Echinoid community structure and rates of herbivory and bioerosion on exposed and sheltered reefs

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A B S T R A C T

Echinoid–habitat relations are complex and bi-directional. Echinoid community structure is affected by the habitat structural and environmental conditions; while at the same time, echinoids may also act as ‘reef engineers’, able to alter marine environments on a wide geographic scale. In particular, echinoids play a major role in bioerosion and herbivory on coral reefs. Through feeding, echinoids reduce algal cover, enabling settlement and coral growth. However, at the same time, they also remove large parts of the reef hard substrata, gradually leading to reef degradation. Here, we compared coral and macroalgal abundance, echinoid community structure and species-specific rates of echinoid herbivory and bioerosion on reefs subjected to different intensities of oceanic exposure. Spatio-temporal variations in coral and macroalgal cover were monitored, and populations of the four most abundant echinoid species on the coral reefs of Zanzibar – Diadema setosum (Leske), D. savignyi (Michelin), Echinometra mathaei (de Blainville) and Echinolithus diadema (Linnaeus) – were compared between the Island’s eastern exposed reefs and western sheltered ones. To account for the effect of management in the context of reef exposure, we included marine protected areas (MPAs) of both types of reef categories (i.e. sheltered and exposed) in our comparison. Coral and macroalgal cover presented a conspicuous contrasting pattern across exposed and sheltered sites. While coral dominance and lack of macroalgae were prominent on sheltered reefs, an opposite trend of low coral cover and moderate–high macroalgal cover were found on exposed reefs. Bioerosion was also significantly higher on exposed reefs than on sheltered ones (4.2–13 and 1.2–3.9 kg CaCO₃ m⁻² year⁻¹, respectively). The highest rates, recorded on Pongwe, with almost 7 kg CaCO₃ m⁻² year⁻¹, are among the highest echinoid bioerosion rates known to date. Management had a substantial effect on habitat and echinoid community structure, as coral cover was significantly higher, macroalgal cover lower, and echinoid densities generally reduced on MPAs regardless of exposure intensity. Our findings suggest that exposed reefs are susceptible to markedly higher degrees of echinoid bioerosion; however, adequate management measures can significantly reduce these rates, consequently altering the reef’s trajectory for degradation.

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1. Introduction

Common coral-reef associated echinoids have a range of different feeding modes. Echinoids are considered to be generalist herbivores as their diets may include algae and seaweed (Klumpp et al., 1993; Lawrence, 1975; Vaililingon et al., 2003), or omnivores due to the inclusion of animal tissue (Briscoe and Sebens, 1988; McClintock et al., 1982), and even the occasional predation of live coral tissue (Bak and van Eys, 1975; Carpenter, 1981; Glynn et al., 1979). This dietary flexibility, coupled with their great abundance on some coral reefs (Bauer, 1980; McClanahan and Kurtis, 1991), place echinoids as keystone species in coral reef environments. As hard-substrate eroders (Bak, 1990; Glynn et al., 1979; Hunter, 1977; Trudgill et al., 1987) they scrape the surface while grazing (Lawrence and Sammarco, 1982), reducing algal cover (Mapstone et al., 2007) and breaking down reef substratum (Bak, 1990; Hawkins and Lewis, 1982). At moderate sea urchin densities this action may facilitate a topographic complexity that favors increased biodiversity (Johnson et al., 2003) and may also enhance coral recruitment (Birkeland and Randall, 1981; Carpenter and Edmunds, 2006; Griffin et al., 2003). However, at high sea urchin densities, echinoids may limit reef growth through predation of coral tissue (Glynn et al., 1979) or extensive coral (Bak et al., 1984; Mokady et al., 1996) and crus- tose coralline algae (CCA) erosion (O’Leary and McClanahan, 2010). Moreover, the indiscriminate nature of echinoid grazing has a profound effect on coral community composition through its control of newly-settled coral spat (Sammarco, 1980, 1982). Consequently, high sea urchin abundance may alter the structure of coral reef communities by eroding the reef’s coral framework, leading to gradual reef degradation.

Many variables have been recognized as important in regulating echinoid food consumption. For example, species composition, body size, population densities (Bak, 1990, 1994; Carreiro-Silva and McClanahan, 2001; Scoffin et al., 1980), attraction to food (Vadas and Elner, 2003), hydrodynamics (Siddon and Witman, 2003), light (Mills...
et al., 2000; Vaitilingon et al., 2003), temperature (Larson et al., 1980), and reproductive stage (Klinger et al., 1997), have all been mentioned as factors influencing echinoid feeding rates and ecological impact. However, beyond the physiological aspects determined by the life histories of particular species, echinoid food consumption, and consequently the rates of herbivory and bioerosion, must be considered in terms of the environmental conditions that exist in their habitats, as gradients in the physical environment may produce variability in the abundance and distribution of echinoid populations (Andrew, 1993; Clemente and Hernández, 2008). Several studies have investigated the relationship between coral reef associated echinoids and their habitat (e.g., Dumas et al., 2007; Graham and Nash, 2013; McClanahan, 1998; McClanahan and Kurtis, 1991; O’leary and McClanahan, 2010; Peyrot-Clausade et al., 2000). These publications suggest aspects such as structural complexity, macroalgal and coral cover, sedimentation, and the presence or absence of predators, as having substantial effects on the composition, distribution, and size of related echinoid populations. For example, marine protected areas (MPAs) protecting various echinoid predators consequently present lower rates of sea urchins compared to reefs with depauperate predatory populations (McClanahan and Kurtis, 1991; McClanahan et al., 1999). Additionally, echinoid communities tend to display strong differences in species distribution between exposed and sheltered reefs, making sea urchin ecology further complex (Dumas et al., 2007).

