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Patterns of distribution and composition of sea urchin assemblages on Brazilian subtropical rocky reefs

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Abstract Sea urchins are a key group of herbivores in both temperate and tropical food webs because they control macroalgal cover, and consequently influence primary productivity and phase shifts on reefs. Despite being abundant on southwestern Atlantic reefs, sea urchin distributions, and their association with abiotic and biotic variables, are poorly known. In this study, sea urchin assemblages were surveyed in 2011 at multiple depths at eight sites in Arraial do Cabo (Brazil, 22°57′S/41°01′W), with sites split between a colder, more wave-exposed location, and a warmer, more sheltered location. The influence of this large-scale physical gradient, along with changes in depth and substrate complexity, on sea urchin densities was then investigated. Predator biomass was low and did not vary significantly among sites. Among the seven species recorded, *Paracentrotus gaimardi*, *Echinometra lucunter* and *Arbacia lixula* were dominant. Linear mixed-effects models indicated that location was important, with mid-sized *P. gaimardi* individuals and *A. lixula* more common at cooler, exposed sites and *E. lucunter* more abundant at warmer, sheltered sites. Sea urchin densities typically decreased with increasing depth, probably caused by changes in factors such as light, wave exposure, and sedimentation. Substrate complexity had a positive effect on the abundance of all species, presumably because of the increased availability of refuges. Physical gradients have important consequences for urchin distributions and their ecological functions at relatively small spatial scales on these reefs, and should be incorporated into herbivore monitoring programmes. Research is also required to examine how differential sea urchin distributions affect benthic dynamics.

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Introduction

Herbivory is an important process shaping natural communities and transferring energy through food webs in autotrophic ecosystems (Choat and Clements 1998). However, there are significant differences between terrestrial and aquatic systems in the mechanism of energy transfer from primary producers to higher trophic levels (Burkepile 2013). In contrast to terrestrial systems, where large vertebrates still perform an important role as vegetal consumers (Asner and Levick 2012), in marine ecosystems they no longer represent strong trophic links in communities (Pandolfi et al. 2003). This is because overfishing in coastal systems has decimated herbivorous megafauna, such as sirenians and turtles (Jackson 1997). Consequently, fishes and sea urchins are now the most important herbivores in reef ecosystems (Hughes et al. 2007a). However, their relative influence on primary producers differs along a latitudinal gradient (Gaines and Lubchenco 1982). On tropical reefs, fish and sea urchins are both important herbivores, while

sea urchins predominate in temperate reef systems (Hughes 1994; Tuya et al. 2004). The functional importance of sea urchins in temperate seas is demonstrated by their formation of vast barren areas when at high densities, decreasing habitat complexity and affecting benthic cover and local community dynamics (Wright et al. 2005).

Given their important functional role on temperate reefs, sea urchin populations have been investigated in relation to abiotic factors such as substrate type (Alves et al. 2001), hydrodynamics (Tuya et al. 2007), and substrate heterogeneity and complexity (Benedetti-Cecchi and Cinelli 1995; Clemente and Hernández 2008). This work has demonstrated that these factors clearly influence sea urchin densities at a range of spatial and temporal scales. In particular, depth influences the density and spatial distribution of sea urchin populations (Agatsuma et al. 2006), since it is a proxy for a number of environmental characteristics including light intensity, hydrodynamics, and temperature (Barnes and Crook 2001). Along with having some influence over local hydrodynamics, substrate complexity has significant effects on sea urchin distributions by directly influencing the availability of shelter and food (Beddingfield and McClintock 2000). Competitive interactions among sea urchin species, such as aggressive behavior, may limit access to shelters and force subordinate species into less-suitable microhabitats (Shulman 1990). Additionally, predation can exert direct top–down controls on sea urchin distributions (Clemente et al. 2009) and enhance competition for shelter.

Brazilian reef areas are poorly mapped, but biogenic and abiogenic reefs are present along the 5,000 km of coast (Amaral and Jablonski 2005), directly or indirectly providing goods and services for more than 40 million people that live in the coastal zone (Jablonski and Filet 2008). Despite the extensive literature on sea urchins, and their considerable ecological importance, virtually nothing is known about the distribution and functional role of sea urchins on tropical and subtropical biogenic reefs and rocky shores along the southwestern Atlantic coast (Ventura et al. 2013). Previous studies on sea urchin biology in the region have been restricted to their reproduction and embryology (e.g., Mourão 2007; Contins and Ventura 2011), their contribution to biodiversity studies (e.g., Xavier 2010), and their influence on algal recruitment (Oliveira 1991). Consequently, despite being conspicuous organisms, there is a very limited understanding of how the distributions of individual species vary within sea urchin assemblages, and how these variations are related to environmental factors.

In this study, we survey sea urchin abundances on subtropical rocky reefs in southeastern Brazil. We assess sea urchin assemblages across a large-scale geographical discontinuity in wind exposure and temperature, and in relation to smaller-scale depth gradients, crevices availability

(substrate complexity) and potential predator abundances. The aim of the study was to link sea urchin abundance patterns to key abiotic and biotic factors on rocky reefs.

