



Sea urchin abundance and habitat relationships in different Brazilian reef types



Rachel Labbé-Bellas^{a,1}, Cesar A.M.M. Cordeiro^{b,*}, Sergio R. Floeter^a, Bárbara Segal^{a,c}

^a Universidade Federal de Santa Catarina, Programa de Pós-graduação em Ecologia, Departamento de Ecologia e Zoologia, Florianópolis – SC, 88010-970, Brazil

^b IRD-UMR 250 Entropie-Labex Corail, Université de Perpignan, Perpignan, 66000, France

^c Instituto Coral Vivo, Arraial d'Ajuda, Porto Seguro, Brazil

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ABSTRACT

Sea urchins exhibit close linkages with the substrate, derived from their life habits such as locomotion and feeding. The main objectives of this study were to evaluate the distribution and abundance patterns of urchins and their relationships with habitat characteristics (habitat complexity, depth, and benthic percent cover) at the microhabitat scale in Brazilian reefs. *In situ* sampling was performed during scuba diving, using 0.5m x 0.5m quadrat counts and the percent cover of the microhabitat variables. Six species of urchins were found in subtropical reefs (Santa Catarina), including a new record of the species *Tripneustes ventricosus*. At the tropical coral reef (Recife de Fora) four species were found but *E. lucunter* was by far the most abundant species ($12.7 \pm 1.1 \text{ ind. m}^{-2}$). At the subtropical rocky reefs, *E. lucunter* mean density in shallow areas was $5.12 \pm 2.1 \text{ ind. m}^{-2}$. Other species were also representative in these reefs, such as *Arbacia lixula* (1.67 ind. m^{-2}) and *Paracentrotus gaimardi* (1.34 ind. m^{-2}). The structure of the assemblages of sea urchins was different between biogenic and rocky reefs, with the latter showing higher species richness but lower abundances of sea urchins. Despite intrinsic differences in studied reefs, the sea urchins abundance was mainly related to structural complexity (reef building organisms, holes and crevices) indicating that, in general, the reef spatial structure is crucial to sea urchin species due to direct and indirect resources provided.

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1. Introduction

Sea urchins have important roles in marine shallow coastal environments by controlling the abundance of macroalgae, and in turn favoring the growth of crustose coralline algae (Lewis, 1958; Paine and Vadas, 1969; Ogden et al., 1973; Sammarco et al., 1974; Johansson et al., 2010), and may enable coral spat settlement (Edmunds and Carpenter, 2001). The phenomenon of urchin effects on algae has been documented in various types of habitats from temperate rocky reefs (Schiel and Foster, 1986; Andrew, 1993; Ling et al., 2015) to coral reefs (Lawrence, 1975; Hughes, 1994). Interest in this topic began in the mid-70s in the temperate reefs of the western coast of North America when a sea urchin proliferation event happened, causing the depletion of macroalgal zones and

transforming them into calcareous algae zones (Lawrence, 1975). Not much later after, a high mortality of the sea urchin *Diadema antillarum* was recorded in the Caribbean between 1983–1984 (Lessios et al., 1984), where its absence contributed to a significant increase in macroalgal dominance (Hughes et al., 1985; Carpenter, 1990). Thus, macroalgal cover and sea urchin density can be considered as two well-known bio-indicators, among others, of reef health condition (Hughes, 1994; McClanahan and Mutere, 1994; Jackson et al., 2001; McManus and Polsenberg, 2004).

Sea urchin distribution can be influenced by abiotic factors (e.g. physical structure, Hernández and Russell, 2009 wave exposure, Tuya et al., 2007), and biotic factors (e.g. predators abundance, McClanahan, 1998). Quantitative studies regarding species/habitat relationships have shown that the urchin–habitat relationship is often species-specific and highly dependent on the assessed scale (Andrew, 1993; Dumas et al., 2007; Entrambasaguas et al., 2008). Other studies, however, state that urchin distribution patterns are complex and relating them to environmental factors is difficult (Adjeroud, 1997; Dumas et al., 2007).

* Corresponding author.

E-mail address: cammcordeiro@gmail.com (C.A.M.M. Cordeiro).

¹ Authors share co-first authorship.

Few studies have assessed benthic community structures in marine hard substratum of the South Atlantic (Oigman-Pszczol et al., 2004; Cordeiro et al., 2014). In Brazil, Rathburn published in 1879 the first study citing the importance of urchins in the benthic community. The author states “*Echinometra lucunter* is an edible urchin, and a rock-burrower that occurs from Pernambuco state until Santa Catarina in the south” (Giordano, 1986). Taking advantage of the wide distributional range of *E. lucunter*, this species was used here as a comparative model within urchin’s assemblages between studied habitats.

