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

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19 **Abstract**

20 *Echinometra viridis* previously was considered a cryptic species unable to control the
21 development and growth of macroalgae on coral reefs. Its role as a herbivore was seen
22 as minor compared to other grazers present on the reef. However, the present disturbed
23 state of some reefs has highlighted the role played by this sea-urchin. Combining field
24 data with experiments on the Caribbean coast of Panama, we demonstrate that the
25 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.

Key words: macroalgae, *Diadema antillarum*, grazing, coral reef resilience, Panama reefs, *Lobophora variegata*, *Halimeda opuntia*.

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

52 excluding the scleractinian corals, the major engineer species in these systems (Hughes,
53 1994). In unfished reefs, both herbivorous fish (parrotfish, surgeonfish) and sea-urchins
54 control macroalgal distribution and abundance (Adam et al., 2015). However,
55 overfishing has reduced fish populations, including sea-urchin predators. This has led
56 sea-urchins to become currently the main herbivores on many reefs (Mumby et al.,
57 2007). The role of herbivorous fish in promoting coral recovery and functionality
58 depends on their diversity, abundance and biomass (Bellwood et al., 2016; Bozec et al.,
59 2016), but in most cases their populations are not sufficient to reduce macroalgal cover.
60 Several authors have also suggested that with present-day reef exploitation, fish are only
61 able to control the most palatable algal species (Williams and Polunin, 2001; Burkepile
62 and Hay, 2008). Nevertheless, the role of fish in controlling macroalgae has been widely
63 discussed and tested, and both field and experimental evidence suggests that sea-urchins
64 are more effective grazers than fish (McClanahan et al., 1996; Mumby et al., 2007).

65 The Caribbean coral reefs are among the most disturbed and threatened in the
66 world (Gardner et al., 2003; Pandolfi et al., 2003; Mora, 2008). In recent decades they
67 have undergone continual large-scale changes in their structure, function and
68 conservation status (McClanahan and Muthiga, 1998; and references therein). Low
69 levels of herbivory have been identified as the major driver of a shift from scleractinian-
70 to fleshy macroalgae-dominated reefs (Hughes, 1994). The reduction in fish grazing
71 through overfishing, in addition to the mass die-off of the sea-urchin *Diadema*
72 *antillarum* in 1983-1984, reduced coral populations to < 5 % of their previous size
73 (Lessios et al., 1988), favouring the present fleshy macroalgal dominance (Mora, 2008).
74 *D. antillarum* has been shown experimentally to contribute to the coral community
75 structure in shallow reefs, promoting the settlement, growth and competitiveness of
76 scleractinians, and reducing macroalgal abundance (Sammarco, 1980). It has been

77 considered the main herbivore in coral reefs subject to heavy human pressure (Hay et
78 al., 1983; Harborne et al., 2009). Despite slight local recoveries, e.g. Jamaica, Belize
79 and Puerto Rico (Miller et al., 2003; Carpenter and Edmunds, 2006; Myhre and
80 Acevedo-Gutierrez, 2007), after the mass mortality event, *D. antillarum* populations
81 have not yet recovered to previous levels (Lessios et al., 2016). Currently, *Echinometra*
82 *viridis* is the numerically dominant echinoid grazer on many reefs in the Caribbean,
83 especially in the Mesoamerican region where it is very abundant (Griffin et al., 2003;
84 Brown-Saracino et al., 2007). Lessios et al. (1984) indicating that after the mass
85 mortality of *D. antillarum*, *E. viridis* showed significant increases in density, probably
86 occupying the grazing niche voided by the *Diadema* die-off. Additionally, overfishing
87 changes the trophic structure of these reefs (Newman et al., 2006), relieving the
88 predation pressure on juvenile and new recruits of *E. viridis*, leading to an increase in
89 their populations (Bologna et al., 2012). However, the key herbivore role of *E. viridis*
90 has already been discussed, especially when compared with *D. antillarum*. McClanahan
91 (1999) studied its ecology, assessing how predators control *E. viridis* distribution, as
92 well as its ability to control macroalgal overgrowth. His results showed that *E. viridis*
93 abundance and grazing are strongly controlled by predation, which limits it to cryptic
94 habitats. Under these conditions, he proposed that this sea-urchin is not able to control
95 fleshy macroalgal growth in exposed habitats as effectively as *D. antillarum*.
96 Conversely other authors have defended the active grazing power of *E. viridis*. For
97 example Aronson et al. (2002) reported that high densities of *E. viridis* kept the
98 abundance of fleshy and filamentous macroalgae low. Along the same lines, Griffin et
99 al. (2003) found that a high density of this echinoderm regulates the composition of
100 macroalgal communities.