Materials and methods

Study site

The region of Arraial do Cabo (Rio de Janeiro, Brazil) was declared a marine extractive reserve in 1997, where only traditional fishers are allowed to exploit natural resources. The Arraial do Cabo region consists of an isthmus and two islands mostly surrounded by rocky shores (Fig. 1). Small-scale upwelling processes often occur because of the prevailing winds and coastal morphology, creating two distinct domains within the study area: west of the isthmus is affected by cold waters (mean annual temperature approximately 18 °C), and the eastern side has comparatively higher mean water temperatures (approximately 23 °C; Valentin 1984). Furthermore, the geography of the area is such that reefs on the western side are generally more wave exposed than those on the eastern side because the latter receives more shelter from prevailing winds. All surveys were conducted between January and May 2011 at eight sites (Fig. 1), with four located on each side of the isthmus. Maximum depths of the sites ranged from 6 to 15 m at sites 1–4, and from 6 to 25 m at sites 5–8. All sites were characterized by a high cover of an epilithic algal matrix (>40 %) and lower cover of crustose coralline algae (~5 %). Sites to the west of the isthmus had higher macroalgal cover (21 %) and lower sessile invertebrate cover (4 %) when compared to eastern sites (8 and 17 %, respectively) (Online Resource Fig 1s).

Sea urchin surveys

Sea urchin assemblages were evaluated at each site by recording the density of individuals present in 40 quadrats (50 × 50 cm) replicated at each 1-m-depth contour, which started from the mean level of neap low tide and extended to the interface of the rocky reef with non-consolidated substratum (i.e., the base of the reef). All quadrats in each depth contour were placed at random, keeping at least 1 m among replicates. The randomized placement of quadrats in each depth contour also avoided spatial dependency across depth gradients as surveys on adjacent depth contours did not start and stop in the same locations. All sea urchins observed were identified and counted in three size classes (<2, 2–5 and >5 cm). Size was considered as the maximum diameter of the test without spines. The smaller size category used in the analyses was defined based on the approximate size of maturity for *Echinometra lucunter*
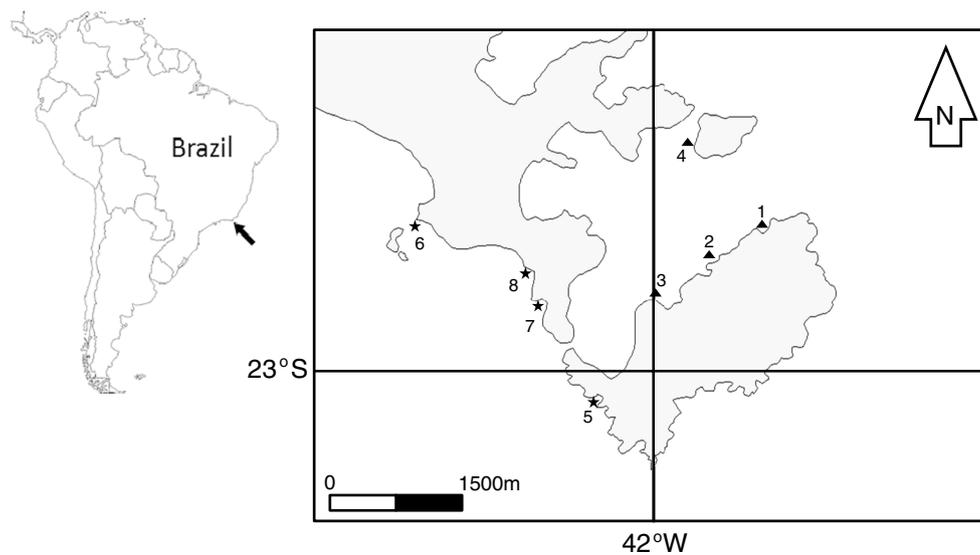
Fig. 1 Map of the Arraial do Cabo region (Rio de Janeiro, Brazil) indicating sampled sites. The maximum depth of each area is shown in parentheses after the site name: 1—Anequim (10 m), 2—Abobrinha (8 m), 3—Maramutá (6 m), 4—Ilha dos Porcos (15 m), 5—Ingleses (25 m), 6—Franceses (6 m), 7—Sometudo (15 m), 8—Sonar (7 m). Sites 5–8 are influenced by cold upwelling water. *Source* NOAA/GSHHG 2.2.2

(Lima et al. 2009) and *Arbacia lixula* (Wangensteen et al. 2013). The size of maturity for *Paracentrotus gaimardi* is not known, but data for *P. lividus* (Spirlet et al. 1998) indicate that maturity occurs at approximately the same size as in *E. lucunter* and *A. lixula* (i.e., approximately 2 cm).

Abiotic factors

The number of crevices (substrate complexity) was evaluated at each site using replicated video-transects (10 min long) positioned at the same depth intervals used for sea urchin surveys. Videos were taken with a digital HD video camera (Sony HF G10 with Light & Motion Bluefin underwater housing) at a fixed distance of 0.6 m from the substrate (field of view = 0.5×0.5 m). Subsequently, fifteen random frames were extracted from the footage and analyzed with CPCe software (Kohler and Gill 2006) to count the number of crevices per 0.25 m^2. Crevices were defined as any cracks or gaps in rocks or among boulders that were wider than 1 cm and provided a potential shelter for sea urchins. It was not possible to measure the deepness of crevices from the video, but it was assumed that each crevice was at least as deep as it was wide (i.e., minimum size was 1 cm wide by 1 cm deep), and hence at least represented shelter to most juvenile sea urchins.

Wave exposure at each site was calculated using linear wave theory (see full details in Harborne et al. 2006) in order to quantify the differences in exposure on both sides of the isthmus. Briefly, online wind data archives (BDMEP 2013) from a land-based meteorological station located at Arraial do Cabo were analyzed to calculate the mean wind speed in eight 45° segments and the proportion of time the wind blew from within each segment. These data were then combined using linear wave equations with depth values and fetch distances in each of the eight directions to calculate wave exposure for each site (see Online Resource for details).

