * Indicate a significant between sites with $P < 0.05$

Table 6 Mean depth and rank values (±SE) of abiotic habitat variables per quadrat ($0.25m^2$) in all five sites at Recife de Fora.

Sites **Habitat variables**	**Forereef-N**	**Forereef-S**	**Patchreef-W**	**Forereef-E**	**Backreef-N**
Depth (m)	2.3(±0.2)	3.2(±0.2)	1.9(±0.1)	4.9(±0.1)	2.3(±0.2)
Habitat complexity	2.6(±0.1)	2.7(±0.4)	2.4(±0.3)	2.1(±0.2)	2.4(±0.3)
Crevice	1.8(±0.1)	2.1(±0.1)	1.3(±0.3)	1.9(±0.1)	2.0(±0.2)

A multivariate analysis (BIOENV) using the combination of seven environmental variables plotted against the biotic similarity matrix, identified crevice cover as the best explaining variable despite its low Spearman rank correlation (p_w= 0.217). The proceeding variables in order of best correlation were: Sand (p_w= 0.209); Sand and Crevice (p_w= 0.204); and Sand, Crevice, and percent cover of Scleractinians (p_w= 0.201). The biotic data only comprised of *Echinometra lucunter,* since *Diadema antillarum* individuals were too infrequent to detect correlations. Therefore, crevice cover was the single habitat variable best explaining the biotic assemblages for all sites. Further exploring this relationship in a linear form, the correlation between square-root transformed rank crevice cover and *E. lucunter* density presented a significant positive correlation (Fig. 10; r = 0.37, P <0.0001). Finally, when considering the relationship between coral richness (scleractinians only) and *E. lucunter* density from all transects, no correlation was detected, although richness was observed highest at low-intermediate *E. lucunter* abundance ranging from 20−120 $ind.20m^{-2}$. No correlation was found between coral cover (percent cover of Scleractinians) and density of *E. lucunter*.

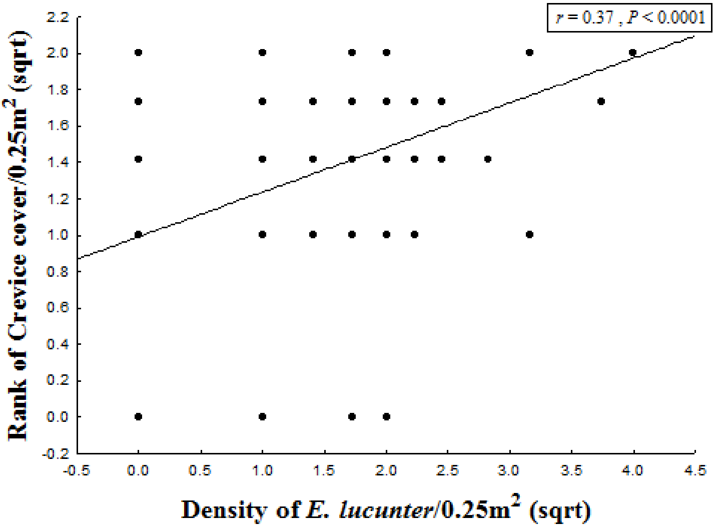

Fig. 10 Scatterplot with line of best fit of the relationship between square-root transformed *E.lucunter* density per quadrat (0.25m^2) and rank crevice cover in each quadrat (*r* = 0.37, *P* <0.0001).

DISCUSSION

Urchin Abundances and Site Characteristics

This study provides a quantitative investigation of the sea urchin assemblage and its relationship with habitat variables at Recife de Fora. In the Caribbean, a study has shown that *Diadema* densities vary from rare to absent across sites, and when seen are very large, patchly distributed (Lessios 1988), and associated to sandy bottoms (Randall et al. 1964; Lessios 1988). Also, McClanahan (1988a) has experimentally shown that another *Echinometra* species, *E. mathaei,* competitively excludes two *Diadema* species from crevice space. This could potentially be complicating the situation for *Diadema,* resulting in their lower numbers at Recife de Fora. Of the four species recorded, *Echinometra lucunter* was by far the most abundant species and is therefore the main focus of interest for discussion. Futhermore, at this assessed microhabitat scale, Euclidean distance showed a tendency of the habitat composition (transects) to group according to site, in a similar pattern to that of *E. lucunter* density. This suggests that a combination of habitat variables (substrate cover of studied groups, depth, habitat complexity, etc.) may be influencing the urchin densities at these sites, possibly explaining the urchin-habitat relationships. For examples, sites of highest crevice cover and habitat complexity also presented high urchin densities at Forereef-S and Backreef-N. Also at these sites, Forereef-S had significantly lower Foliose algae cover while Backreef-N presented significantly higher foliose cover.