The present study aims to evaluate the composition and abundance of sea urchin assemblages in two Brazilian reef types (rocky and coral), with emphasis in the contribution of *E. lucunter* as a common factor, and determine its relationships with habitat variables at the microhabitat scale. Specifically, we performed this study at rocky reefs of Santa Catarina and a coral reef of Bahia (Recife de Fora) to understand the urchin assemblages and their relation to habitat structure habitat complexity, depth, and percent cover of benthos. For both reef types, we evaluated (1) urchin densities, (2) urchin–habitat associations at the microhabitat scale, and (3) discussed the differences between urchin assemblages and habitat relationships in the two different reef systems (rocky and coral).

2. Material and methods

2.1. Study areas

Two study regions were selected to assess urchin–habitat relationships in two reef types (rocky and coral reefs) (Fig. 1). The rocky reef areas of Santa Catarina (SC) are situated in the transition belt between the subtropical and warm-temperate regions of the Southwestern Atlantic (Garreaud et al., 2009; Bouzon et al., 2012). The tropical reef, Recife de Fora, is close to the largest extension of the continental shelf of Bahia (BA), the Abrolhos Bank, (the most complex reef system in the South Atlantic; Castro and Pires, 2001).

2.2. Sea urchin counting

Sampling was conducted during the daytime in the summer–spring months (December 2011–April 2012) in rocky shores of three islands off the coast of Santa Catarina Island (Brazil): Campeche Island, Xavier Island, and Arvoredo Island (Fig. 1). The annual average sea surface temperature in these rocky reefs is 22.5 °C, ranging from 17 °C in the winter to 27 °C in the summer (PO.DAAC, 2015). The second sampling campaign was conducted in five sites during the spring of November 2012 at Parque Municipal Marinho do Recife de Fora (herein referred to as Recife de Fora), a 29 km² patch reef area that lies 5 km offshore in south of Bahia (Brazil) (Seoane et al., 2012). Recife de Fora is composed by biogenic reefs, with rounded formations that do not surpass 20 m depths (Laborel, 1969), and sea surface temperature varies from 24° to 28 °C in that region (Ghisolfi et al., 2015).

All sea urchin counts and assessment of the habitat variables were conducted with SCUBA in 20 × 1 m belt transect along the reef substrate to help guide the placement of the quadrats. Along the transect, a 0.5 × 0.5 m PVC quadrat was placed at alternating sides at every meter for a total of 12 quadrats in each transect. In Santa Catarina (SC) and Recife de Fora (BA), transects were laid out between depths of 3–7 m and 2–5 m respectively. Ten transects were performed in all sites in SC, but Campeche Island, with only six transects, due to its limited area. At Recife de Fora, three transects were placed at each of the five sites due to its patchy formation. Sea urchins in quadrats were identified *in situ* to the species level and their abundances were recorded, totalizing 310 quadrats sampled in SC and 180 in BA. Also in each quadrat,

we assessed the relative substrate cover along with an evaluation of habitat complexity. Classes of substrate cover (scleractinian corals and milleporids, epilithic algal matrix, crustose coralline algae, macroalgae, bare substrate – rock and sand, crevice, other sessile invertebrates – anemones, ascidians, sponges, bryozoans, *Palythoa* sp., gorgonians) were estimated in five categories (≤ 5 , 6–25, 26–50, 51–75, 75%–100%) for each sampled quadrat. Habitat complexity was obtained through a semi-quantitative method, and evaluated only by RL-B, performing a visual assessment of complexity following the criteria in the Table 1.

2.3. Data analysis

Detrended correspondence analysis (DCA) was applied to sea urchin abundance in order to evaluate the ordination of assemblages in sampled regions, and data was transformed using the Hellinger transformation (Legendre and Legendre, 2012) prior to its use. The SIMPER routine (Clarke and Warwick, 2001) was then applied to identify the relative contribution of species to the differences found between regions. The same procedure was applied to substrate cover data, with the additional analysis of similarity ANOSIM supplemented by the Monte-Carlo test (4999 permutations) to test for significance in differences.

The relationship between sea urchin species abundance and environmental factors was investigated using redundancy analysis (RDA). All data was transformed using Hellinger transformation, and the environmental data was then standardized by the margin maximum and multiplied by the number of non-zero items (Legendre and Legendre, 2012). The significance of axes and the relative contribution of each environmental variable were tested with a Monte-Carlo test (Reduced model, 4999 permutations).