Zanzibar Island (Unguja, Tanzania) is situated on the continental shelf of Tanzania between 50°40′ and 60°30′ south of the equator, 35 km from the mainland. Being an island surrounded by coral reefs, exposed to strong eastern winds and with a sheltered west coast, makes Zanzibar an ideal study location for echinoid ecology. Located off the East-African shoreline, the island’s coral reefs are fundamental to the entire marine environment and of great economic importance for the large human population that depends on them for a livelihood (Jiddawi, 1997; Khatib, 1997; Mbijje et al., 2002; Ngoile and Horrill, 1993). Small patches of mangrove forest and shallow patches of fringing reefs occur along the more sheltered western coast, while on the more exposed eastern coast fringing reefs slope up to a narrow coastal lagoon backed by sand beaches or fossil coral cliffs (Richmond, 2002). The eastern and western sides of the island are subject to markedly different wave and current intensities; reefs on the eastern ocean-facing side are exposed to the Indian Ocean (IO) and are susceptible to strong waves and currents, while reefs in the Zanzibar channel, on the island’s western side, are sheltered from direct exposure to the IO (Bergman and Öhman, 2001; Ngoile, 1990). Swell waves generated in the IO can travel undisturbed for thousands of miles before hitting the Island’s eastern reefs. These swell waves occur off the east coast of Zanzibar for much of the year, changing their orientation from north-east (between October and March) to south-east (between March and October) depending on monsoonal season (McClanahan, 1988b; Zanzibar Department of Environment and MACEMP, 2009). In contrast to the north-east monsoon, the south-east monsoon is characterized by high cloud cover, rain, high wind energy, decreased temperatures and light, and rougher seas, with velocities of the East African Coastal Current (EACC) increasing to a speed of four knots (McClanahan, 1988b). The semi-diurnal tides have mean spring amplitude of 3.3 m, with associated tidal currents being stronger on the east coast, where currents up to three knots are common (Bergman and Öhman, 2001).

Here, we studied coral and macroalgal cover, echinoid community structure and associated rates of herbivory and bioerosion on exposed and sheltered coral reefs. The following hypotheses were tested: (1) Coral and macroalgal cover vary between exposed and sheltered reefs. (2) Echinoid community structure, and consequently the intensity of echinoid-induced bioerosion, are influenced by the degree of oceanic exposure (e.g., the exposure to higher intensities of waves, currents, tides, etc.). (3) Rates of echinoid herbivory and bioerosion on marine-protected areas are lower than on unprotected sites. Finally, we present data on spatio-temporal variations of coral and macroalgal cover, and a detailed account on echinoid community structure and associated rates of herbivory and bioerosion around the Island of Zanzibar, WIO.

2. Methods

2.1. Study sites

Coral communities and associated echinoid populations were studied on six reefs surrounding Zanzibar Island (Fig. 1). The sites were selected to represent sheltered and exposed reefs in terms of oceanic exposure. To test for effects of marine protected areas, MPAs from both exposure categories (i.e. sheltered and exposed) were selected. However due to the scarcity of MPAs in the region, only one such site per exposure category was available for this analysis. Three sites, Bawe (06°08.7′S; 039°08.2′E), Changu (06°06.8′S; 039°09.8′E), and Chumbe (06°16.3′S; 039°10.2′E), were selected on the sheltered western side of the main island facing the Zanzibar Channel. The site at Changu is located ca. 5.5 km from Zanzibar Town and a similar distance from the site at Bawe. Chumbe is located ca. 12 km south of Zanzibar Town, and has been a private nature reserve, developed and managed by the Chumbe Island Coral Park (CHICOP), since 1992 (Nordlund and Walther, 2010). The sites on the exposed eastern side of Zanzibar were Kiwengwa (06°00.9′S; 039°24.6′E), Pongwe (06°01.9′S; 039°25.2′E), and Mnemba (05°48.3′S; 039°21.3′E). The

Fig. 1. Map of Zanzibar showing the six study sites, Double circles indicate sites are marine-protected areas.
2.2. Coral and macroalgal cover

Three surveys were conducted between 2006 and 2008 (November 2006, March 2007, and April 2008). At each site, 12 20 × 1 m belt-transects were randomly placed to sample the composition of coral assemblages at depths of 3–5 m using SCUBA. Each belt-transect was subdivided into 20 1 × 1 m quadrats, which were photographed with a digital camera (Olympus C-5060) attached to a 1 × 1 m PVC-frame. The percentage coral and macroalgal cover was calculated from the photographs taken in the field.

2.3. Echinoid community structure

Species assemblages and densities were quantified in March 2008. Ten randomly placed belt-transects, measuring 20 × 0.5 m, were conducted at each site, at depths of 1–5 m using SCUBA. All echinoids within a transect were recorded and identified to the species level. When present, the size frequency distributions (SFD) of the dominant species (i.e. Diadema setosum, Diadema savignyi, Echinometra mathaei and Echinolatia diadema) from each site were estimated. Estimations were based on length measurements of the first 100 individuals encountered in randomly placed one square meter quadrates. The length was measured underwater to the nearest 0.5 mm as the longest axis at the ambitus, using thin blade Vernier calipers. The mean size of individuals in the population was then calculated for each species at each site.