Sea urchin biomass estimates

Values of biomass were estimated based on size–weight relationships computed using data from the locally most abundant sea urchin species (*A. lixula*, *E. lucunter*, and *P. gaimardi*) (see Online Resource for full details). Sea urchins from a wide range of sizes were collected at different depths from the survey sites ($n = 200$ for each species). The individuals were placed on trays for 5 min in order to drain excess water, then weighed and measured. All specimens were then returned to the collection location. Values of biomass and diameter were log-transformed and analyzed with linear regression to establish the relationship between the variables. The values obtained were applied to calculate biomass values from sea urchin densities. Since sea urchins were grouped into three size classes, the conversion to biomass values was achieved by multiplying sea urchins densities for each size class by the weight of a sea urchin representing the midpoint of the size class (i.e., 1.5, 3.5, and 5.5 cm assuming a typical maximum size of 6 cm). The values for the three size categories were summed to generate total sea urchin biomass.

Potential predator abundances

In order to assess the abundance of potential predators of sea urchins at each site, fishes were counted along underwater visual census transects (20 × 2 m) distributed across the depth profile. Eight to twelve transects were surveyed at each site. Fishes observed within the transect were recorded and grouped according to their species and length (10-cm-interval size classes), and their biomasses were calculated following length–weight relationships (e.g., Froese and Pauly, 2013). As there are few comprehensive data on the identity of sea urchin predators in Brazil, the classification of species as potential predators was based on a combination of literature from other locations (McClanahan 1995, 1998) and data on the diet of species found locally (Froese and Pauly 2013). The species considered here as potential predators are members of the families Diodontidade (*Chilomycterus spinosus*, *Diodon hystrix*, *D. holacanthus*), Tetraodontidae (*Sphoeroides spengleri*), Monachantidae (*Stephanolepis hispidus*), Sparidae (*Diplodus argenteus*), and Labridae (*Bodianus pulchellus*, *B. rufus*, *Halichoeres poeyi*).

Data analysis

The east and west sides of the isthmus represent significant differences in two major abiotic factors, with cold water upwelling and high wave exposure to the west, and warmer, calmer water to the east. For example, wave exposure analysis indicated that western sites are 120 times more wave exposed than eastern sites (see Online Resource). Consequently, large-scale temperature and exposure gradients, both of which can have important influences on sea urchin assemblages, covary within the study area, and their relative importance cannot be distinguished. Therefore, the combined influence of these natural gradients was represented in the analyses as a categorical variable named 'location' (east or west). Any significant influences of this location variable are subsequently interpreted as being caused by changes in temperature and/or wave exposure.

Densities of the three size classes and total biomass of each sea urchin species were analyzed using linear mixed-effects models (LMMs). The fixed factors for the sea urchin models were continuous estimates of depth, number of crevices, predator biomass, and the categorical factor 'location.' However, because of their rarity within the study area, the mean abundance of predators was first tested using ANOVA of the log-transformed biomass values, using location (east/west) and site as fixed factors. This analysis aimed to establish whether there were any significant differences within the study area. The LMMs also included interaction terms between all fixed factors. Since surveys from multiple depths were conducted at each site, site

was included as a random factor. Data analysis was done using R software (R Development Core Team 2008) and the package nlme (Pinheiro et al. 2013). Colinearity among predictive variables was checked by calculating Pearson's index of correlation, and normalization procedures (log transformation) were applied to variables prior to analyses to reduce kurtosis. The model selection was based on best-fit with stepwise selection and the Akaike information criteria using the drop1 function (MASS library, Venables and Ripley 2002). Significant interactions among factors were analyzed for each pair of interacting factors using predictions for the dependent variable based on best-fit models (see Online Resource for details of interaction analyses).

Results

Abiotic variables and potential predators

The number of crevices across all depths and sites was higher at eastern sites (mean ± SE = 2.3 ± 0.2 crevices 0.25 m^{-2}, $n = 540$) than at western sites (mean ± SE = 1.0 ± 0.1 crevices 0.25 m^{-2}, $n = 795$).

Diplodus argenteus was the dominant species (70.4 % of total biomass) among potential predators, followed by *S. hispidus* (9.2 %) (Online Resource Fig 2s). The mean biomass of potential predators was slightly higher at eastern (1–4; mean ± SE = 1,332.38 ± 219.82 g 40 m^{-2}, $n = 89$) than at western sites (5–8; mean ± SE = 1,062.36 ± 118.61 g 40 m^{-2}, $n = 83$), but differences were not significant between locations (ANOVA, $F_{(1,163)} = 1.5$, $p = 0.22$) or among sites (ANOVA, $F_{(5,163)} = 1.96$, $p = 0.07$). In order to avoid spurious correlations, limit the number of variables compared to the number of sites surveyed and following the parsimony principle, the biomass of potential predators was therefore not included as a variable in the LMMs, because there was no significant variation at the spatial scales examined (location and site).

Sea urchin distributions

Seven sea urchin species were found at the survey sites, consisting of 42,497 individuals. *P. gaimardi* represented 70.7 % of the total abundance. *E. lucunter* was the second most abundant species (27.3 % of individuals), followed by *A. lixula* (1.7 %), *Lytechinus variegatus* (0.002 %), *Eucidaris tribuloides* (<0.01 %), *Tripneustes ventricosus* (<0.01 %), and *Diadema antillarum* (<0.01 %). Since *L. variegatus* (104 individuals), *E. tribuloides* (17), *T. ventricosus* (17), and *D. antillarum* (1) were found at very low abundances, they were not included in subsequent analyses.

