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Macroalgal communities on multi-stressed coral reefs in the Caribbean: Long-term changes, spatial variations, and relationships with environmental variables

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ABSTRACT

Long-term changes in macroalgal cover, spatial variation between macroalgal communities, and relationships with environmental variables and benthic groups were assessed in coral reefs along the Caribbean coast of Panama. Sampling was conducted in two regions: Western and Central. Data collected between 2000 and 2012 showed a continuous increase in macroalgal abundance, although patterns differed according to region and site. There were differences in macroalgal communities between regions, as well as within regions between different wave-exposure levels. There were also differences between sites within regions exposed to the same level of wave action. Multivariate analysis found that wave exposure along with herbivore density (*Echinometra viridis*) and sedimentation were the variables that explained most of the variability between communities. Other variables such as *Echinometra lucunter* and *Diadema antillarum* densities, fish density, productivity, and live coral cover had significant relationships with community structure, but explained less of the variability.

1. Introduction

Macroalgae are becoming a predominant and essential organism in benthic reef communities around the tropics (Knowlton, 2001; Bellwood et al., 2004). Since the late twentieth century, there have been profound changes in the structure and abundance of coral reefs (Pandolfi et al., 2003; Baker et al., 2008; Fong and Paul, 2011). A major number of scleractinian coral species are now in decline and at a high risk of extinction. It has been predicted that some coral reefs will collapse entirely within the next few decades (Carpenter et al., 2008; Crabbe, 2008). Reef-forming coral species compete with macroalgae for space, however the rise in abundance of macroalgae has not only been driven by the decline of corals. Macroalgae have also flourished as a result of anthropogenic changes (Pandolfi et al., 2003; Aronson and Precht, 2006) such as the depletion of herbivores, and an increase in nutrient runoff into coastal waters (McCook, 1999; Aronson and Precht, 2001; Fabricius, 2005; McClanahan and Karnauskas, 2011). Once established, macroalgae may dominate other sessile organisms like corals in the struggle for substrate (McCook et al., 2001). Macroalgae are also ecological engineers and can reorganize the communities (Spalding and Jarvis, 2002; Lambo and Ormond, 2006).

Due to their key role in structuring the reefs, macroalgal studies are now more relevant than ever. Conservation priorities therefore need to take account of temporary changes within macroalgal communities, as well as factors that determine macroalgal community spatial distribution and structure (Hughes et al., 2003; Tribollet and Vroom, 2007; Vroom and Timmers, 2009). Macroalgal research is already a core component of most reef monitoring programs but these studies rarely, if ever, investigate the long-term dynamics of macroalgae (e.g., Edmunds, 2002; Nugues and Bak, 2008), nor do they often study the effect of multiple environmental variables on spatial variability (Águila-Ramírez et al., 2003; Vroom et al., 2005). On the other hand, short-term changes such as seasonal variability have been well documented (Águila-Ramírez et al., 2003; Ateweberhan et al., 2006; Lefébre and Bellwood, 2010). It is important to identify the factors that determine macroalgal community structure on the coral reefs because macroalgae affect coral recruitment and coral exclusion (McCook et al., 2001; Mumby et al., 2005; Diaz-Pulido et al., 2010). Furthermore, the predominance of one functional group of macroalgae may be indicative of the state of conservation of a reef since its abundance is related with different successional stages (Diaz-Pulido and McCook, 2002).

The coral reefs in the Caribbean are among the most disturbed and threatened in the world (Gardner et al., 2003; Pandolfi et al., 2003; Mora, 2008). Since the 1980s when monitoring programs began in Panama, the area occupied by scleractinian coral species has reduced by 50–

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70% (Guzman, 2003). In the last thirty years, warming events have contributed to the decline of these reefs due to anomalously high temperatures and coral bleaching (Baker et al., 2008). Mass coral bleaching occurs when the thermal tolerance of corals and their photosynthetic symbionts (zooxanthellae) is exceeded. Episodes of elevated sea temperatures over the past involve loss of zooxanthellae (Hoeg-Guldberg, 1999). The 2005 warming event alone resulted in mortality of 40% of the coral colonies in Bocas del Toro (on the western Panama coast) (Eakin et al., 2010). The number of herbivores exerting top-down control on macroalgae has also fallen. In 1983, populations of the sea-urchin *Diadema antillarum,* a major herbivore on these reefs, were reduced by >93% as a result of a mass mortality event (Lessios et al., 1984). Decades later, *Diadema antillarum* has still not recovered on most Caribbean reefs (Lessios, 2005). Only in some places (e.g., Jamaica, Costa Rica or Puerto Rico) is recovery of their populations reported (Edmunds and Carpenter, 2001; Lessios, 2016). This has also contributed to greater community dominance by macroalgae (Carpenter, 1990). Other anthropogenic factors have also accentuated the rise in macroalgal dominance. Artisanal fisheries have decimated populations of reef fish (Harper et al., 2014) and in the coastal zone and river basins the impact on the reefs of sedimentation and enrichment by nutrients has increased, due to indiscriminate deforestation and the construction and operation of the Panama Canal (Guzman, 2003; Guzman et al., 2008; Cramer, 2013). Other factors include oil spills (Guzman et al., 1991) and traditional coral mining by the Guna people (Guzman et al., 2003).