2.4. Echinoid gut contents analysis

Individual rates of bioerosion and herbivory of the dominant sea urchin species at each site were determined in experiments conducted at the Institute of Marine Sciences (IMS) in Zanzibar City during March 2008. Throughout this study, the term ‘bioerosion’ refers to the total amount of newly eroded CaCO$_3$ from the hard reef substrate, which is largely composed of scleractinian corals and crustose coralline algae (CCA). These rates, together with species densities, were then used to estimate annual echinoid bioerosion and herbivory rates per square meter for each species at each site. The total bioerosion and herbivory rates for the entire Zanzibar region were evaluated by pooling all sites together.

Ten individuals of each species from each site were collected from the field and brought to the lab. Sampled individuals were chosen according to the mean sizes of each species at the different study sites, as determined by the size frequency distribution (SFD) estimations noted above. Collection was carried out on the reef-flats, in early morning, at a depth of 3 m, using SCUBA diving. Individual sea urchins were separately placed in sealed containers underwater to avoid loss of material during transfer. At the lab, the sea urchins were measured and weighed after being blotted for five minutes on filter paper. They were then dissected under a binocular to extract the gut wall from the gut contents. Extractions were followed by repeated rinses with distilled water. The gut contents were then analyzed in terms of organic and inorganic fractions, with the latter being further separated into calcium carbonate (CaCO$_3$) and non-soluble residue fractions (e.g. quartz grains, sponge spicules, and silt). Analysis of the organic fraction followed a modification of the ignition-loss method (Dean, 1974). The total extracted gut content was dried in a preheated oven (WTB Binder 1505) at 60 °C for 48 h (or until a stable weight was reached) and weighed with a Shimadzu AW220 analytical balance to the nearest 0.0001 g. The low drying temperature of 60 °C was necessary to minimize the loss of volatile, especially lipoid, constituents. The samples were then transferred to a furnace (Carbolite 1200 °C Ashing-plus furnace) and burned at 550 °C for 6 h in order to eliminate the organic material. After drying, the samples were weighed again. The difference in weights before and after ashing was used as a measure of the organic matter in the sea urchin's gut. The CaCO$_3$ fraction was then determined by acidic digestion of the residual material after removal of the organic matter. 1.13 N hydrochloric acid (HCl) was used to dissolve the CaCO$_3$, 0.5 g subsamples of residual ashed material were incubated for 10 min with 25 ml 1.13 N HCl. Following incubation and complete dissolution of CaCO$_3$, the solution of HCl and residual material was filtered on 0.22 µm PTFE filters (Millipore Hydrophilic Durapore Membrane disk filters), using a suction filter system. Prior to filtration the filters were dried in a pre-heated oven at 60 °C for 24 h, and weighed to obtain the filter’s dry weight. Following filtration the filters were dried as before and reweighed. The weight of the residual material retained in the filter was calculated by subtracting the filter's dry weight before filtration from the dry weight after filtration. This weight corresponds to the non-soluble residue fraction. Subtracting the weight of the non-soluble residue fraction from the total ashed weight resulted in the weight of CaCO$_3$ in the gut. The results obtained in the analysis are expressed in terms of percentage of each fraction in the sea urchin gut for each species at each site.

2.5. Estimating the rates of bioerosion and herbivory

The daily food consumption could be estimated based on two parameters: the average amount of food in the gut, and the number of hours necessary for complete gastric evacuation (Bajkov, 1935; Elliott, 1972; Elliott and Persson, 1978). The average amount of food in the gut was calculated for each species at each site as previously described. The rates of gastric evacuation for the echinoid species studied were obtained from Carreiro-Silva and McClanahan (2001). To calculate the daily ingestion rates, the average amount of food in the gut and the rates of gastric evacuation were used in an equation developed by Elliott and Persson (1978). Assuming an exponential rate of gastric evacuation and a constant rate of food consumption, the daily rates of food consumption could be calculated using the equation:

\[ F = \frac{C}{R} \]

where the daily food consumption (F) could be estimated from the average amount of food (C) in the stomach at the time of sampling, and the rate of gastric evacuation (R) (see Carreiro-Silva and McClanahan, 2001).

The two assumptions at the basis of this model – an exponential rate of gastric evacuation and a constant rate of food consumption – were previously validated for the echinoid species of the current study. An exponential rate of gastric evacuation was demonstrated in all species of the current study by conducting gut emptying experiments (Carreiro-Silva and McClanahan, 2001; McClanahan and Kurtis, 1991; Mokady et al., 1996). The assumption of a constant rate of food consumption is widely accepted (e.g. McClanahan and Kurtis, 1991; Mokady et al., 1996), and is supported by field observations (Carreiro-Silva and McClanahan, 2001; Glynn et al., 1979; Klumpp et al., 1993) as well as controlled field experiments (Downing and El-Zahr, 1987), and is in agreement with our own observations of sea urchins actively feeding during all hours of the day.