Paracentrotus gaimardi was the most abundant species, both at eastern and western sites (Fig. 2a). Smaller

individuals (<2 cm) were common and contributed to more than 60 % of the total abundance. Larger individuals (2–5 and >5 cm) were found across all depths and were more abundant at western sites, and this is reflected in the higher biomass values at these sites (Fig. 2a). The results of the LMM indicated qualitatively similar models for the densities of individuals in the first two size classes of this species, with significant negative correlations with increasing depth (Table 1). The density of the largest individuals was not significantly correlated with depth, but total biomass decreased with increasing depth. Although densities were higher at western sites, location was a significant factor

only within the best-fitting LMM for urchins sized 2–5 cm (Fig. 2a; Table 1). The density of all size classes and the biomass of *P. gaimardi* were positively correlated with the number of crevices (Tables 1, 2; Fig. 2b). The number of crevices also had a significant interaction with location for larger sized individuals (Table 1) indicating that the availability of shelter was more important at western sites (Online Resource Fig 7s).

Echinometra lucunter was the second most abundant species in this study and was found in significantly higher densities at eastern sites (Fig. 3a; Table 1). The density and biomass of *E. lucunter* were significantly negatively
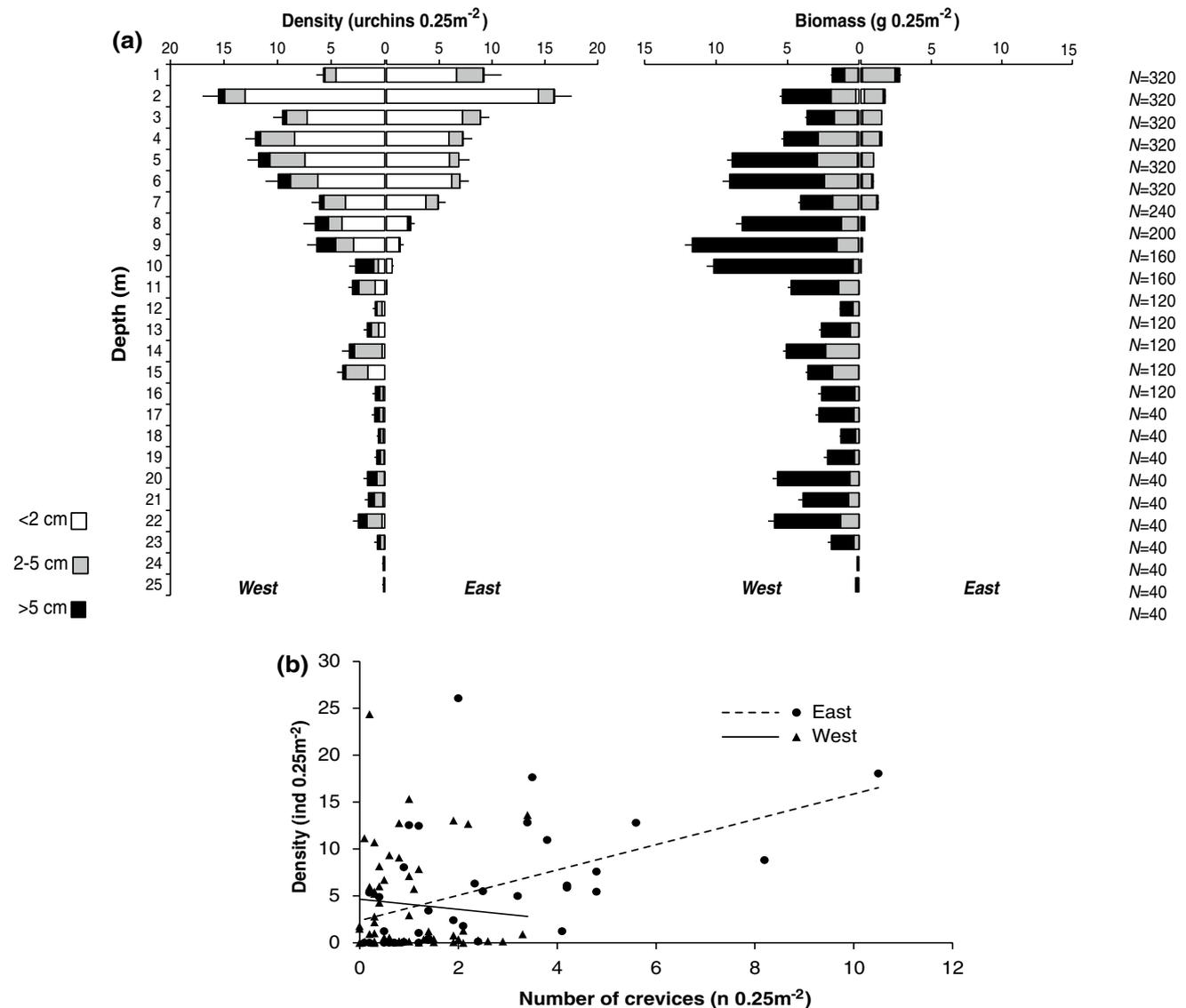

Fig. 2 *Paracentrotus gaimardi*: **a** density and biomass (mean ± SE) according to size classes on both the east and west of the isthmus and across depth profiles. The number of replicates across all eight sites at each depth is indicated on the *right side* of the figure. **b** *Scatter plots* of density of individuals <2 cm and number of crevices (crev-

ices 0.25 m^{-2}) at eastern and western sites. *Regression lines* are only indicative of the relationships within the minimal adequate linear mixed-effects models, which include multiple explanatory variables, interaction terms, and random effects, and are provided to aid visualization of the bivariate trends

Table 1 Minimal adequate linear mixed-effects models (fixed effects only) for the densities of the three most abundant sea urchin species