A generalized linear mixed model (GLMM) was applied to the data on *Echinometra lucunter* abundance in order to investigate the influence of the same environmental factors to this species that was conspicuous to all sampled sites. Due to the overdispersion found in data, we used a negative binomial model in the GLMM. For that, the function *glmer.nb* from the package *lme4* (Bates et al., 2015) was applied to the full model, which included all environmental factors as continuous variables, the region (Santa Catarina and Bahia) as fixed factor, and the sites as random factor nested with regions. After that, the model was reduced through sequentially removing terms based in the Akaike information criteria (AIC) (Zuur et al., 2009), comparing the full model with nested models in which one of the predictor variables was dropped (using the ‘ANOVA’ function in the R base statistics distribution). If the ANOVA found a dropped variable to have no significant effect on the model, it was removed. Interactions were examined and dropped in the same fashion.

3. Results

3.1. Sea urchin species

Six sea urchin species were detected during this study in both regions, from which all were already registered for Recife de Fora region, and five for the state of Santa Catarina (Table 2). One species was a new record for Santa Catarina state (1 individual of *Tripneustes ventricosus* Lamarck, 1816), inside the MPA REBIO Arvoredo, near Arvoredo Island on a sandy bottom at 4 m depth (supplementary material).

A total of 310 urchins were counted in the five study sites in Bahia, and 666 individuals for all three sites in Santa Catarina. *Echinometra lucunter* was the most abundant and frequent species in both sampled regions (Table 2), followed by *Diadema antillarum* and *Arbacia lixula*, in Bahia and Santa Catarina, consequently.