Arantes (2012) has previously characterized two of our high urchin density sites, Forereef-N and Forereef-S as: exposed, situated along the reef edges, with high wave exposure and a predominant eastern wave direction. *E. lucunter* is known to be more abundant in high wave action sites, suggesting that these sites may provide a more energy efficient environment where food avaliability in relation to energy loss is maximized (Johansson et al. 2010). As well, the high abundance of this species at these sites may well be due to the species ecological and biological adaptations to a high-wave energy environment (Johansson et al. 2010). The proximity of Backreef-N to Forereef-N could be responsible for the similar and high densities although, many other factors like recruitment, for example, acting at both macro and micro scales, can be influencing urchin densities at these sites.

As for the low-density sites, Arantes (2012) characterizes Patchreef-W and Forereef-E as sites comprising of macroalgal cover greater than 25%, higher than we observed in our study. Arantes (2012) also describes

Forereef-N as having a similar macroalgal cover, which may be why it groups with Patchreef-W and Forereef-E in our study. Additionally, Patchreef-W differs from the rest of our sites, located on the sheltered side of the reef, and is the only site where we registered the occurrence of *Palythoa caribaeorum*. Forereef-E was also unique in terms of habitat composition, since it presented zero to minimal Gorgonian and Milleporid cover.

Despite variations in some habitat variables (biotic and abiotic) among sites, in general all five sites presented a fairly homogenous composition, thus supporting our finding from the multivariate analysis (BIOENV): crevice cover is the single and best explanatory variable influencing the abundance of *E. lucunter.* As for *Diadema antillarum*, one study has shown that the species is better explained by sediment type than biotic cover (Dumas et al. 2007), which was not assessed in our study. Also this species occurred too infrequently to detect habitat correlations with its presence.

The Pearson *r* correlation corroborates the above BIOENV result, as it indicates a low-moderate and linear correlation between crevice cover and *E. lucunter* density. This relationship is interchangeable, meaning that it is not clear which variable depends on the other. Could it be that *E. lucunter* density increases with percent cover of crevices or the reverse? *E. lucunter* is generally found in holes in the substrate of shallow rocky areas on reefs, particularly in locations of surf and wave surge. As well, this species erodes cavities or burrows in rock to create a protective chamber from the currents hardly ever leaving their crevices (Abbott et al., 1974; McGhehee 1992). Deducting from this excavating behaviour it is therefore acceptable to assume the reverse, where the percent cover of crevices increases with urchin density.

Implications for Coral Reef Conservation

Functional redundancy, is one of the four cornerstones of reef resilience along with spatial heterogeneity, connectivity and response diversity (Nystrom et al. 2008). The history of herbivory in the Caribbean reefs illustrates how the loss of a single species can have large-scale, devastating impacts if not counterbalanced by functionally redundant species (Dietzel 2011). At Recife de Fora, besides the presence of a few individuals of *D. antillarum*, *E. lucunter* is the only urchin capable of excavating and inhabiting the reef. This highlights the fragility of this system, such that the creation of holes and the enhanced topographic complexity are affected by the urchins’ behaviour. Also, many small invertebrates depend on these holes for refuge and studies have shown that cryptobenthic fishes positively correlate with microhabitat complexity, *i.e.* number of holes (Willis and Anderson 2003; Dalben and Floeter 2012). Moreover, Patzner (1999b) recorded the effect of sea urchins as a hiding place for juvenile benthic fishes in the Mediterranean Sea (Dalben and Floeter 2012), therefore enhancing the diversity of the reef system.