To estimate the true scale of reef degradation (i.e. the scraping off of new material from the reef’s hard substratum), the source of CaCO$_3$ found in the sea urchins’ guts must be considered (Scoffin et al., 1980). It is therefore essential to distinguish between reworked sediment (i.e. recycling of previously eroded sediment) and newly-eroded sediment (Bak, 1990; Hunter, 1977; Mokady et al., 1996). The measure of reworked sediment can then be subtracted from the total amount of CaCO$_3$ in the gut, and the remaining portion considered as a direct representation of the reef’s framework erosion. However, to date there is little consensus over the way to adequately estimate the amounts of
echinoid sediment consumption (i.e. reworked sediment). Mainly, it has not been concluded whether sediment ingestion by echinoids is a process driven by behavior, or merely an outcome of environmental conditions (e.g., sediment load). Our estimates of the proportion of reworked sediment and gut turnover rates for *D. setosum*, *D. savignyi*, and *E. diadema* are based on Carreiro-Silva and McClanahan (2001), and for *E. mathaei* from McClanahan and Kurtis (1991). These estimates represent the highest values of reworked sediment for these species available from the literature and as such would yield the most conservative (i.e. low) bioerosion estimations. Still, as the impact of sedimentation on echinoid sediment consumption could not be elucidated at this point, these values should be treated with caution.

2.6. Statistical analysis

Data analyses were performed using R software for statistical computing (Team, 2013). All data were tested for normality and homogeneity of variance prior to deciding upon the appropriate statistical test. As data violated test assumptions of normal distribution and homoscedasticity, and as data transformations failed to bring the data to meet the assumptions of parametric statistical tests, permutation analysis was performed. Permutations were performed using the lmPerm package (Wheeler, 2010) for data analysis, allowing all permutations of Y (i.e. Perm = “Exact”). Temporal variations in coral and macroalgal cover were tested using permutation analysis of variance (pANOVA), and spatial differences (i.e. between sites and sea facing sides) using a nested design pANOVA with year < site < side. Differences in sea urchin densities were tested using a two-way pANOVA with sites and species as factors. Size frequency distributions were compared using pair-wise Kolmogorov–Smirnov tests and adjusted for multiple testing using the Bonferroni correction to minimize false-discovery-rate. Gut content fractionation was tested using one-way pANOVA. The Tukey Honest Significant Difference (HSD) method which controls for the Type I error rate across multiple comparisons was used when appropriate.

3. Results

3.1. Coral community structure

Western sites presented significantly higher coral cover in comparison to eastern sites (pANOVA, p < 0.01; Fig. 2A). Throughout the years of the surveys trends of coral cover have remained consistent within
sites (pANOVA, p > 0.05 for all sites) except for the site of Mnemba where a constant decline in coral cover had been recorded (pANOVA, p < 0.01), displaying the sharpest reduction of coral cover between March 2007 and April 2008. Of the western sites, Chumbe recorded the highest coral cover (64%–72%) throughout the three years of the survey. The lowest coral cover was recorded on Kiwengwa, with cover less than 0.5%. Macroalgal cover presented an opposite trend to coral cover (Fig. 2B). While the western sites presented negligible macroalgal cover, the eastern sites presented significantly higher algal cover (pANOVA, p < 0.001), reaching more than 50% at some locations (Fig. 2B). The highest macroalgal cover throughout the duration of the surveys (ca. 35%–52%) was recorded on Kiwengwa on the Island’s eastern exposed side. Temporal variations in macroalgal cover indicate no change at the western sites (pANOVA, p > 0.05 for all sites), and significant increases in percentage cover for both Mnemba and Kiwengwa (pANOVA, p < 0.001 for all; Fig. 2B). In the Mnemba MPA macroalgal cover increased seven-fold from March 2007 to March 2008, and at Pongwe in macroalgal cover constantly increased from ca. 1% to 9% and 33% from 2006 to 2008.

3.2. Echinoid community structure

Sea urchin populations varied in species assemblages and population densities both within and between sites, and across the western and eastern sides of the Island (Fig. 3). Variations in densities were significant between sites (pANOVA, p < 0.001), and species (pANOVA, p < 0.001). D. setosum dominated the western sheltered sites (i.e. Changu, Bawe and Chumbe) followed by E. mathaei which instead dominated the exposed eastern ones (i.e. Kiwengwa and Pongwe) (Fig. 3). E. mathaei densities were more than seven-fold higher on the eastern sites than on the western ones (ca. 14 and 2 ind m⁻², respectively), but were always absent from marine-protected areas on both sides. The two MPAs, Mnemba (east), and Chumbe (west), differed from neighboring sites in both species assemblages and densities (Fig. 3). For the eastern reefs Mnemba presented low sea urchin densities (1.62 ± 1.0 ind m⁻²) and no E. mathaei, a sharp contrast to the high echinoid densities at Kiwengwa and Pongwe (20.50 ± 12.0 and 30.19 ± 10.6 ind m⁻², respectively) (pANOVA, p < 0.001; Fig. 2). On the western side, Chumbe had low density of E. mathaei compared to Changu and Bawe (pANOVA, p < 0.05) but similar densities of D. setosum (pANOVA, p > 0.05).

