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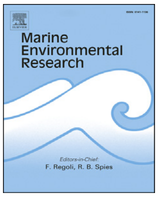

Assessing the herbivore role of the sea-urchin *Echinometra viridis*: Keys to determine the structure of communities in disturbed coral reefs

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ABSTRACT

Echinometra viridis previously was considered a cryptic species unable to control the development and growth of macroalgae on coral reefs. Its role as a herbivore was seen as minor compared to other grazers present on the reef. However, the present disturbed state of some reefs has highlighted the role played by this sea-urchin. Combining field data with experiments on the Caribbean coast of Panama, we demonstrate that the current community organization on disturbed coral reefs in the Mesoamerican Caribbean is largely due to the action of *E. viridis*. It is the most abundant sea-urchin species, together with two others (*Diadema antillarum* and *Echinometra lucunter*). Field data also indicate that the relationship between its density and the abundance of macroalgae is stronger and it is more negative in impact than those of the other two. However, the niche this urchin exploits most efficiently is confined to leeward reefs with low levels of sedimentation. Outside these habitats, their populations are not decisive in controlling macroalgal growth. Grazing experiments showed that *E. viridis* consumes more fresh macroalgae per day and per weight of sea-urchin, and is a more effective grazer than *D. antillarum* or *E. lucunter*. *E. viridis* showed food preferences for early-successional turf macroalgae (*Acanthophora spicifera*), avoiding the less palatable late-successional and fleshy macroalgae (*Lobophora variegata*, *Halimeda opuntia*). However, it becomes a generalist herbivore feeding on all varieties of macroalgae when resources are scarce. *H. opuntia* is the macroalga that most resists *E. viridis* activity, which may explain its wide distribution.

1. Introduction

Rapid decline of coral reef health, and phase shifts towards macroalgae-dominated systems, have highlighted the key role of grazing as a force making coral species resilient (Ledlie et al., 2007). When herbivores are decimated or excluded, a boom in macroalgal growth occurs (Norström et al., 2009). If they are not removed by herbivores, they can become the predominant organisms on the reefs and may end up excluding the scleractinian corals, the major engineer species in these systems (Hughes, 1994). In unfished reefs, both herbivorous fish (parrotfish, surgeonfish) and sea-urchins control macroalgal distribution and abundance (Adam et al., 2015). However, overfishing has reduced fish populations, including sea-urchin predators. This has led sea-urchins to become currently the main herbivores on many reefs (Mumby et al., 2007). The role of herbivorous fish in promoting coral recovery and functionality depends on their diversity, abundance and biomass (Bellwood et al., 2016; Bozec et al., 2016), but in most cases their populations are not sufficient to reduce macroalgal cover. Several authors have also suggested that with present-day reef exploitation, fish are only able to control the most palatable algal species (Williams and Polunin, 2001; Burkepile and Hay, 2008). Nevertheless, the role of fish in controlling macroalgae has been widely discussed and tested, and both field and experimental evidence suggests that sea-urchins are more effective grazers than fish (McClanahan et al., 1996; Mumby et al., 2007).

The Caribbean coral reefs are among the most disturbed and threatened in the world (Gardner et al., 2003; Pandolfi et al., 2003;

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Mora, 2008). In recent decades they have undergone continual large-scale changes in their structure, function and conservation status (McClanahan and Muthiga, 1998; and references therein). Low levels of herbivory have been identified as the major driver of a shift from scleractinian-to fleshy macroalgae-dominated reefs (Hughes, 1994). The reduction in fish grazing through overfishing, in addition to the mass die-off of the sea-urchin *Diadema antillarum* in 1983–1984, reduced coral populations to <5% of their previous size (Lessios, 1988), favouring the present fleshy macroalgal dominance (Mora, 2008). *D. antillarum* has been shown experimentally to contribute to the coral community structure in shallow reefs, promoting the settlement, growth and competitiveness of scleractinians, and reducing macroalgal abundance (Sammarco, 1980). It has been considered the main herbivore in coral reefs subject to heavy human pressure (Hay et al., 1983; Harborne et al., 2009). Despite slight local recoveries, e.g. Jamaica, Belize and Puerto Rico (Miller et al., 2003; Carpenter and Edmunds, 2006; Myhre and Acevedo-Gutiérrez, 2007), after the mass mortality event, *D. antillarum* populations have not yet recovered to previous levels (Lessios et al., 2016). Currently, *Echinometra viridis* is the numerically dominant echinoid grazer on many reefs in the Caribbean, especially in the Mesoamerican region where it is very abundant (Griffin et al., 2003; Brown-Saracino et al., 2007). Lessios et al. (1984) indicating that after the mass mortality of *D. antillarum*, *E. viridis* showed significant increases in density, probably occupying the grazing niche voided by the *Diadema* die-off. Additionally, overfishing changes the trophic structure of these reefs (Newman et al., 2006), relieving the predation pressure on juvenile and new recruits of *E. viridis*, leading to an increase in their populations (Bologna et al., 2012). However, the key herbivore role of *E. viridis* has already been discussed, especially when compared with *D. antillarum*. McClanahan (1999) studied its ecology, assessing how predators control *E. viridis* distribution, as well as its ability to control macroalgal overgrowth. His results showed that *E. viridis* abundance and grazing are strongly controlled by predation, which limits it to cryptic habitats. Under these conditions, he proposed that this sea-urchin is not able to control fleshy macroalgal growth in exposed habitats as effectively as *D. antillarum*. Conversely other authors have defended the active grazing power of *E. viridis*. For example Aronson et al. (2002) reported that high densities of *E. viridis* kept the abundance of fleshy and filamentous macroalgae low. Along the same lines, Griffin et al. (2003) found that a high density of this echinoderm regulates the composition of macroalgal communities.