101 In previous studies in Western Caribbean Panama, Guzman and Guevara (1998)
102 pointed out the herbivorous role of the species in Bocas del Toro reefs, and Sangil and
103 Guzman (in review) found that *E. viridis* was a principal factor, together with wave
104 exposure and sedimentation, that significantly influences the structure of macroalgal
105 communities on the Caribbean coast of Panama. Its grazing effect appeared to be more
106 intense than other sea-urchins and herbivorous fish. Coral communities are spatially
107 variable, depending on the extent of wave and wind exposure, and proximity to the
108 mainland (Guzman and Guevara, 1998). The coral community in the coast of Panama
109 generally forms a highly diverse mosaic with varying conservation status (Guzman,
110 2003).

111 In order to solve the herbivore role that *E. viridis* plays in Caribbean coral reefs,
112 we combined field data with some experiments on the coast of Panama. Firstly we
113 analyzed in the field the spatial distribution of *E. viridis* together with *D. antillarum*,
114 and *Echinometra lucunter* and the abundance of total non-crustose macroalgae, and the
115 upright calcareous *Halimeda opuntia* and *L. variegata*. The relationship between sea-
116 urchin density and macroalgal cover, and how changes in density can affect preferred
117 habitat with selected environmental variables and with the cover of the two benthic
118 groups under study (corals and macroalgae) have been explored. In these assessments
119 we considered two different regions (Western and Central Caribbean Panama), and two
120 environments (windward and leeward reefs). Secondly, considering that *L. variegata*
121 and *H. opuntia* are two of the most abundant non-crustose macroalgae in the Caribbean,
122 including Panama (Williams and Polunin 2001; Sangil and Guzman, in review), while
123 *A. spicifera* is highly palatable but infrequent on coral reefs (Hay 1981). We tested
124 under experimental conditions (laboratory and field) the grazing activity of *E. viridis*,
125 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.

Materials and methods

Study area

The Caribbean coast of Panama is situated between latitude 8.6–9.6N and longitude 82.5–77.3W, and spans 1,295 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 scleractinian 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).

Field studies

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 x 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).

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 were square-root transformed. Sums of squares type III (Anderson et al., 2008) were employed to account for unbalanced design.

Spearman’s correlations were used to test the relationships positive or negative between the density of *E. viridis*, *E. lucunter* and *D. antillarum* with the cover of non-crustose macroalgae, *H. opuntia*, *L. variegata* and *A. spicifera*.