Analyses of size frequency distributions revealed significant differences in size distributions (Table S1 in Electronic Supplementary Material; ESM) and average sea urchin sizes among species (Table 1) and sites (Table 2, Fig. S1). Sea urchins from the eastern sites were larger than their western conspecifics. For example, the mean diameter of E. diadema was highest on Pongwe, followed by Changu and Bawe (ca. 100, 96, and 78 mm, respectively) (pANOVA, p < 0.001). Similarly, E. mathaei presented relatively small individuals on Changu and Bawe (ca. 36 and 34 mm, respectively), while those from Kiwengwa and Pongwe were significantly larger (47 and 38 mm, respectively) (pANOVA, p < 0.001). D. savignyi was significantly larger on Bawe compared to Changu and Pongwe (pANOVA, p < 0.001). D. setosum presented significantly smaller individuals than their conspecifics on Changu and Bawe (pANOVA, p < 0.002). Sea urchin densities on the eastern MPA at Mnemba were too low to adequately perform size frequency estimations.

3.3. Echinoid gut contents analysis

In all four species, the inorganic portion was larger than the organic portion (Fig. 4). Interspecific differences were found in the CaCO₃ and organic matter portions, where E. diadema had a significantly larger proportion of organic matter and a smaller proportion of CaCO₃ than all other species (pANOVA, p < 0.01). D. setosum presented significantly higher CaCO₃ content and lower organic matter than all other species (pANOVA, p < 0.001). No significant differences in the non-soluble portions were observed among species (pANOVA, p > 0.05).

Intraspecific comparisons of gut contents revealed significant differences in the proportions of CaCO₃ and organic matter among species between sites (Fig. 4). However, while species like E. mathaei presented increased proportions of organic matter on exposed reefs in comparison to sheltered reefs, the results for the other species were not so clear. The proportion of organic gut content of E. diadema on Changu was about 40%, compared to less than 20% on adjacent Bawe. The organic content in the gut of E. diadema on the only exposed reef with sufficient sea urchin abundances, Pongwe, was around 20%. D. savignyi displayed a reverse pattern with Bawe around 25% organic gut composition compared to 10% on Changu and 15% on Pongwe. D. setosum presented similar CaCO₃ and organic matter proportions on all sheltered sites (~10%) (Fig. 4).

![Fig. 3. Sea urchin densities at the different study sites around the Island of Zanzibar. Densities were measured in 20 m x 0.5 m belt transects (n = 10 transects per site), Bars indicate average species specific densities per m⁻² (mean ± SD) from surveys conducted in March 2008. Western sites and eastern sites are denoted W and E, respectively. Significance groupings as inferred from Tukey HSD analyses are presented as lowercase letters to indicate groupings among species within sites, and as uppercase letters among sites.](image-url)
3.4. Rates of ingestion, herbivory, and bioerosion

Significant differences in rates of ingestion, herbivory and bioerosion were found between sites and species. The greatest rates of ingestion were found for _D. diadema_, with a daily CaCO3 consumption rate of (11.43 ± 1.6 g CaCO3 ind−1 day−1), more than three-fold that of _D. setosum_ (3.59 ± 0.4 g CaCO3 ind−1 day−1), 5.7-fold that of _D. savignyi_ (2.00 ± 0.2 g CaCO3 ind−1 day−1), and almost 24-fold that of _E. mathaei_ (0.48 ± 0.05 g CaCO3 ind−1 day−1) (Table 1). _E. diadema_ also had the greatest rates of herbivory per day (3.87 ± 0.8 g algae ind−1 day−1) than any of the other species; 7.7-fold more than _D. savignyi_ (0.50 ± 0.1 g algae ind−1 day−1), 9.7-fold more than _D. setosum_ (0.40 ± 0.2 g algae ind−1 day−1), and almost 30-fold more than _E. mathaei_ (0.13 ± 0.02 g algae ind−1 day−1). _E. diadema_ also presented the highest individual rate of bioerosion (3.46 ± 0.47 g CaCO3 ind−1 day−1), _D. setosum_ average bioerosion rate (0.95 ± 0.1 g CaCO3 ind−1 day−1) was less than a third of that of _E. diadema_ while almost twice the rate of _D. savignyi_ and _E. mathaei_ (0.56 ± 0.05 and 0.48 ± 0.05 g CaCO3 ind−1 day−1, respectively) (Table 1).

Gross annual bioerosion was higher on the eastern exposed reefs in comparison to the western sheltered ones (ANOVA, F = 52.97, p < 0.001; Fig. 5). The highest bioerosion rates were recorded on Pongwe, with more than 6.9 kg CaCO3 m−2 eroded annually. Kiwengwa presented the second highest bioerosion levels (4.2 kg CaCO3 m−2 year−1), slightly higher than Bawe (3.9 kg CaCO3 m−2 year−1) and twice the erosion rates at Changu (2.1 kg CaCO3 m−2 year−1). The lowest bioerosion rates were recorded on Chumbe, with only 1.2 kg m−2 year−1 CaCO3 eroded (Table 2, Fig. 5).

4. Discussion

The magnitude of echinoid grazing, and consequently the rates of herbivory and bioerosion, are believed to be determined by three fundamental variables: species identity, body size and population densities (Bak, 1994). These variables are both governed by the habitat’s physical conditions and at the same time, influence the structure and composition of the habitat itself (reviewed by Steneck, 2013). For example, factors such as habitat structural complexity (Graham and Nash, 2013), exposure to surf (Ebert, 1982), and regulation by predation (McClanahan and Kurtis, 1991; McClanahan and Shafir, 1990), are all known to influence echinoid community structure on coral reefs. On the other hand, reef degradation through bioerosion is often associated with high sea urchin abundance (Bak, 1990; Scoffin et al., 1980), direct coral predation (Carpenter, 1981; Glynn et al., 1979), and echinoid control of newly-settled spat (Sammarco, 1980, 1982). The type and intensity of environmental conditions are likely to regulate echinoid communities both directly (e.g., inability of certain species to resist strong currents) (Tuja et al., 2007), and indirectly through shaping coral reefs structure to either favor or exclude specific echinoid species (Dumas et al., 2007; McClanahan and Kurtis, 1991; McClanahan and Shafir, 1990).