Despite being a protected area, Recife de Fora suffers from overfishing and presents low abundances of large herbivorous fish, especially *Sparisoma amplum* (Ranzani, 1842) (0.06±0.02 ind.3m^{-2}) (Chaves et al. 2010), a fish that performs some of the functional roles (excavation by erosion) of urchins. In the Carribean, the sister species of *S. amplum*, *Sparisoma viride*, is known as the most important excavating grazer (Bruggemann et al. 1996). *S. amplum* is also responsible for reef bioerosion (Francini-Filho et al. 2008), especially for large individuals, since they have a more profound effect on the reef (Bruggemann et al. 1994; Bonaldo and Bellwoord 2008; Lokrantz et al. 2008). Therefore, we suggest that sea urchins are the primary herbivores at Recife de Fora. Also, Recife de Fora has already been hit by shifting baselines, and fishers perceptions on fish species status have rapidly shifted (Bender et al. 2013). The pattern of this shifting perspective is also evident across fishers of different ages and species catches of what is considered now a large individual (Bender et al. 2013). These findings also point to an altered state of the reef community.

At Recife de Fora, no correlations were detected between Scleractinians (richness and cover) and urchin density. There is little evidence of this relationship in literature, but since urchin herbivory controls algal cover, we thus assumed that coral cover will increase, although some urchins can also be facultative corallivores (Glynn et al. 1979, 1990a; Lewis and Rotjan 2008). Therefore, we expected that an intermediate urchin density would indirectly maximize coral richness, cover and diversity. Evidence of this from another study, but with another species, shows that while settlement of coral spat is highest in the absence of the urchin *Diadema*, survivorship of juvenile corals is low due to algal overgrowth (Edmunds and Carpenter 2001). A study conducted in six coral reef lagoons of Kenya, observed a strong negative correlation between coral richness and sea urchin density (McClanahan and Mutere 1994), yet these *Echinometra* of Kenya are different than *E. lucunter* of the Western Atlantic. The same authors also suggest the possibilily that reduced abundance; perhaps size, and species richness of hard corals are attributable to intense sea urchin grazing or spine abrasion on hard substrate. At Recife de Fora, it is possible that we did not observe any correlation of this kind because the reef was primarily dominated by a single species *(E. lucunter*) and maybe has not reached an urchin barren state *i.e* the highest urchin disturbance level possible. The highest density of *E. lucunter* at Recife de Fora was 30 ± 1.2 ind.m^{-2}. When comparing to other studies, this density can be considered as relatively intermediate. For example, for densities of *E. lucunter* in other reefs of Bahia, like in Back Door-Ilhéus, Cuevas (2005) recorded a low 3.4 ind.m^{-2} in wave-cut benches (rocky shore platforms). This site is made up of crystalline rocks that may difficult the rock-burrowing process of *E. lucunter* (Cuevas 2005). Cuevas (2005) has also recorded densities of 17.3 ind. m^{-2} in coastal coral reef platforms of Península de Maraú, an area under the influence of two Offshore Petroleum projects (Silva and Souza Filho 2011). Situated closest to Recife de Fora, densities between 3 ind.m^{-2} and 10 ind.m^{-2} have been recorded in a coastal coral reef plateau at Coroa Vermelha: a site heavily impacted by fishing and diving tourism (Pelaes and Martins 2007). Thus, comparing to Recife de Fora, the greater anthropogenic impacts at Coroa Vermelha may be responsible for a lower urchin density. In rocky reefs of Rio de Janeiro, densities vary between 3.33 ± 1.56 and 65.28 ± 8.95 ind.m^{-2} (Calderon et al. 2007). In rocky reefs of Santa Catarina, studies have recorded mean densities of 4 ind.m^{-2} (Dalben and Floeter 2012) and 5.12 ± 2.09 ind.m^{-2} in three shallow rocky reefs between 1−5 m (Labbe-Bellas et al., *in prep*), similar to the depths studied at Recife de Fora. Extreme densities of 100 ind.m^{-2} (Ogden 1977; O'Leary and McClanahan 2010) have been reported in a Carribean Patchreef and can create undesirable states such as urchin barrens. Higher *E. lucunter* densities in coral reefs, such as Recife de Fora, than in rocky reefs, could be due to the greater ability of *E. lucunter* to excavate in calcareous reefs and therefore also leading to a greater crevice cover. On the contrary, in rocky reefs, densities did not respond to crevice cover since urchins cannot excavate as easily (Labbe-Bellas et al., *in prep*). Finally, comparing the situation at Recife de Fora with other studies, we suggest that this reef has not yet attained an undesirable urchin barren state.