Sea-urchin habitat use and environmental drivers

175 In order to identify the habitat of the three sea-urchin species and their relation with
176 sessile benthic groups and selected environmental variables, we applied a distance-
177 based linear model routine (DistLM) (Legendre and Anderson. 1999). The variables
178 considered were depth, wave exposure, sedimentation, percentage cover of live corals
179 (branching, foliose, massive and encrusting, soft and anemones), and percentage cover
180 of macroalgae (CCA, microalgae, filamentous, foliose corticated, corticated, erect
181 calcified and leathery macroalgae). Depth of each quadrat was determined with a dive
182 computer. Wave exposure was calculated from a topographical wave exposure index
183 (fetch), derived at each site from the sum of the products of the distance of each location
184 from the nearest coast (km) by the wind intensity ($\text{m}\cdot\text{s}^{-1}$) for the sixteen cardinal points
185 (*sensu* Burrow et al., 2008). Distances were calculated using ArcGIS9[®]. Wind data for
186 the Caribbean coast of Panama was obtained from the Smithsonian Tropical Research
187 Institute Databases (between 2004-2013) (www.stri.si.edu). Sedimentation was
188 indirectly estimated using the percentage cover of sand in the quadrats. Percentage
189 cover of live corals and macroalgae was obtained for each quadrat in which urchins
190 were counted. Prior to the DistLM analysis, the draftsman plot method with the
191 corresponding Pearson correlation coefficients was used to explore the relationships
192 between the environmental variables (Clarke and Gorley, 2006). This test was
193 performed to detect any possible relationship between variables, so as to discard those
194 strongly correlated. Because the correlations between variables were low in our case
195 ($R < 0.5$), no variable was excluded. The analysis, based on similarity matrices, used the
196 Bray–Curtis index for the biological data. The method used stepwise selection, an
197 adjusted R^2 criterion and 9,999 permutations. Following recommendations by Clarke
198 and Gorley (2006), sea-urchin densities were square-root transformed and variables
199 were normalized. A distance-based redundancy analysis (dbRDA) was used to visualize

the relationships between seaweed assemblages and the environmental variables, based on the multivariate regression model generated by the DistLM analysis (McArdle and Anderson, 2001).

Experimental studies

Consumption rate

In order to test the differences in consumption rate of the macroalgae *L. variegata*, *H. opuntia* and *A. spicifera* by the sea-urchins *E. viridis*, *E. lucunter* and *D. antillarum*, we performed an experiment in aquariums. Thirty similar-sized specimens ($\pm$ s.e.) (shell diameter *E. viridis* = 30.69 ± 0.91 , *E. lucunter* 37.58 ± 0.83 , *D. antillarum* = 60.54 ± 1.33 mm) of each urchin species were selected and weighed. Separately, each specimen was placed in a 1 liter plastic container for *Echinometra* species, 3 liters for *D. antillarum*, within an aquarium, with continuous aeration and water circulation for four days in starvation (Fig. 1S). Later, 10 specimens of each species were fed for two days with weighed quantities of *L. variegata*, 10 with *H. opuntia* and 10 with *A. spicifera*. Fresh macroalgae offered varied from 5 g for *Echinometra* species and 30 g for *D. antillarum*. After two days, the fresh algae were reweighed with a precision balance and the consumption rate was expressed as grams of algae consumed per gram of sea-urchin per day. Differences in consumption rate were tested using permutational analysis of variance (ANOVAs). The analysis design based on Euclidean distances with 4999 permutations consisted of a two-way model, where ‘sea-urchin species’ with three levels (*E. viridis*, *E. lucunter* and *D. antillarum*) and ‘macroalgae species’ with three levels (*L. variegata*, *H. opuntia* and *A. spicifera*) were treated as fixed factors.

Food preferences

225 These were evaluated both in field (sites 4, 7, 11; Fig. 1) and in the laboratory. In the
226 field, 10 g fresh fragments of each macroalga (*L. variegata*, *H. opuntia*, *A. spicifera*)
227 were inserted in a 75 cm length of rope (Fig. 2S). This experiment was replicated at
228 three sites (4, 7, and 11), at which *E. viridis* density was 12.16 ± 3.31 , 2.53 ± 0.85 ,
229 4.29 ± 1.11 indiv $\cdot 0.25$ m⁻² respectively. At each, 7 ropes were placed between coral
230 colonies of *Millepora alcicornis* and *Porites furcata*, at a minimum distance of 5 m
231 apart. Grazing on macroalgae was evaluated for 24 hours, after this the fragments were
232 reweighed. The difference between the weights before and after the experiment was
233 expressed as a percentage of consumed macroalgae. Differences were analyzed using
234 permutational analysis of variance (ANOVAs), with a two-way model based on
235 Euclidean distances with 4999 permutations. ‘Macroalgae species’ with three levels (*L.*
236 *variegata*, *H. opuntia* and *A. spicifera*) was treated as fixed factor, while ‘site’, with
237 three levels (Sites 4, 7, 11) was treated as random factor.