4.1. Coral and macroalgal cover

We found marked differences in coral and macroalgal cover, echinoid community structure, and rates of herbivory and bioerosion between exposed and sheltered reefs. That coral cover is low in areas of high algal cover has been thoroughly discussed in the scientific literature, and is often associated with algal predominance over scleractinian corals in competition for environmental resources (reviewed by McCook et al., 2001). Respectively, our data present opposite trends of coral and algal cover: where coral cover was low, algal cover was high and vise versa. This pattern was evident in all of the sites studied regardless of the level of ocean exposure or protection (i.e. MPA and non-MPA), reflecting the generality of these coral–algal interactions. Nonetheless, between-site differences corresponded to the degree of habitat
exposure: while exposed reefs had high algal and low coral cover, sheltered reefs presented an opposite trend. It appears that coral communities on Zanzibar’s exposed reefs are being competitively excluded by algae, while on sheltered reefs coral communities are sustained through algal regulation. Of particular interest is the Mnemba MPA on the north-eastern exposed side. Our data show a significant decrease in coral cover and, at the same time, a significant increase in macroalgal cover between 2007 and 2008 (Fig. 2). Though coral cover at this site is historically low (Bergman and Öhman, 2001; Ngoile, 1990), our measurements reflect the lowest ever recorded coral cover in what is considered Zanzibar’s oldest established MPA (Obura et al., 2002). Nonetheless, management at this site seems effective, judging by the abundance of herbivorous and predatory fish on the site (Brokovich, pers. comm.). The abundance of predatory fish may account for the lack of sea urchins (McClanahan and Kurtis, 1991), while the abundance of herbivorous fish may compensate for the lack of echinoids in regulating algal cover at that site. Thus, though the reason for Mnemba’s coral cover loss is not resolved at this stage, it might be a consequence of global changes and the overall large-scale coral decline (Bellwood et al., 2004; Hughes, 2003). In contrast coral cover on the Chumbe MPA was exceptionally high throughout the duration of the study. Some of the mechanisms that work to maintain such high coral cover may be attributed to the extensive and efficient protection these reefs receive (e.g., no take zone, diving restrictions and strict anchoring regulations). However, in contrast to the reefs on Changu and Bawe, the geographical location of Chumbe, away from the big urban center of Zanzibar Town, is likely to further reduce indirect anthropogenic stressors, such as water pollution, that may also contribute to the prosperity of the latter reefs.

4.2. Echinoid community structure

Multiple environmental, ecological, and biological factors concurrently occurring on coral reefs may make it difficult to elucidate the resulting echinoid species distributions (Dumas et al., 2007; Johansson et al., 2013). Nonetheless, echinoid community structure in terms of species composition, densities, and average body size, varied considerably between sheltered and exposed reefs. Of the four dominant echinoid species found around the Island of Zanzibar, the two most abundant species, *D. setosum* and *E. mathaei*, were also the most affected by the level of habitat exposure. While *D. setosum* was prevalent on sheltered sites, it was absent on exposed sites where *E. mathaei* predominated (Fig. 3). *D. setosum* is known to be restricted to quiet or protected waters (Ebert, 1982). In exposed areas, the large overall volume (body and spines) of *Diadema* may prevent it from resisting the strong currents and surf, causing it to detach from the substrate, as demonstrated in *Diadema* on the reefs of the Canarian Archipelago (Tuya et al., 2007). Despite high macroalgal cover (Fig. 2B) and presumably low predation pressure as a result of intense fishing activity in the area (Jiddawi and Öhman, 2002; Ngoile et al., 1988), *D. setosum* spatial distribution is most likely a result of physical variables (e.g., surf, currents, etc.) rather than biotic factors (e.g., predation, food availability, etc.).
In contrast to *D. setosum*, *E. mathaei*, though present at most western sites, predominated the eastern exposed sites (Fig. 3). Similar to Russo’s findings from reefs with stronger water flow (Russo, 1977), our data show higher densities and a larger average body size of *E. mathaei* on the exposed reefs. These patterns of size and abundance might be attributed to food limitations and availability in the two different reef environments. As *E. mathaei* is generally sedentary, limited to the proximity of its burrows (Langdon, 2012; Young and Bellwood, 2011), in late successional algal communities it was suggested to rely on drift algae for a large part of its diet (Johansson et al., 2013; McClanahan and Muthiga, 2001; Russo, 1977). The significantly higher macroalgal cover and stronger currents on the eastern exposed reefs generate large amounts of drift algae, thus increasing food accessibility for populations of *E. mathaei*. However, in comparison to *D. setosum*, *E. mathaei*’s distribution is thought to be less susceptible to environmental variables (Dumas et al., 2007). *E. mathaei*’s proliferation throughout the exposed unprotected sites might also be attributed to its ability to competitively exclude other echinoid species (McClanahan, 1988a). In this context of inter-specific competition, variations in the echinoid guild of the Bawe site will be interesting to follow during the next few years, as *E. mathaei* densities there are constantly rising (Bronstein, unpublished data) and are now as high as those of *D. setosum* (Fig. 3, Bronstein, unpubl. data).