Variables	Paracentrotus gaimardi						Echinometra lucunter						Arbacia lixula					
	<2 cm		2–5 cm		>5 cm		<2 cm		2–5 cm		>5 cm		<2 cm		2–5 cm		>5 cm	
	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value	Coeff.	p value
Depth (D)	−0.78	<0.001	−0.14	0.024	–	–	−0.48	<0.001	−0.15	<0.001	−0.16	0.002	–	–	–	–	–	–
Location—east (L)	–	–	−0.28	0.049	−0.09	0.15	0.89	<0.001	0.50	<0.001	0.61	<0.001	na	na	na	na	na	na
Crevices (C)	0.80	<0.001	0.49	<0.001	0.31	0.005	–	–	–	–	–	–	–	–	–	–	0.19	<0.001
D × L	–	–	–	–	–	–	−0.75	<0.001	−0.51	<0.001	−0.63	<0.001	na	na	na	na	na	na
D × C	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
L × C	–	–	–	–	−0.32	0.007	–	–	–	–	–	–	na	na	na	na	na	na
D × L × C	–	–	–	–	–	–	–	–	–	–	–	–	na	na	na	na	na	na

na not applicable

×: interaction term, –: non-significant term ($p > 0.050$)

correlated with depth (Tables 1, 2). The total density of all size classes and biomass was significantly positively correlated with the number of crevices (Tables 1, 2; Fig. 3b). The model for the density of all size classes of *E. lucunter* also contained a significant interaction term between depth and location. These interactions had the same pattern and indicated that location had a higher negative influence on density at shallow depths than in deeper water (Online Resource Fig 8s to 10s).

Only the data from western sites were used in the LMM analysis of *A. lixula*, since this species was found in <1 % of samples at eastern sites, leading to a highly right-skewed data distribution that was inappropriate for the assumptions of the LMM analyses. Similarly, the smaller size class (<2 cm) of this species only occurred in <1 % of samples and was not included in further analyses. Larger individuals of *A. lixula* (>5 cm) contributed to 65 % of the total abundance of this species at western sites. The highest density of these larger urchins and total biomass of *A. lixula* were observed at intermediate depths (Fig. 4a). A quadratic depth term was tested in the LMMs for the biomass and density values to account for this apparent pattern, but it was not significant and was removed during model selection. The density of individuals with intermediate size (2–5 cm) was not significantly correlated with any of the tested factors (Table 1). The mean density of larger individuals was positively correlated with the number of crevices (Table 1; Fig. 4b), and the biomass of *A. lixula* had a marginally significant positive correlation with number of crevices (Tables 1, 2).

Discussion

The three dominant sea urchin species reported in this study are common components of subtidal communities along the tropical and subtropical coast of Brazil (Sanchez-Jerez et al. 2001). However, the patterns and drivers of their abundance and distribution have not previously been described in detail, despite *P. gaimardi* and *A. lixula* having a broad, amphi-Atlantic distribution (Lessios 2010; Lessios et al. 2012). This study has demonstrated significant differences in how sea urchin species are distributed across physical gradients. In general, depth and location were important factors for all three species, having species-specific effects on densities and biomass. Species abundances typically decreased with increasing depth, and this could be because of a multitude of reasons. Depth directly influences light, sedimentation, nutrient concentration, hydrodynamics, and temperature. For example, wave exposure decreases with increasing depth, which creates variation in wave-induced turbulent fluxes (Ortega-Borges et al. 2009), affecting the spatial distribution of sea urchins as a selective

Table 2 Minimal adequate linear mixed-effects models (fixed effects only) for the total biomass of the three most abundant sea urchin species

Variables	Paracentrotus gaimardi		Echinometra lucunter		Arbacia lixula	
	Coeff.	p value	Coeff.	p value	Coeff.	p value
Depth (D)	−0.37	0.003	−1.28	0.000	–	–
Location—east (L)	–	–	–	–	na	na
Crevices (C)	0.77	0.002	0.678	0.025	0.358	0.058
D × L	–	–	–	–	na	na
D × C	–	–	–	–	–	–
L × C	–	–	–	–	na	na
D × L × C	–	–	–	–	na	na

na not applicable

×: interaction term, –: non-significant term ($p > 0.050$)

force according to adhesion power (Tuya et al. 2007). Turbulent fluxes can also influence sea urchin recruitment rates by hindering or preventing larvae from settling (Hereu et al. 2004). The factors correlated with depth also affect algal growth and the strength of biotic interactions, and consequently determine the suitability of microhabitats for species along this vertical axis (Garrabou et al. 2002). Thus, depth can produce species-specific variability in sea urchin distribution patterns according to the availability of resources and the physiological tolerance of individual species (Clemente and Hernández 2008), constraining less-tolerant species to less-suitable microhabitats.

The geographical characteristics of Arraial do Cabo leads to a strong discontinuity in physical conditions to the east and west of the isthmus. For example, wind-driven upwelling events cause cooler waters to the west of the isthmus, which also has higher wave energy (Valentin 1984). This natural gradient was represented here by the factor 'location,' and we can only speculate on the relative importance of exposure and temperature in our data set. In spite of mean annual temperatures being an important factor characterizing the eastern and western sites, lower temperatures can also affect the eastern sites during upwelling events (Valentin et al. 1987; Coelho-Souza et al. 2012). Furthermore, although lower temperatures could affect the larval development, recruitment, and settlement of sea urchin species (e.g., Miller and Emlet 1999; Gianguzza et al. 2011), the studied species are present on both sites of the isthmus. In addition, *E. lucunter*, *A. lixula*, and *P. gaimardi* have latitudinal distributions extending to regions with mean temperatures lower than those observed in Arraial do Cabo (e.g., Florianópolis, Brazil; CAMMC, personal observation). This may indicate that temperature is potentially acting as a modulating factor, rather than a limiting factor, for sea urchin distributions, but further studies are required to distinguish how wave exposure and temperature are affecting sea urchin abundances in the area.