238 The laboratory experiment consisted in offering simultaneously the three species
239 of macroalgae to sea-urchins, in two 90 x 90 cm tanks (200 L). In each, 50 similar-sized
240 specimens of *E. viridis* (30.53 ± 0.98 in the tank 1, and 30.23 ± 0.89 mm in the tank 2)
241 were kept without food for 4 days, then 4 replicates of each fresh macroalga were
242 offered to them systematically (see Fig. 3S). The replicates consisted of fragments of
243 approximately 100 cm² stitched to dead branches of *Porites*, forming a small bush. The
244 experiment was conducted for eight days; every day at the same time a photograph of
245 each replicate was taken to calculate the percentage of macroalgae not consumed per
246 day, images were analyzed using the public domain NIH ImageJ software (Rasband,
247 2007), and the number of sea-urchins in contact with each replicate was noted. The
248 percentage of non-consumed macroalgae, as well as number of sea-urchins associated
249 with each macroalga bush were tested with permutational ANOVAs, using a three-way

model based on Euclidean distances with 4999 permutations, in which ‘macroalgae species’ with three levels (*L. variegata*, *H. opuntia* and *A. spicifera*) was treated as fixed factor, and ‘time’ with 9 levels (day 0 to day 8) and ‘tank’ with two levels (tank 1, tank 2) were treated as random factors. The use of permutational procedures to generate a correct distribution of each *pseudo-F* statistic solves the problem of sample non-independence when repeated measures are used (Anderson et al., 2008).

Cage experiment

An herbivore exclusion experiment was performed to test the growth of macroalgae (*L. variegata*, *H. opuntia* and *A. spicifera*) with and without *E. viridis* populations. To exclude herbivores, plastic mesh cages with dimensions 0.50 x 0.30 x 20 cm made of 0.5 cm diameter mesh were used. Inside each cage, as well as outside close to the cage, a replica of each species of macroalgae was placed. Fragments of approximately 100 cm² of macroalgae were attached to concrete blocks (Fig. 4S). The experiment was conducted at two locations (sites 2, 3; Fig. 1) for 4 months. *E. viridis* density at each was 7.64 ± 1.72 , and 6.72 ± 1.79 indiv · m⁻² respectively. Four groups of samples, caged and uncaged replicas, with a minimum distance of 3 m between them were placed at each site. Percentage macroalgal increase was calculated from photographs of each sample taken before and after experiments using the NIH ImageJ software. Differences in the percentage macroalgal increase were analyzed using permutational ANOVAs, with a three-way model based on Euclidean distances with 4999 permutations, in which ‘macroalgae species’ with three levels (*L. variegata*, *H. opuntia* and *A. spicifera*) and ‘herbivores’ with two levels (caged, uncaged) were treated as fixed factor, while ‘site’ with two factors (site 2, 3) was treated as random factor nested in ‘herbivores’.

Experimental data were square-root transformed. *A posteriori* pairwise comparisons were used to explore significant terms. Statistical analyses were performed using PRIMER-E® v.6 + PERMANOVA+ (www.primer-e.com) and SPSS 17 for Windows.

Results

Spatial variability

The mean number ($\pm$ s.e.) of sea-urchins considering all samples was 2.56 ± 0.23 indiv. $\cdot 0.25 \text{ m}^{-2}$ for *E. viridis*, 0.30 ± 0.04 indiv. $\cdot 0.25 \text{ m}^{-2}$ for *E. lucunter*, and 0.06 ± 0.01 indiv. $\cdot 0.25 \text{ m}^{-2}$ for *D. antillarum*. The number of *E. viridis* differed significantly between ‘region’, ‘wave exposure’ and ‘site’. *E. lucunter* showed significant differences from factors ‘wave exposure’ and ‘site’, whereas *D. antillarum* showed differences per the factor ‘site’ (Table 1). Regarding ‘region’, the number of *E. viridis* was higher in Western Panama, while per ‘wave exposure’ it was higher on the leeward reefs. *E. lucunter* was more abundant on the windward reefs. The number of *E. viridis*, *E. lucunter* and *D. antillarum* showed great variability within each region and level of wave exposure (Fig. 2). The mean percentage cover of non-crustose macroalgae considering all samples was 28.10 ± 2.10 ; for *H. opuntia* it was 5.73 ± 0.42 , and *L. variegata* showed 4.87 ± 0.47 . These taxa only presented differences for the factor ‘site’ (Table 1, Fig. 2).

