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

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ABSTRACT

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), *Diadema savignyi* (Michelin), *Echinometra mathaei* (de Blainville) and *Echinothrix 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 $CaCO_3$ m^{-2} $year^{-1}$, respectively). The highest rates, recorded on Pongwe, with almost 7 kg $CaCO_3$ 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.

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; Vaïtilingon 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 crustose 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

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et al., 2000; Vaïtilingon 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 easterly 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; Mbije 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°48.5′S; 039°21.3′E). The

Fig. 1. Map of Zanzibar showing the six study sites. Double circles indicate sites are marine-protected areas.