In previous studies in Western Caribbean Panama, Guzman and Guevara (1998) pointed out the herbivorous role of the species in Bocas del Toro reefs, and Sangil and Guzman (in review) found that *E. viridis* was a principal factor, together with wave exposure and sedimentation, that significantly influences the structure of macroalgal communities on the Caribbean coast of Panama. Its grazing effect appeared to be more intense than other sea-urchins and herbivorous fish. Coral communities are spatially variable, depending on the extent of wave and wind exposure, and proximity to the mainland (Guzman and Guevara, 1998). The coral community in the coast of Panama generally forms a highly diverse mosaic with varying conservation status (Guzman, 2003).

In order to solve the herbivore role that *E. viridis* plays in Caribbean coral reefs, we combined field data with some experiments on the coast of Panama. Firstly we analyzed in the field the spatial distribution of *E. viridis* together with *D. antillarum*, and *Echinometra lucunter* and the abundance of total non-crustose macroalgae, and the upright calcareous *Halimeda opuntia* and *L. variegata*. The relationship between sea-urchin density and macroalgal cover, and how changes in density can affect preferred habitat with selected environmental variables and with the cover of the two benthic groups under study (corals and macroalgae) have been explored. In these assessments we considered two different regions (Western and Central Caribbean Panama), and two environments (windward and leeward reefs). Secondly, considering that *L. variegata* and *H. opuntia* are two of the most abundant non-crustose macroalgae in the Caribbean, including Panama (Williams and Polunin, 2001; Sangil and Guzman, in review), while *A. spicifera* is highly palatable but infrequent on coral reefs (Hay, 1981). We tested under experimental conditions (laboratory and field) the grazing activity of *E. viridis*, including food preference, and the consumption rate of *L. variegata*, *H. opuntia* and *A. spicifera* by the three sea-urchin species. Finally a cage experiment was performed for 4 months to test the growth of the studied macroalgae with and without *E. viridis* populations. Field experiments were conducted on leeward reefs characterized by high abundance of *E. viridis* and low density of herbivorous fish.

2. Materials and methods

2.1. Study area

The Caribbean coast of Panama is situated between latitude 8.6–9.6N and longitude 82.5–77.3W, and spans 1295 km of coastline between Costa Rica and Colombia (Fig. 1). In this region, coral reefs are one of the major marine ecosystems influenced by extensive fringing mangrove forest and seagrass beds. Although their development varies along the coast they are most extensive on the leeward side of island systems such as in Central Panama, from Colon to Guna Yala, and on the Western coast in Bocas del Toro (Guzman, 2003). Macroalgae, recently spreading over these coral reefs, are the main benthic group in cover terms and the principal competitors of the scelactrinian coral species. Macroalgal abundance varies strongly with the degree of wave exposure, nutrient concentration, sedimentation and turbidity, and in relation to herbivore density (Guzman, 2003; Sangil and Guzman, in review).

2.2. Field studies

2.2.1. Field data collection

Fieldwork was conducted by snorkeling and scuba diving between 0.5 and 10 m depth at 29 sites, 17 on the Western and 12 on the Central Panama coast, between September 2013 and April 2014 (Fig. 1). At each site, between 18 and 24 quadrats (50 × 50 cm) were taken randomly to estimate *in situ* the number of sea-urchins *E. viridis*, *E. lucunter* and *D. antillarum*, and the percentage of coral and macroalgal cover from high resolution photographs using the visual scanning method (*sensu* Murray, 2001). For later analyses, coral species (see Table 1S) were grouped according to McCook et al. (2001) into branching, foliose, massive and encrusting, and soft corals and anemones; and macroalgal species (see Table 2S) into: crustose coralline (CCA), microalgae, filamentous, foliose corticated, corticated, erect calcified and leathery macroalgae (*sensu* Steneck and Dethier, 1994).

2.2.2. Spatial variability

Permutational analyses of variance (ANOVAs) (Anderson et al., 2008) were performed to test spatial differences in sea-urchin density (*E. viridis*, *E. lucunter*, *D. antillarum*) and macroalgal cover (total non-crustose *H. opuntia*, *L. variegata*) around the reefs along the Caribbean coast of Panama. The analysis used Euclidean-distances similarity with 4999 permutations and consisted of a three-way model where 'region' (two levels: Western *vs* Central Panama) and 'wave exposure' (two levels: windward *vs* leeward) were treated as fixed factors. 'Site' (29 levels) was treated as random factor and was nested in 'region × wave exposure'. Data