In our study we attempted to discover the current status of macroalgae on the coral reefs around the Caribbean coast of Panama, as well as the pattern of change over the last decade. In order to answer these questions we examined: (i) non-crustose macroalgal cover in time-series data collected between 2000 and 2012; (ii) the spatial variability of macroalgal communities in two different regions (western and central Caribbean Panama) and at two different levels of wave exposure (windward and leeward) and (iii) the structure and composition of macroalgal communities in relation to the variables depth, selected oceanographic parameters, sand cover, benthic groups, sea-urchins and herbivorous fish.

2. Materials and methods

2.1. Data collection

The study area is situated on the Caribbean coast of Panama at latitude 8.6–9.6N longitude 82.5–77.3W. It spans 1295 km of coastline between Costa Rica and Colombia (Fig. 1). Here, reef corals are one of the main engineer species in the coastal ecosystems, however the abundance of coral communities is highly variable spatially in diversity and structure, depending on the wave exposure, turbidity, nutrients and proximity to the mainland (D'Croz and Robertson, 1997; Guzman, 2003). In comparison, coral reefs from the entrance to the Panama Canal to the limit with Guna Yala region are the most affected by coastal and industrial development, being generally poorly developed and of low diversity. In contrast, the most developed coral reefs in western Panama are found on the leeward side of island systems in Bocas del Toro, where hundreds of cays, islands, and islets are surrounded by fringing reefs (Guzman, 2003).

2.1.1. Long-term change monitoring

Coral reefs were sampled by snorkeling and scuba diving between the years 2000 and 2012 at 9 sites, 5 in the western Panama region (WPR) (sites 2, 6, 10, 13, 15), and 4 in the central Panama region (CPR) (sites 18, 19, 25, 26) (Fig. 1). These sites were sampled once per year in the same season September–October, except the CPR reefs, which were not sampled in 2007 due to logistic restrictions. At each site, 3 to 5 permanent 30 × 1 m transects were marked out in water 0.5 to 10 m deep, parallel to the coastline. Using this type of fixed transects offsets the methodological difficulties arising from environmental heterogeneity in coral reefs, therefore permitting the detection of relatively small changes over time. Percentage macroalgal cover within each transect were measured in situ using thirty quadrats (100 × 100 cm, subdivided into 10 × 10 cm). Only non-crustose macroalgae were counted.

2.1.2. Relationships with environmental variables and spatial variability

Fieldwork was conducted by snorkeling and scuba-diving at 29 sites, 17 in WPR and 12 in CPR (Fig. 1). Each site was sampled once, between September 2013 and April 2014. Samples were obtained from reefs between 0.5 and 10 m deep. Percentage species cover was estimated using photographs of quadrats (50 × 50 cm, subdivided into 10 × 10 cm). At each site, between 18 and 24 high resolution photographs of reef communities were taken randomly with a Nikon D7000 camera with Nauticam D7000 housing and two Sea&Sea YS100 strobes. The dominant seaweed species were identified in situ and percentage cover was estimated using the visual scanning method (sensu Murray, 2001). Some conspicuous species were collected for later laboratory identification. Filamentous blue-green algae (cyanobacteria), small red filamentous species (Ceramiales), green filamentous (Chlorophyta and Phaeophyceae), and crustose coralline algae (CCA) (except *Neogoniolithon strictum* and *Peyssonnelia* spp.) were treated as groups in later analyses due to the difficulty of identification in situ. Number of species (species density) per unit area (Simpson, 1964), and Shannon–Wiener diversity were calculated for each sample (Shannon and Weaver, 1949).

2.1.3. Environmental variables and benthic groups

Fifteen environmental variables and benthic groups were considered and associated with each quadrat in the multivariate analysis: depth, temperature, productivity, wave exposure, sand cover, branching coral, foliose corals, massive and encrusting corals, soft corals and anemones, *Echinometra viridis*, *Echinometra lucunter*, *Diadema antillarum*, surgeonfish, damselfish, parrotfish, and sea-chubs. Depth of each quadrat was determined from a dive computer. We obtained mean values of sea surface temperature and productivity (chlorophyll A concentration $mg \cdot m^{-3}$) from the Bio-Oracle (a geospatial database over an eight year period 2003–2010) to characterize the study sites (Tyberghein et al., 2012). Wave exposure was calculated from a topographical wave-exposure index, derived at each site from the sum of the product of the distance of each location to the nearest coast (km) × the wind intensity ($m \cdot s^{-1}$) in the sixteen cardinal points (see Burrows et al., 2008). Distances were calculated using GIS. Wind data for the Caribbean coast of Panama was obtained from the Smithsonian Tropical Research Institute Databases (between 2004 and 2013) (www.stri.si.edu). Sand cover was estimated using the percentage cover of sand in each quadrat. Percentage cover of live corals was estimated from the quadrats and grouped into the following categories: branching coral, foliose corals, massive and encrusting corals, and soft corals and anemones (McCook et al., 2001). Table 1S shows the species in each group. The sea urchins *Echinometra viridis*, *Echinometra lucunter*, and *Diadema antillarum* were counted using the same quadrats. To estimate the abundance of herbivorous fishes we used a stationary visual count method (Bortone et al., 1989). In this method the observer takes a position at the center of a circle with a radius 5.6 m (100 m^2) and records the number (abundance), and size (cm) of individuals of each species. Only herbivorous species were recorded (Froese and Pauly, 2015). At each site, six replicate surveys were performed the same day the macroalgae were sampled. In later analyses the species were grouped into the following four herbivorous groups: surgeonfish, damselfish, parrotfish, and sea-chubs. Table 2 shows the herbivore species sampled. Fish biomass was estimated using species-specific size-biomass relationships (Froese and Pauly, 2015).