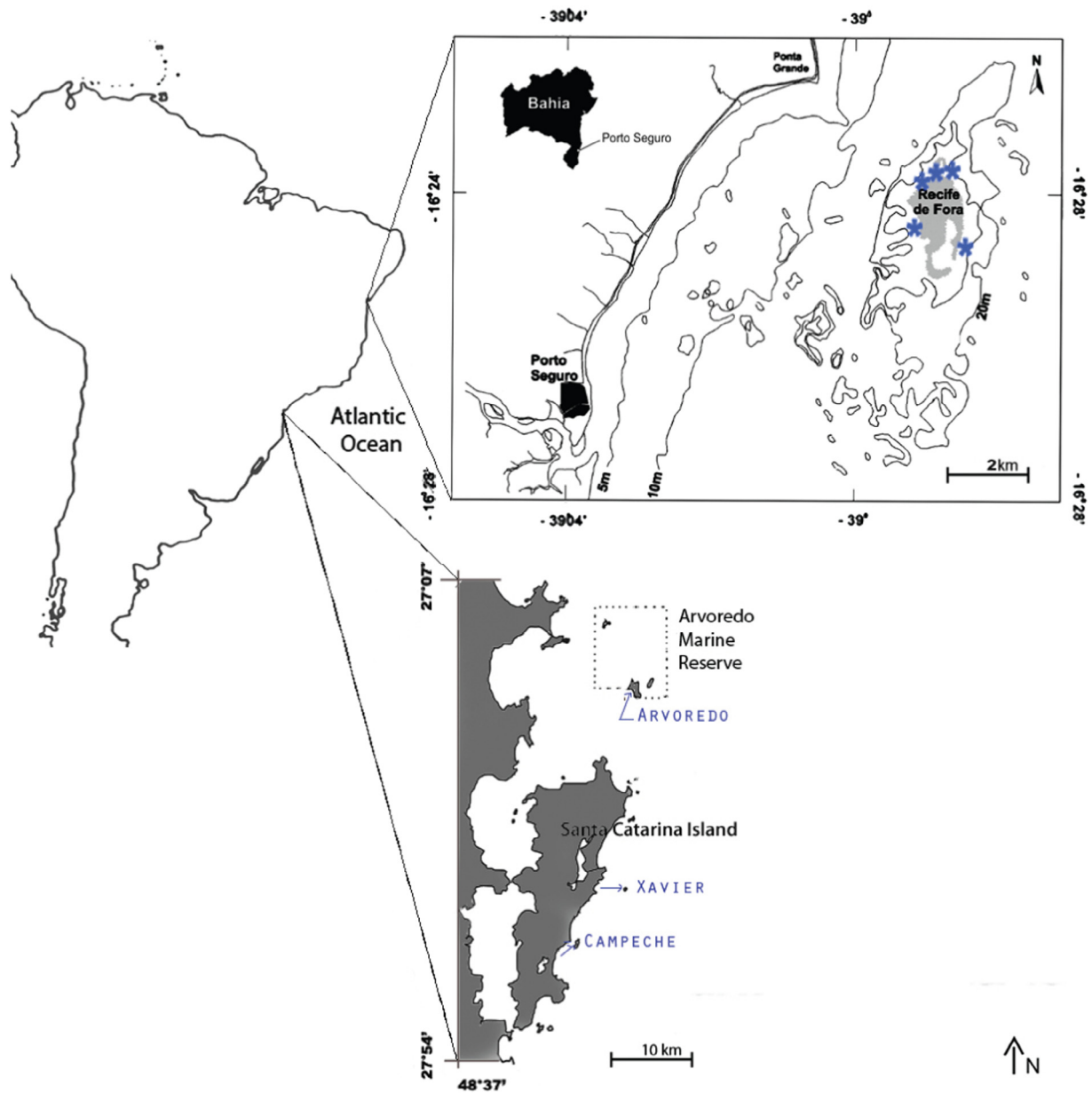


Fig. 1. Map of sampled reef areas in Brazil.

Table 1

Criteria for ranking habitat complexity in each quadrat (0.5 m × 0.5 m).

Source: Adapted from Polunin and Roberts (1993), Spalding and Jarvis (2002) and Graham et al. (2007).

Rank	Topographic complexity	Coral cover*
1	Rocks of ≤0.5 m diameter or sandy or flat surface (0 holes)	(0%–5%)
2	Rocks of ≤1 m diameter or flat surface (1–2 holes)	(5%–25%)
3	Rocks of >1 m diameter or few surface inclinations (1–2 holes)	(25%–50%)
4	3–5 holes and different surface inclinations	(50%–75%)
5	>5 holes and many surface inclinations	(>75%)

* Only measured at Recife de Fora (BA).

The rocky reefs of Santa Catarina showed a more evenly distributed abundance among species when compared with the biogenic reefs of Bahia, with a significantly different assemblage (ANOSIM, $R = 0.13$, $p < 0.001$, 4999 permutations). The rock boring sea urchin *E. lucunter* represented 97.7% of all individuals found in biogenic reef and 57.6% of total in rocky reefs. Only *Paracentrotus gaimardi* and *Arbacia lixula* in SC were more representative with 16.1% and 20.7% of local total abundance, consequently.

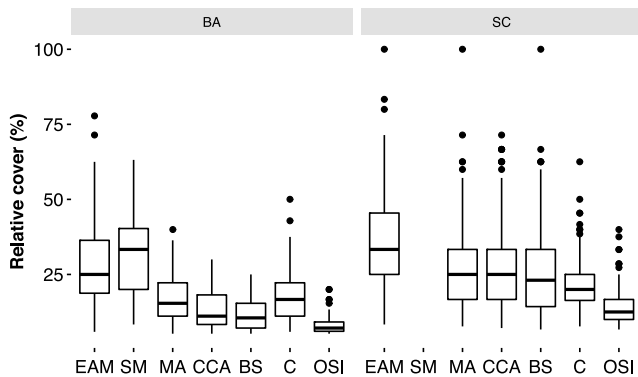
3.2. Environmental factors

Biogenic and rocky reefs showed significant differences between mean values (\pm s.e.) of structural habitat complexity ($F_{1, 490} = 18.2$, $p < 0.001$) and depth ($F_{1, 490} = 281.2$, $p < 0.001$), where the first had higher complexity (2.5 ± 0.08) but lower depth (3.0 ± 0.09 m) when compared to rocky reefs (2.1 ± 0.05 ; 5.2 ± 0.09 m).

Table 2Total abundance, median and quantiles (0.25 m²) of sea urchin species in Brazilian reefs.

Species	FO%	N	Q.25%	Median	Q.75%	Max.
Bahia						
<i>Arbacia lixula</i>	–	–	–	–	–	–
<i>Diadema antillarum</i>	1.7	4	1	1	1.5	2
<i>Echinometra lucunter</i>	64.4	303	1	2	3	16
<i>Eucidaris tribuloides</i>	0.6	1	1	1	1	1
<i>Lytechinus variegatus</i>	1.1	2	1	1	1	1
<i>Paracentrotus gaimardi</i>	–	–	–	–	–	–
<i>Tripneustes ventricosus</i>	–	–	–	–	–	–
Santa Catarina						
<i>Arbacia lixula</i>	25.6	138	1	1	2	8
<i>Diadema antillarum</i>	–	–	–	–	–	–
<i>Echinometra lucunter</i>	28.8	384	1	3	5	50
<i>Eucidaris tribuloides</i>	4.2	13	1	1	1	1
<i>Lytechinus variegatus</i>	6.1	24	1	1	1.5	2
<i>Paracentrotus gaimardi</i>	11.5	107	1	2	4	12
<i>Tripneustes ventricosus</i>	–	1	–	–	–	–