The number of crevices was positively correlated to at least one abundance metric of each species. Number of crevices is a measure of substrate complexity, which has been reported as enhancing grazing rates (Clemente and

Hernández 2008) and survival of recruits (Hereu et al. 2004). Both of these factors directly influence the distributional patterns of sea urchins (Clemente and Hernández 2008). Furthermore, the availability of shelter provided by complexity reduces predation rates (Guidetti and Dulcic 2007) and can cause aggregations of some sea urchin populations (Andrew 1993), both of which could be important additional drivers of the observed positive relationships between complexity and sea urchin densities.

Paracentrotus gaimardi was dominant on both sides of the isthmus and across all depths, indicating its high adaptability and plasticity. However, at a larger geographical scale, *P. gaimardi* is considered vulnerable by Brazilian environmental authorities, mainly due to its restricted distribution on the southeastern and south coast (Calderón et al. 2009). Within the study area, populations of this species was mainly composed of small individuals (<2 cm), which are not usually included in most surveys because of problems with density fluctuations attributed to unpredictable recruitment events (Cameron and Schroeter 1980). Despite the negligible biomass of the smallest size classes of *P. gaimardi* (<1 % of the total), the high densities of juveniles (>60 % of total) indicate the importance of including this demographic category in population studies. Furthermore, small individuals are clearly important in local food webs due to the naturally high mortality rates of this size class (Hereu et al. 2004; Uthicke et al. 2009), coupled with the fact that they constitute part of the diet of several predators (Clemente et al. 2009). However, their potential impact on benthic assemblages is likely to be low because grazing is generally strongly correlated with biomass. Similarly, the relative contribution of *P. gaimardi* to grazing pressure in Arraial do Cabo is likely to be greater at sites on the western side of the isthmus where larger individuals are more abundant.

The ecological importance of *E. lucunter* remains understudied, even though it is the most common sea urchin species on Brazilian tropical and subtropical reefs (Calderón et al. 2007). As already described for other species of the same genus (McClanahan and Muthiga 2007), *E. lucunter* is commonly found in high densities at depths shallower
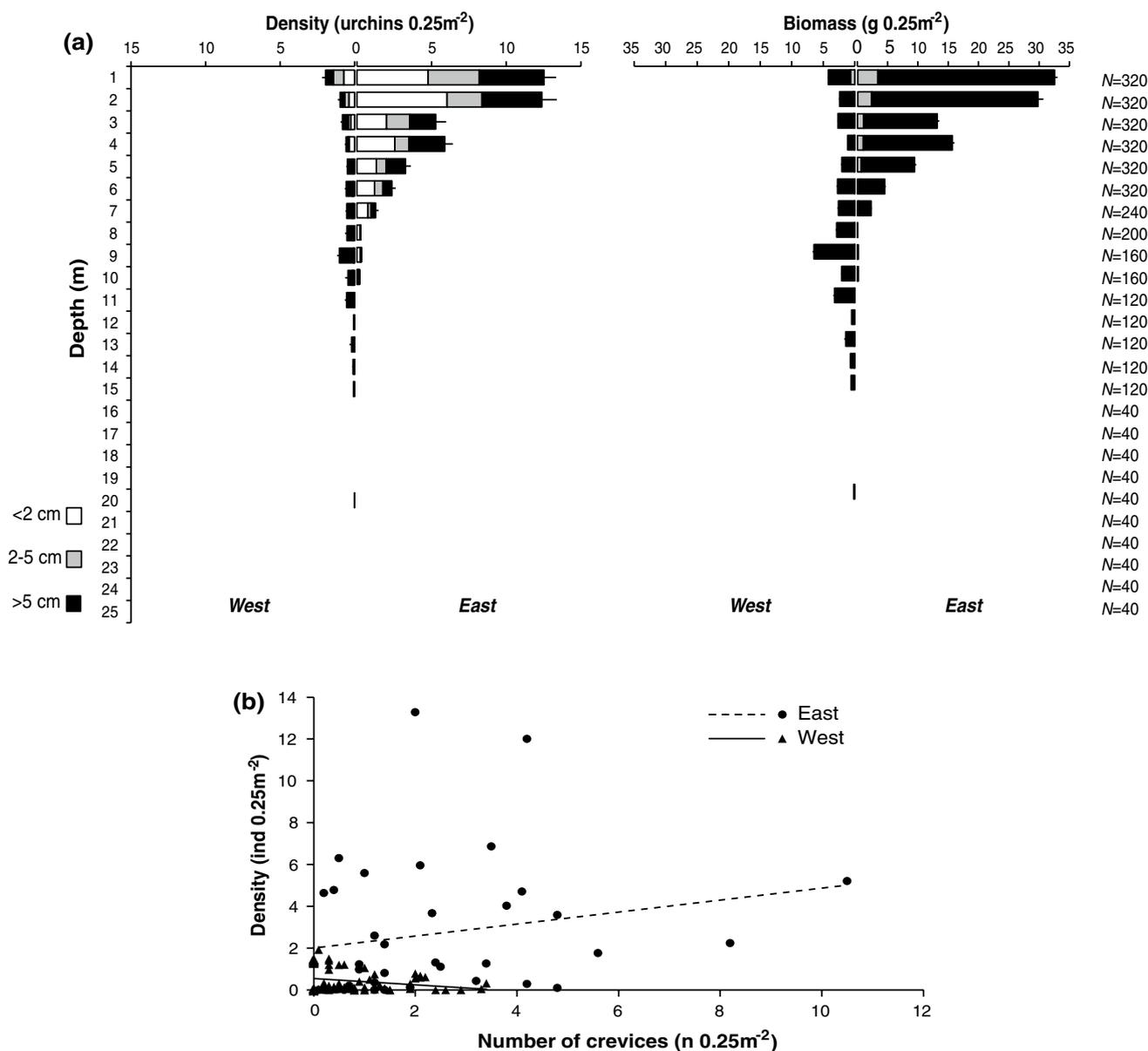
Fig. 3 *Echinometra lucunter:* **a** density and biomass (mean ± SE) according to size classes on both the east and west the isthmus and across depth profiles. The number of replicates across all eight sites at each depth is indicated on the *right side* of the figure. **b** *Scatter plots* of density of individuals <2 cm and number of crevices (crev-ices 0.25 m⁻²) at eastern and western sites. *Regression lines* are only indicative of the relationships within the minimal adequate linear mixed-effects models, which include multiple explanatory variables, interaction terms, and random effects, and are provided to aid visualization of the bivariate trends