To conclude, reef resilience at Recife de Fora should be considered a topic of concern for reef managers and conservationists. The presence of mainly one species, *E. lucunter,* was a surprising result and became a topic of concern when we compared our findings with those from a subtropical rocky reef system in Santa Catarina, Brazil (Labbe-Bellas et al., *in prep).* It has been thought that marine species diversity peaks at the equator and declines towards higher latitudes (Pianka 1966; Whitman et al. 2004; Iken et al. 2010). Nevertheless, Iken et al. (2010) state that some taxa do not follow this latitudinal gradient, which could be the case for sea urchins at Recife de Fora and Santa Catarina. At Recife de Fora, we observed one primary urchin grazer compared to five species in the more subtropical reefs of Santa Catarina (latitudes 27° S–29°S). At Recife de Fora, *E. lucunter* overwhelms the functional role of urchin herbivory, being more abundant than in the subtropical reefs of Santa Catarina. Although little is known regarding the functional roles of different herbivores in the Southwestern Atlantic and how redundant their functions are in the reef, this situation seems to represent an example of low functional redundancy. Therefore, we suggest that if this almost single functional herbivore is removed at Recife de Fora, or its population is depleted by a future catastrophic event; the reef system could suffer severe impacts. This stresses the importance of maintaining a strict protection level in order to conserve reef herbivores (both fish and urchins).

The present study is the first urchin species-habitat study performed in northeastern Brazil, and these results explore such a relationship at a microhabitat scale. Future studies should incorporate other factors, like wave exposure, that occur at a larger scale. For example, using the wave exposure data obtained by Arantes (2012), we detected a trend of higher abundance in more exposed reef sites. Therefore, further studies, over larger spatial and temporal scales, are needed to better advance our findings on which habitat variables best explain the sea urchin assemblages. Monitoring programs should also be implemented to obtain a better understanding of sea urchin assemblages and habitat associations, which will allow us to make inferences on proper reef system functioning and management actions.

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CONCLUSÕES

Esse estudo amostrou 695 ouriços dentro de 26 transectos, entre 1 e 10 m em tres recifes rochosos de Santa Catarina, dos quais a grande maioria foi de *Echinometra lucunter*. Das cinco espécies encontradas em Santa Catarina, apesar de terem densidades mas baixas, também foram representativas: *Arbacia lixula* (1,67 ind.m^{-2} na ilha do Xavier) e *Paracentrotus gaimardi* (1,34 ind.m^{-2} na ilha do Arvoredo). Considerando apenas a faixa rasa (comparável com a profundidade amostrada no recife coralíneo da Bahia) a média geral de *E. lucunter* 5,1±2.1 ind.m^{-2} entre 1 e 5 m. As ilhas se diferenciaram em termos de composição e abundância de ouriços e também das variáveis ambientais avaliadas. Além disso, o novo registro da espécie *Tripneustes ventricosus* nos leva a concluir que a escassez de estudos na região ou respostas as mudanças climáticas recentes, podem estar relacionados a novos padrões de distribuição de espécies.

Nessa escala do microhabitat estudada, o conjunto de variávies que melhor explicou as assembleias de ouriços foi a complexidade de habitat e a profundidade, mas com uma baixa correlação. Estudos que avaliam mais que uma espécie ao mesmo tempo com as variáveis ambientais são complexos, e muitas vezes não apresentam altas correlações. Contudo, os resultados aqui apresentados corroboram com outros estudos, que mostram que a relação entre echinodermos e o habitat é espécie-específica, possivelmente devido às preferências de nicho (recurso, risco de predação, reprodução, etc), pouco conhecidas para ouriços. Esse estudo apresentou, pela primeira vez no Brasil, associações entre assembleias de ouriços e variáveis do habitat. Por exemplo, das variáveis estudadas, a espécie *Arbacia lixula* foi melhor explicada pela porcentagem de cobertura de alga foliosa na ilha do Xavier e negativamente associou com a cobertura de esponja, possivelmente refletindo o efeito dessa espécie na estruturação da comunidade bêntica. Já a espécie *E. lucunter* se mostrou associada com a ilha do Arvoredo e com a cobertura de anemonas e alga crostosa coralina. Portanto, para responder melhor a pergunta sobre se há relação entre as assembleias de ouriços e as variáveis do habitat, estudos sobre a relação ouriço-habitat precisam ser observados de acordo com cada espécie e em escalas maiores englobando outras variáveis que também influenciam as assembleias de ouriços. É importante também salientar que as variáveis estudadas ocorrem em gradientes inter-relacionados, dificultando a identificação da distribuição das espécies de ouriços, especialmente porque a densidade tende a variar em curtas distâncias e a agregação tende a aumentar dependendo da escala espacial (Dumas et al. 2007).