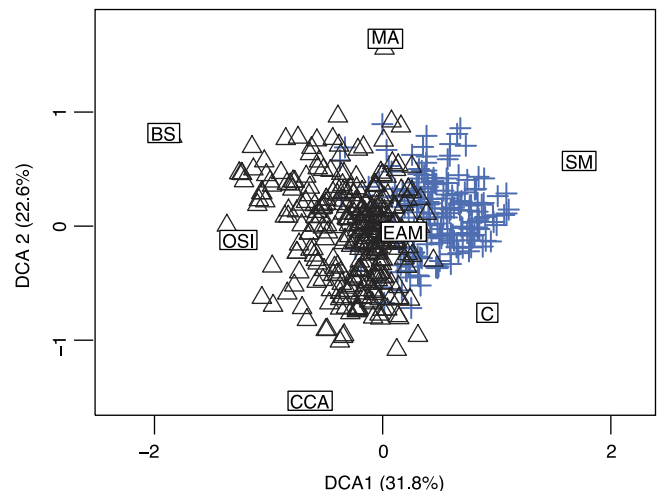
FO—Frequency of occurrence, Q.—quantile, max.—maximum.

**Fig. 2.** Substrate cover of biogenic reefs of Recife de Fora and rocky reefs of Santa Catarina, Brazil. EAM—epilithic algal matrix, SM—scleractinian and milleporid corals, MA—macroalgae, CCA—crustose coralline algae, BS—bare substrate, C—crevice, OSI—other sessile invertebrates, BA—Recife de Fora, SC—Santa Catarina.

Epilithic algal matrix was the dominant type of cover at all sites (Fig. 2), and the other types of cover showed similar trends in both biogenic and rocky reefs, with the exception of Scleractinian and milleporid corals (SM), that was only found in biogenic reefs. Despite some overlap, the samples for benthic cover of biogenic and rocky reefs showed significant dissimilarities (ANOSIM, $R = 0.36$, $p = 0.002$, 4999 permutations) according to sampled regions (Fig. 3). Scleractinian and milleporid corals (SM) contributed with 26% of the dissimilarity found between regions. After the removal of this category present only in biogenic reefs, macroalgae (MA) was the type of cover with higher contribution for the dissimilarities found (19.5%), followed by crevices (19.0%) and CCA (18.2%), being only the last two significant for differences (SIMPER, $p = 0.01$, 4999 permutations).

3.3. Sea urchin abundance and environmental variables

In the analysis of sea urchins and environmental variables in all reefs the reduced model was significant with six of nine tested variables, with the first three axes being significant ($F_{6, 309} = 13.1$, $p < 0.001$). Only the variables that contributed significantly to axis are shown in Fig. 4. Axes 1 and 2 of the RDA accounted for 93.6% of explained variance ($R_{adjusted} = 0.19$, Fig. 4(a)), and the third axis is not shown in figures due to the low contribution to the model explanation. The first axis was positively associated with depth and CCA, and negatively with SM, while the second axis was negatively influenced by: crevice (C), SM, depth and complexity (Fig. 4(a)). *Echinometra lucunter* was positively associated with SM, while *A.*

**Fig. 3.** Detrended correspondence analysis of benthic cover in biogenic reefs of Recife de Fora and rocky reefs in Santa Catarina. Axis 1 and 2 explained variation 31.8% and 22.6%, respectively. Triangles represent samples of biogenic reefs from Recife de Fora, and crosses, rocky reefs from Santa Catarina. EAM—epilithic algal matrix, SM—scleractinian and milleporid corals, MA—macroalgae, CCA—crustose coralline algae, BS—bare substrate, C—crevice, OSI—other sessile invertebrates.

lixula was linked to higher depths, and *P. gaimardi* with BS and CCA (Fig. 4(a)). At biogenic reefs, *E. lucunter* was highly dominant in abundance (99.8%) and a separate analysis for this regional level was unfeasible. This way, a second RDA, at the region level, was performed only for the rocky reefs sites. In this second analysis, the first three axes were significant ($F_{6, 309} = 3.59$, $p < 0.001$), explaining 89% of the total variance ($R_{adjusted} = 0.08$). The most influential variables for the first and second axes were depth (−0.52) and complexity (−0.50), indicating that these are the principal factors, among the tested variables, influencing the sea urchin assemblages in the region.