Regardless of the level of exposure, no *E. mathaei* were recorded on the two MPAs, Chumbe and Mnemba. Predation is probably the prevalent regulatory agent affecting *E. mathaei* proliferation on marine-protected areas (McClanahan and Kursit, 1991; McClanahan and Muthiga, 1989). Exclusion by predation can thus explain the sharp contrast between the extremely high *E. mathaei* densities observed on reefs adjacent to the Mnemba MPA, in contrast to their absence from within the protected zone. Alternatively, the effects of predation might still be evident even when echinoids are not completely excluded as in the case of Mnemba. Strong predation pressure of *D. setosum* in the MPA of Chumbe could be assumed from their bimodal size frequency distribution (Fig. S1), as mid-sized individuals are most susceptible to predation while large predator-immune sea urchins and newly recruited individuals are more likely to escape predation (Ojeda and Dearborn, 1991; Scheibling and Hamm, 1991; Tegner and Levin, 1983). In unprotected reefs, the difference in *E. mathaei* proliferation between exposed and sheltered reefs may also be attributed to human exploitation through fishing. Reduced fishing success on sheltered reefs may be attributed to the relatively high coral cover and structural complexity of these reefs, which may provide more refuge from fishing for potential *E. mathaei* predators in comparison to bare exposed reefs (McClanahan, 1997). Alternatively, the strong surf and currents associated with exposed reefs may restrict fishing by forcing fishermen away from exposed sites or limit fishing duration, allowing more echinoid predators to avoid being caught.

4.3. Bioerosion and herbivory

Accurate assessments of the proportion of reworked sediments in the diet of echinoids are still inconclusive, as evident from the variety of methodologies that have been used to obtain them. These methodologies, often yielding considerably different results, may include the use of petrographic sections of fecal pellets (Bak, 1990; Hunter, 1977; Scoffin et al., 1980), CaCO₃ evaluations in the guts of urchins from noncarbonated substrates (Mokady et al., 1996), and even comparisons to other echinoids that are presumed to be non-eroding species (Carreiro-Silva and McClanahan, 2001). Nonetheless, except for the biases that originate from using different methodologies, it is still largely debated whether ingestion of loose sediment (reworked sediment) by sea urchins is merely a by-product of their grazing activity (i.e. unintentional sediment ingestion) and such a consequence of sediment loads, or an active strategy of intentional grazing that is governed by the life histories of the different species. In the current study, we have observed, on several occasions, groups of *Diadema setosum* actively feeding on filamentous algae on loose sediments (Bronstein, unpublished data). Such activity would imply a nutritional strategy for utilizing an available resource through intentional sediment ingestion. These observations, despite being far from conclusive, should serve to underline gaps in our understanding of this process, and stress the need to further elucidate the issue of echinoid reworked sediment evaluations.

Sheltered sites experienced lower degrees of bioerosion in comparison to exposed sites. Of the sheltered sites, the highest degree of bioerosion was recorded on Bawe, being over three-fold higher than that recorded on Chumbe, and almost twice as high as that of Changu (Table 2). Some of these differences may be attributed to differences in species composition and abundance on these reefs. While in Bawe four different echinoid species contributed to the total bioerosion, in Chumbe *D. setosum* was the sole contributor, and although similar species compositions were observed on Bawe and Changu, the abundance of *E. mathaei* on Bawe was 3.8 times higher than on Changu. Gross bioerosion on Bawe is still more than two-fold higher than that on Chumbe, even when only *D. setosum* is considered, and despite similar abundance and algae cover on Chumbe. Apparently the higher gross bioerosion on Bawe may instead be attributed to the higher average body size of *D. setosum* on these reefs, as rates of food consumption are known to increase with sea urchin size (Bak, 1990; Klumpp et al., 1993). However, this argument seems inadequate here as *D. setosum* on Bawe present rates of bioerosion almost twice as high as those on Changu, despite having similar average body size. Other currently unaccounted for variables, such as the hardness or particular type of substrate available for grazing, may account for these differences.

Bioerosion rates on the exposed sites were highest on Pongwe, with more than 6.9 kg CaCO₃ m⁻² year⁻¹. The higher gross bioerosion on Pongwe compared to Kiwenga, despite the higher total sea urchin abundance on the latter site (ca. 15.5 and 20.3 ind m⁻², respectively), may be attributed to differences in species composition between the two sites. While on Pongwe there are three species comprising the reef-eroding echinoid guild, the reefs of Kiwenga were solely occupied by *E. mathaei*. As different species may occupy different niches on the reef, interspecific competition may be reduced allowing more resources for feeding. Although intraspecific food consumption is expected to increase as sea urchins grow larger (Bak, 1990; Klumpp et al., 1993), the individual rates of food consumption for the larger mean sized *E. mathaei* from Kiwenga were lower than those from Pongwe. The high *E. mathaei* abundance on Kiwenga inevitably increases interspecific competition which consequently utilizes resources that might otherwise be channeled to feeding.