than approximately 10 m. This pattern was observed in Arraial do Cabo and was reflected in the negative correlation between density and depth for all size classes and for total biomass. The high abundances in shallow waters may reflect adaptive advantages conferred by the species' resistance to environmental stress as compared to sympatric species (Lawrence 2013), allowing it to occupy the shallowest reef areas that normally have a high cover of fast-growing algae (Witman and Dayton 2001). However, further research into the behavioral and morphological features of

E. lucunter is needed to elucidate the nature of the mechanisms that confer such advantages in these environments.

Arbacia lixula is considered crucial in barren habitat maintenance in the Mediterranean Sea (Agnetta et al. 2013). This species is a subject of concern due to its range expansion because of its affinity for warm waters, which may threaten the balance of benthic communities (Gianguzza et al. 2011). Along the Mediterranean coast, *A. lixula* can be the dominant species in shallow areas with high wave exposure (Tuya et al. 2007), and this is reflected in
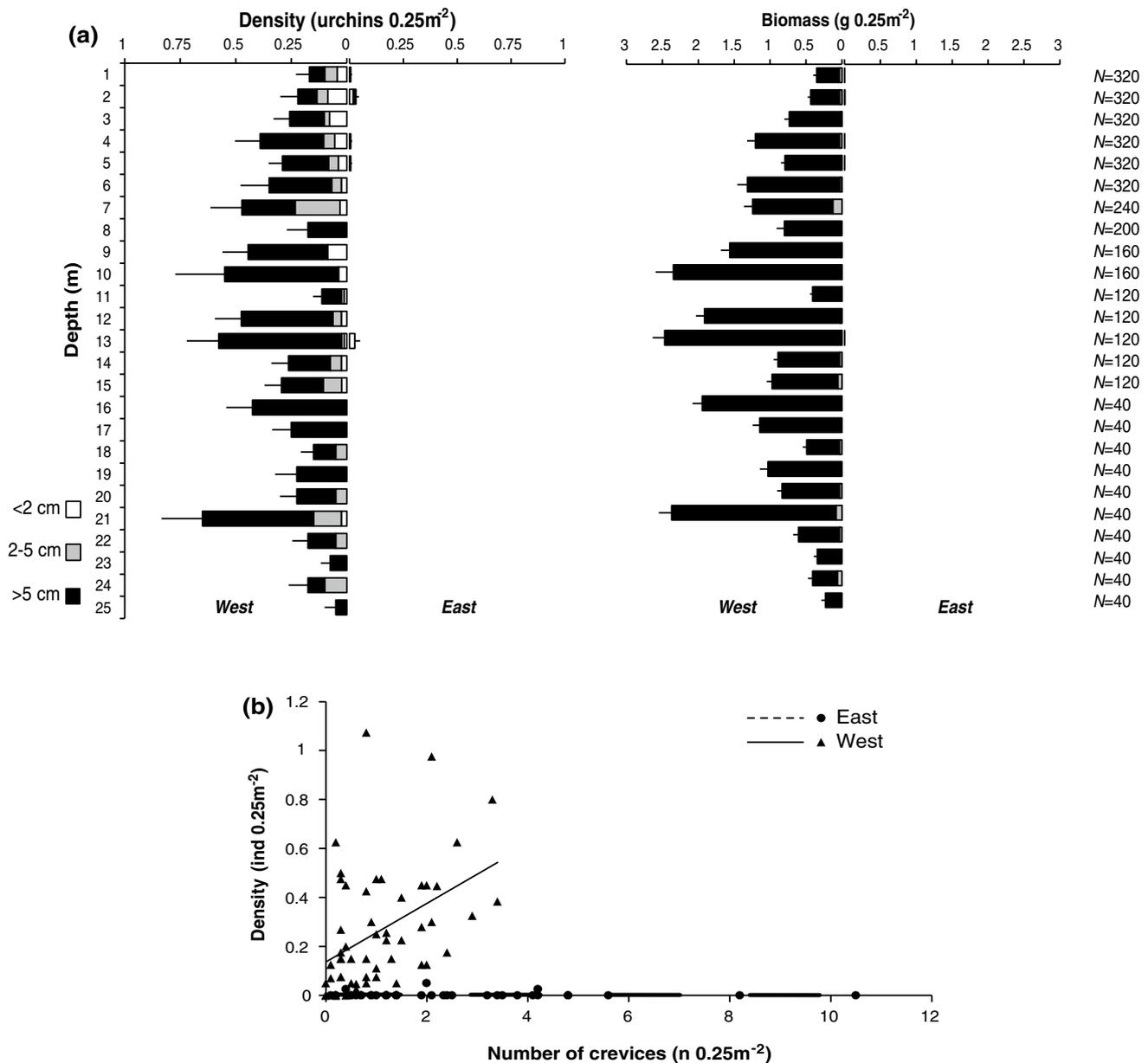
Fig. 4 *Arbacia lixula:* **a** density and biomass (mean ± SE) according to size classes on both the east and west of the isthmus and across depth profiles. The number of replicates across all eight sites at each depth is indicated on the *right side* of the figure. **b** *Scatter plots* of density of individuals >5 cm and number of crevices (crev- ices 0.25 m^{-2}) at eastern and western sites. *Regression lines* are only indicative of the relationships within the minimal adequate linear mixed-effects models, which include multiple explanatory variables, interaction terms, and random effects, and are provided to aid visuali- zation of the bivariate trends