Additionally, *A. lixula* was again associated to greater depths and complexity, but *E. lucunter* was more associated with CCA and BS, and *P. gaimardi* was not influenced by any of the tested variables (Fig. 4(b)).

The GLM model performed only for *E. lucunter* indicated that MA and Depth were the only significant variables explaining the variance in densities of this species at the studied reefs (Table 3(a)). Both variables were negatively correlated with the abundance of *E. lucunter* in the studied reefs, indicating an association with shallow areas with low cover of macroalgae. The same relationship with depth can be observed in RDA diagrams both for all reefs and for

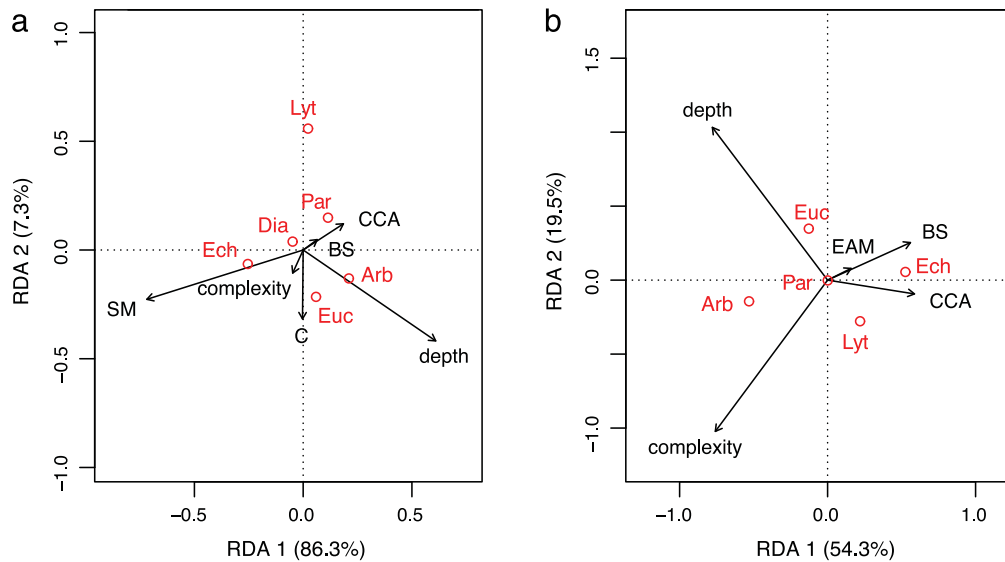


Fig. 4. Redundancy analysis of sea urchin species and environmental variables for (a) all sampled reefs, and only for (b) rocky reefs. Arb—*Arbacia lixula*, Dia—*Diadema antillarum*, Ech—*Echinometra lucunter*, Euc—*Eucidaris tribuloides*, Lyt—*Lytechinus variegatus*, Par—*Paracentrotus gaimardi*, EAM—epilithic algal matrix, SM—scleractinian coral and milleporids, CCA—crustose coralline algae, BS—bare substrate, C—crevice. The explained variation for axis 1 and 2 is showed in each figure.

Table 3

Summary of generalized linear mixed-effect models statistics for effects of environmental factors influencing the abundance of *Echinometra lucunter* in Brazilian reefs, with (a) tested variables, Akaike information criteria (AIC) and χ^2 2-test statistics. (b) Final model (estimates, standard error and p -values).

(a)	Variable	d.f.	AIC	Pr(χ^2)
	Full model	12	1304.5	–
	EAM	11	1303.7	0.592
	BS	10	1301.1	0.557
	C	9	1299.8	0.405
	Complexity	8	1298.4	0.295
	Region	7	1298.4	0.215
	OSI	6	1298.4	0.159
	CCA	5	1298.8	0.116
	Depth	4	1302.5	0.018*
	MA	3	1308.8	0.004*

(b)	Variable	Estimate	s.e.	p
	Intercept	0.79	0.55	0.148
	Depth	–0.22	0.09	0.019*
	MA	–0.01	0.01	0.005*

* Indicates that p -value is significant ($p < 0.05$).

rocky reefs (Fig. 4), which reflects the non-influence of the factor Region that divided biogenic and rocky reefs.