The main differences in bioerosion between the eastern and western reefs should rather be attributed to *E. mathaei*, which total erosion was more than 12 times higher on eastern reefs. These rates are higher than those reported for *E. mathaei* from the Red Sea 0.5–0.9 kg CaCO₃ m⁻² year⁻¹ (Mokady et al., 1996); Ennewat Atoll 0.08–0.33 kg CaCO₃ m⁻² year⁻¹ (Russo, 1980); Marshall Islands 3.3 kg CaCO₃ m⁻² year⁻¹ (Russo, 1980); Kenya 1.3 kg CaCO₃ m⁻² year⁻¹ on unprotected reefs (Carreiro-Silva and McClanahan, 2001); and Moorea, French Polynesia 0.37 kg CaCO₃ m⁻² year⁻¹ (Bak, 1990), but lower than the exceptionally high rates reported from the Arabian Gulf 9.9–15.3 kg CaCO₃ m⁻² year⁻¹ (Downing and El-Zahr, 1987). Another difference between exposed and sheltered reefs is the absence of *D. setosum* on the eastern reefs. However, the lack of *D. setosum* bioerosion is diminished by the high bioerosion rates of *E. mathaei*.

One important contributing factor to different bioerosion rates is body size. The larger body size of *E. diadema* may act in two ways to facilitate its exceptionally high herbivory and CaCO₃ consumption rates (Table 2): (a) the larger Aristotle’s lantern (the sea urchin’s feeding apparatus) and intestines, associated with larger body size (Black et al., 1982; Ebert, 1980), may increase the volume of food ingestion and digestion; and (b) a larger body may reduce the risk of predation (McClanahan and Muthiga, 1989), increasing the duration of food foraging at the expense of seeking shelter. In addition to quantity, body size
may also determine the quality of the food consumed. For example, in two similarly-sized _Diadema_ populations (67.8 ± 6.2 mm and 69.9 ± 6.1 mm, mean ± SD, for _D. setosum_ and _D. savignyi_, respectively) in Kenya, no difference was observed in the organic and CaCO₃ portions of the two species (Carreiro-Silva and McClanahan, 2001). In contrast, a significant size difference in similar species in Zanzibar (45.3 mm and 53.8 ± 0.3 mm, mean ± SE, for _D. setosum_ and _D. savignyi_, respectively), revealed a higher proportion of organic matter in the larger _D. savignyi_. As larger _Diadema_ individuals are potentially more mobile and less prone to predation, they may exploit feeding grounds inaccessible to smaller individuals, consequently maximizing organic matter consumption.

The two MPAs, Chumbe on the west and Mnemba on the east, differed from neighboring unprotected sites in both echinoid species composition and abundance, and consequently in the rates of bioerosion. For example, on Mnemba, echinoid densities were so low that sea-urchin-induced bioerosion was considered negligible. Similarly on Chumbe, despite the presence of _D. setosum_, bioerosion rates were the lowest recorded per site (excluding Mnemba). As predation controls echinoid proliferation (McClanahan, 1998), and fishing may in turn reduce potential predators (McClanahan et al., 1999), sea urchin populations on highly exploited reefs are expected to proliferate. Consequently, except for protected areas, where fishing restrictions are enforced, extensive reef exploitation may have favored sea urchin proliferation, which is accelerating reef degradation through bioerosion.

In addition to regulation of community structure, the type of substratum has also been shown to directly affect echinoid rates of bioerosion. Hibino and Van Woesik (2000), for example, found substrate age to be an important factor affecting bioerosion rates by _E. mathaei_; older substrates lost on average more carbonate than did recently dead coral on experimental tiles. As echinoid populations on sheltered reefs, in the current study, inhabit fairly flourishing reefs, they encounter mostly young substrata (mostly coral and coralline alga) of recently accreted origin. In contrast, the exposed reefs on Zanzibar’s eastern side are showing continued signs of deterioration and loss of hard-coral cover (Mbjie et al., 2002). Thus, with little accretion for the loss of substrata, echinoid bioerosion is expected to accelerate with time, as older and faster eroding parts of the reef are constantly being exposed. Apart from sea urchins already being key drivers of the carbonate budget on most coral reefs (Scoffin et al., 1980), as coral cover declines the system will become less sensitive to drivers of calcification and ever more sensitive to echinoid bioerosion (Perry et al., 2012). Moreover, intense erosion of CCA will not just eliminate a significant ingredient of the reef framework, but may also hinder reef recovery as some species are known to chemically induce recruitment of corals and oocorals (Harrington et al., 2004; Heyward and Negri, 1999; Morse et al., 1996).

Sea urchin erosion may temporarily act to increase the complexity of exposed reefs by enhancing to the 3-dimensional structure of abraded benthic environments, consequently facilitating increased diversity in these habitats. However, as echinoid populations continue to proliferate, resources will eventually dwindle, and intensifying competition might work to exclude other benthic species, leading to reduced biodiversity. Consequently, in areas of low coral cover and limited regulation of echinoid proliferation, such as on Zanzibar’s exposed unprotected reefs, sea urchin bioerosion may ultimately lead to a negative carbonate budget and consequently to reef degradation. Our data suggest that these processes are happening faster on exposed rather than sheltered reefs. These differences may be attributed to the complete dominance of the sea urchin _E. mathaei_, having higher densities and a larger average body size than on sheltered reefs. Nonetheless, the establishment of marine protected areas can dramatically slow this process, and facilitate the sustainability of the reef framework by providing efficient regulation over echinoid populations.

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