Brazil by the higher densities at western sites in Arraial do Cabo. The preference of this species for more wave-exposed sites may be related to the adhesion strength it possesses for attaching to rocks (Tuya et al. 2007). The formation of aggregations with interlocked spines could also provide increased benthic adhesion under conditions of high wave exposure (Tuya et al. 2007), and this behav- ior was observed in this study (CAMMC, personal obser- vation). However, despite being able to deal with more

energetic habitats, *A. lixula* was less abundant than *P. gaimardi* or *E. lucunter* at all sites. In a recent study, Gian- guzza et al. (2011) demonstrated that larvae of *A. lixula* had higher survival rates at increased temperatures (22–26 °C). The western sites of Arraial do Cabo are affected by cold upwelling events (Valentin 1984), but despite the appar- ently preferable temperatures for larvae at eastern sites, only a few individuals <2 cm of this species were found on either side of the isthmus. Thus, the lower abundance of

A. lixula at all sites is more likely to be related to competitive exclusion by other sea urchins, resulting in this species being restricted to toward marginal, high-exposure habitats.

Sea urchin species can coexist in the same area, because the niche of each species may vary according to food preferences, type of foraging, and morphological adaptations (McClanahan 1988; Bonaviri et al. 2011). However, sympatric sea urchin species are usually considered as belonging to the same trophic guild (Entrambasaguas et al. 2008), and so there are likely to be at least some competitive interactions. The clear dominance of *E. lucunter* at eastern sites may be attributed to behavioral and foraging characteristics. Despite not being witnessed during our surveys, McClanahan and Muthiga (2007) observed that some *Echinometra* species exhibit aggressive behavior toward sympatric species when competing for shelter. Furthermore, Boudouresque and Yoneshigue (1983) analyzed the diet of *P. gaimardi* and *E. lucunter* at both sides of the isthmus in Arraial do Cabo, and observed that these species feed on different food sources at eastern sites, but have the same diet at western sites. Potentially, aggressive behavior toward *P. gaimardi* could provide *E. lucunter* with a competitive advantage at eastern sites, preventing the subordinate species accessing some environmental resources, such as shelter and more energy-rich food sources. Conversely, as *P. gaimardi* is better adapted to high wave exposure and low-temperature conditions, it may be able to compete more successfully with *E. lucunter* for the same food sources at western sites.

Previous studies have demonstrated that both *A. lixula* and *P. lividus* can coexist even at relatively high densities in the Mediterranean due to non-overlapping feeding preferences (Privitera et al. 2008; Bonaviri et al. 2011). Despite the lack of information on interspecific diet differences among Brazilian species, *A. lixula* and *P. gaimardi* could have a similar coupled ecological function on barren formation on southwestern Atlantic rocky shores, based on similarities of distributional patterns (Bulleri et al. 1999). Similar to the observations about their conspecifics in the Mediterranean (Bonaviri et al. 2011), the density and biomass of *P. gaimardi* in Brazil are typically greater than those of *A. lixula*. This could imply that in Arraial do Cabo *P. gaimardi* is the primary grazer at western sites, while *A. lixula* has a secondary role.

In addition to interspecies competition, the presence of predators is a common biotic variable considered in the study of sea urchin populations (e.g., McClanahan 1995, 1998; Guidetti and Dulcic 2007). In this study, the biomass of potential predators was relatively low, and not significantly different across the sites surveyed, suggesting that the presence of this trophic group has little or no influence on sea urchins in Arraial do Cabo. The region has been intensively fished for a long period (Floeter et al. 2006), and the functional role of predators appears to have been significantly reduced. On reefs where predator densities are higher, they have an important influence on sea urchin dynamics (e.g., McClanahan 1998), and this functional role could potentially be restored in protected areas in Arraial do Cabo.

This study highlights that three coexisting sea urchin species have related, but different, abiotic and biotic controls of their distribution at a relatively small spatial scale. This partial segregation of species suggests differences within the assemblage of grazers on either side of the isthmus, which is an important consideration for analyses of ecological processes in the area. For example, many reef areas have been facing serious declines in roving herbivore fish populations (Hughes et al. 2007b; Comeros-Raynal et al. 2012), and Brazilian waters are no exception (Francini-Filho et al. 2010; Bender et al. 2012). Therefore, it is crucial to fully understand the ecology of sea urchins because they are now the major herbivores in some habitats. For example, the results of this study suggest that there is a higher impact of sea urchin grazing on benthic dynamics in shallow reefs to the east of the isthmus. However, in situ estimates of grazing pressure for sea urchin species and other herbivore groups would help to clarify the patterns and drivers of this important ecosystem process across spatial and physical gradients. Furthermore, as important grazers, sea urchins are a key target for conservation initiatives. Such initiatives are likely to include monitoring of sea urchin populations, and our data clearly demonstrate the importance of stratifying monitoring across key physical gradients, such as depth and exposure. For example, environmental change may have very different effects to the east and west of the isthmus at Arraial do Cabo because of the natural variation in physical conditions and sea urchin assemblages. Perhaps even more importantly, a greater understanding is needed of how biotic and abiotic variables, including sea urchin distributions, physical gradients, and anthropogenic stressors, shape the composition of benthic assemblages in the region.

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