O recife de coral na Bahia apresentou o dobro de ouriços encontrados em Santa Catarina, nas quais 1.336 indivíduos eram da espécie *E. lucunter* (média de 12,7 ±2.1 ind.m^{-2}). Nessa escala do microhabitat, uma variável que está potencialmente explicando as densidades de ouriços no Recife de Fora é a cobertura de buracos (p_w=0.217). Individualmente, observou-se uma correlação baixa-moderada com a cobertura de buracos e a densidade de *E. lucunter* (r = 0.37, P <0.0001). Uma vez que *E. lucunter* habita ambientes agitados em recifes de corais (Johansson et al. 2010), a existência de buracos é importante para buscar refúgio contra os predadores (McClanahan & Muthiga 2001) e ondas (McGhehee 1992; Johansson et al. 2010), e possibilitar a alimentação de algas arribadas (“drifting”) nesses lugares ricos em nutrientes (Abbott et al., 1974; Russo, 1977; Grunbaum et al., 1978; Ogden et al., 1989; McGhehee 1992). Portanto, no Recife de Fora, *E. lucunter* escava melhor o substrato e prefere os locais agitados, resultando em uma correlação encontrada com a cobertura de buraco e densidade.

Através da redução de macroalgas pelos ouriços, seria esperado que um certo nível de distúrbio pudesse permitir uma maior abundância e riqueza de corais. No entanto, não houve nenhuma correlação significativa entre a riqueza e abundância de corais e a densidade de *E. lucunter*, como se esperava.

É importante ressaltar que nos dois tipos de recife, a correlação não sugere uma relação de causa e efeito, mas ilustram os fatores que potencialmente podem influenciar ou ser influenciados pela presença de ouriços nesses locais. Além do tipo de formação recifal os ambientes também são diferentes por muitos outros motivos (e.g. latitude, temperatura, etc). Assim, as diferenças potenciais observadas nesse estudo podem ser resultado não só das diferenças de base desses sistemas. É também importante considerar os fatores influenciando as assembleis dos ouriços na macro escala como a exposição de ondas e efeitos antropogênicos. Muitas vezes, um erro commun dos ecológos é tentar explicar a variabilidade através de ordenações e análises de correspondência canônica (Condit et al. 2002). Portanto, o mesmo autor conclui que precisa-se também considerar os efeitos aleatórios atuando na estruturação das assembleias de organismos.

No recife coralíneo, onde existem poucos peixes herbívoros com a mesma função de bioerosão dos ouriços, foi encontrada apenas uma espécie com abundância suficiente para cumprir esse papel. Nos recifes rochosos de Santa Catarina, apesar das espécies apresentarem densidades mais baixas, o papel funcional dos ouriços herbívoros é distribuído entre as cinco espécies encontradas. Assim, comparando os padrões encontrados nos dois tipos de recifes estudados, percebe-se uma menor redundância funcional no recife de coral da Bahia, potencialmente implicando em uma menor resiliência do sistema. Além disso, percebemos diferenças nas densidades da espécie *E. lucunter*, com maior densidade média no recife de coral e uma correlação com a cobertura de buracos. No recife rochoso, a sua densidade média foi menor e as assembleias de ouriços correlacionaram com complexidade do habitat (também, só que mecanismos diferentes). A correlação com buracos encontrada para Bahia é a mesma correlação encontrada para Santa Catarina (com a complexidade de habitat), só que no Recide de Fora o buraco é um resultado do comportamento de *E.lucunter* escavando o recife e assim, criando uma maior complexidade do habitat.

Desta forma, o entendimento dos processos que controlam as populações de ouriços em diferentes tipos de recifes é um desafio com consequências para o manejo dos habitats recifais, especialmente frente às crises recifais mundiais (Bellwood 2004, 2006; Graham et al. 2007).

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