4. Discussion

This study investigated for the first time urchin species–habitat relationships, in two different Brazilian reef systems, at the microhabitat scale. Also, we evaluated the association of *E. lucunter* and environmental variables in two extremes of its distribution. The structure of the assemblages of sea urchins were different between biogenic and rocky reefs, with the latter showing a higher richness of species but lower abundances of sea urchins. Despite obvious differences in origin and formation, reefs of both regions were covered mainly by EAM, with the differentiation between them being related to the presence of reef building organisms (scleractinian corals and milleporids) in Recife de Fora. SM along with Complexity were important variables associated to sea urchins abundance for all reefs indicating that, in general, the reef spatial structure is crucial to sea urchin species due to resources provided, such as refuge from predation, shelter and

food resources, as cited by previous authors (Benedetti-Cecchi and Cinelli, 1995; McClanahan, 1998; Clemente and Hernández, 2008).

The record of a new occurrence of *T. ventricosus* in a marginal reef site of the South Atlantic adds approximately 500 km further south to the species known distribution range. This tropical species occurs in coastal reef areas from Bermuda (Caribbean) and Southern Florida (USA) (32°N) down to Rio de Janeiro State (22°S) in Brazil (Lawrence, 2007; Cordeiro et al., 2014). The same species has also been observed in oceanic islands in the Atlantic such as Fernando de Noronha, Atol das Rocas and Trindade (Brazil), Ascension Island (UK) and, in the Western Atlantic African coast from Gulf of Guinea to Walvis Bay in Namibia (Lawrence, 2007). The previous absence of this species in Santa Catarina may reflect the low sampling effort over benthic communities locally, but possible changes in the species' distributional range should not be excluded. *Triploneustes ventricosus*, although registered in Bahia's Echinoderm Inventory (Magalhães et al., 2005), was not observed at Recife de Fora reefs, which reinforces the usual low abundances of the species.

It has been thought that marine species diversity peaks at the equator and declines towards higher latitudes (Pianka, 1966; Witman et al., 2014), however some taxa do not follow this latitudinal gradient (Iken et al., 2010). Despite the low richness found here, four species in the tropical reefs (BA) and six species for subtropical reefs (SC), this fact is not a clear sign that there is maybe an anti-tropical gradient in the Brazilian coast for sea urchins. However, concerning the functional role of these echinoderms, the different composition of assemblages may influence on the grazing pressure over the substrate cover locally. At Recife de Fora we observed one dominant species (*E. lucunter*) while in the subtropical reefs (SC), the sea urchins' assemblage is more evenly arranged. This equitability among species may potentially alter the role of sea urchin species locally (Cordeiro et al., 2014). Although little is known regarding the functional roles of different grazers in the Southwestern Atlantic and how redundant their functions are in the reef, the urchins effect on the benthic substrate, by scraping and removing other organisms should be recognized as an important structuring force in benthic communities. Thus, the overwhelming abundance of *E. lucunter* at Recife de Fora seems to represent an example of low functional redundancy. Such disparities in species proportions are not easily answered, and factors such as biogeography (Byrnes et al., 2013),

predators' density (McClanahan, 1998) and economical/traditional exploration (Andrew et al., 2002) must be taken in consideration. The species *Arbacia lixula* and *Paracentrotus gaimardi* do not occur in tropical waters (Kroh and Mooi, 2016) probably associated with species specific constraints due to the temperate origins of these taxa (Lessios, 2010). Then the biogeography history of the regions could be a factor explaining the observed pattern. Additionally, Recife de Fora suffers from overfishing (Chaves et al., 2010), which could suggest a low density of sea urchins predators. However, Santa Catarina is known as one of the Brazilian states with higher fishing activities (Bastos and Petrere, 2010), but none of the sampled regions have registers of intense capture of sea urchins for consumption or commerce (Ventura et al., 2013).

Factors associated to species environmental demands can also explain population's variation at local scale (Tuya et al., 2004). The presence of factors associated to habitat physical structure (e.g. crevices, SM) and complexity itself were associated to differences in sea urchin assemblages here, denoting the importance of this variable although the correlations found were not high. Entrambasaguas et al. (2008) suggests the same low correlation with variables indicating heterogeneous and/or complex habitats. This low correlation 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 (Nishihira et al., 1991; Chiappone et al., 2002; Dumas et al., 2007).

As well, our findings corroborate with other studies such that relationships between echinoderms and habitat are species-specific, probably due to niche preferences (resources, predation risk, and reproduction). For example, in our study we observed associations of urchin species with habitat variables, possibly explained by a preferred feeding strategy (Dumas et al., 2007). This feeding preference, although, may vary among regions. All 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 and Borzone, 2005), which could be the case for Santa Catarina. In the Mediterranean, 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, where *A. lixula* feeds mainly on encrusting corallines while *P. lividus* feeds on non-encrusting macrophytes. On the other hand, Wangensteen et al. (2011) used stable isotopes analysis to counterinterview the long established herbivory for both species, indicating omnivorous, and even carnivorous signatures for *Arbacia lixula*. A similar coupled ecological role is suggested for *A. lixula* and *P. gaimardi* in the rocky reefs of Rio de Janeiro (Brazil) in an upwelling area (Cordeiro et al., 2014), which could be the same case observed here for SC. However, further investigations considering stable isotopes must be conducted on Brazilian rocky reefs to clarify this matter.

Echinometra lucunter is the most conspicuous sea urchin in Brazil. High densities have been recorded in rocky reefs of Rio de Janeiro, ranging from 3.3 to 65.3 ind m⁻² (Calderon et al., 2007; Cordeiro et al., 2014). Dalben and Floeter (2012) also recorded similar mean densities to those found in the present study at Santa Catarina. When comparing both our study sites, differences between *E. lucunter* density in coral and rocky reefs could be due to the greater ability of *E. lucunter* to excavate in calcareous reefs, increasing the structural complexity and leading to gain in shelter. Since *E. lucunter* prefers exposed environments in coral reefs (Johansson et al., 2010), the presence of holes is important such that it provides refuge against predators (McClanahan and Muthiga, 1988) and wave surge (McGhehee, 1992; Johansson et al., 2010), and facilitates feeding on "drifting" algae (Abbott

et al., 1974; Russo, 1977; Grunbaum et al., 1978; Ogden et al., 1989; McGhehee, 1992). However, as found here, all densities are highly variable among samples and regions, which leads to weaker correlations. McClanahan and Muthiga (2013) indicated as a characteristic of the genus *Echinometra* a strong homing behavior and an aggregated distributional pattern, which could help explain the observed variations of urchin densities. From the tested factors here, at the microhabitat scale, the factors that best explained the *E. lucunter* abundances at all reefs were macroalgae cover and depth, both with negative correlations. Concerning the depth, *E. lucunter* is commonly found in shallow depths, as other species of the same genus (McClanahan and Muthiga, 2013), maybe associated to niche characteristics such as a high tolerance to wave surge and feeding preferences (Cordeiro et al., 2014). Sea urchins are great macroalgae consumers usually associated to barren formations when at high densities, both in tropical (Hughes, 1994) and temperate reefs (Tuya et al., 2004). Although no strong association was found for CCA (dominant benthic group in barren habitats), the negative relation with MA cover is an indicator of the potential role of this species as key herbivore locally.

It is important to validate that in both reef types, correlation does not imply cause and effect, but illustrates the factors that may possibly influence or be influenced by the presence of sea urchins in these areas. Besides the difference in reef formation, the environments also differ for other motives (e.g. latitude, temperature, etc.). Thus, the potential differences observed in this study could be result of not only the reef system's framework. It is also important to consider the factors that influence the urchin assemblages at the macro-scale, such as wave exposure. 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. Understanding the processes that control sea urchin populations in different reef types and spatial scales is a challenge, with consequences for the management of reef habitats. Future studies on the functional role of sea urchins as herbivores and grazers in different reef types of the Southwestern Atlantic, an extensive area yet possessing little to no information, are warranted.

5. Conclusions

This study is the first considering multiple species of sea urchins in reefs with different frameworks in the Brazilian coast, having the structural complexity as the common ground for both reef areas. *Echinometra lucunter* was observed as a highly adaptable species due to its wide range of occurrence across different reef types in the Brazilian coast, being also the most conspicuous sea urchin species. In the tropical reefs, *E. lucunter* was dominant with over 95% of the total abundance of species. However, despite being also abundant in subtropical reefs, the role of *E. lucunter* as the main grazer is probably shared with *Paracentrotus gaimardi* and *Arbacia lixula*. In the analysis of sea urchins species we also observed the presence of *Tripneustes ventricosus* at subtropical reefs, which constitutes in an extension of the previous known range of the species by 500 km. Finally, the observed correlations between sea urchins' densities and the environmental indicators showed that, even across different reef types, the structural complexity of the reefs is the main feature influencing sea urchins in the Brazilian coast.

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