Spearman’s correlation found negative and significant relationships between the number of *E. viridis* and non-crustose macroalgae cover. *H. opuntia* and *L. variegata*. *E. lucunter* showed positive and significant relationships with non-crustose macroalgae and *H. opuntia*, and negative with *L. variegata*. However *D. antillarum* showed negative relationships with non-crustose macroalgae (Table 3).

300

301 *Sea-urchin habitat use and environmental drivers*

302 The DistLM analysis showed there was significant variation between sea-urchin data
303 and descriptive variables, except for depth and microalgae (Table 2). The marginal test
304 (Table 2a) examined the significant variation between urchins and each separate
305 variable in turn. Urchin data were explained by each variable as follows: wave exposure
306 (13.50%), foliose corticated macroalgae (6.12%), branching corals (4.43%), soft corals
307 and anemones (4.01%), geniculate coralline macroalgae (2.24%), filamentous
308 macroalgae (2.02%), leathery macroalgae (1.96%), CCA (1.82%), sedimentation
309 (1.71%), erect calcified macroalgae (1.47%), foliose corals (1.20%), corticated
310 macroalgae (0.73%), and massive and encrusting corals (0.63%). However, in the
311 sequential test assessing the effect of all variables together, significant variables and
312 values for each variable differed (Table 2b) as follows: wave exposure (13.52%),
313 sedimentation (4.57%), foliose corticated macroalgae (3.43%), soft corals and
314 anemones (1.76%), geniculate coralline macroalgae (1.44%), filamentous macroalgae
315 (1.35%), erect calcified macroalgae (1.32%), foliose corticated macroalgae (0.68%),
316 and CCA (0.615%). The variation explained by these nine variables was 28.69%. In the
317 dbRDA analysis (Fig. 3a), erect calcified and foliose corticated macroalgae were
318 positively correlated with the first axis, whereas foliose corals, and soft corals and
319 anemones were negatively correlated with the first axis. CCA was correlated positively
320 with the second axis, whereas sedimentation was negatively correlated with it. Wave
321 exposure was partially correlated with the first axis or both axes. Geniculate coralline
322 and filamentous macroalgae were partially correlated with positive values of the first
323 axis and negatively with the second axis. When sea-urchin density data were overlaid
324 (Fig. 3b), *E. viridis* increased in density with negative values of the first axis. *E.*

325 *lucunter* was partially correlated with positive values of both axes, whereas *D.*
326 *antillarum* was partially correlated with negative values of the first axis and with
327 positive values of the second.

328

329 *Experiments*

330 Consumption rate showed significant differences per factor ‘sea-urchin species’ and per
331 factor ‘macroalgae species’ (Fig. 4a,b, Table 3S). *A posteriori* tests for levels of the
332 factor ‘sea-urchin species’ found differences between the three urchin species.
333 Consumption rate was higher in *E. viridis*, while minimal in *E. lucunter*. *Diadema*
334 showed intermediate values (Fig. 4a). Pairwise comparisons at the levels of the factor
335 ‘macroalgae species’ found significant differences between *L. variegata* and *A.*
336 *spicifera*, and between *H. opuntia* and *A. spicifera*, whereas the latter was more
337 consumed than the other species. *L. variegata* and *H. opuntia* were consumed equally
338 (Fig. 5b).

339 Food preferences in the field showed significant differences per factor
340 ‘macroalgae species’ (Fig. 5, Table 4aS). *A posteriori* tests for levels of this factor found
341 differences between all pairs of comparisons. *A. spicifera* was the most consumed,
342 followed by *L. variegata*, while *H. opuntia* was the least consumed. Analysis of food
343 preferences in the laboratory found significant interaction between ‘macroalgae species
344 x time’ (Fig 6a, Table 4bS), showing consumption preferences affecting macroalgae, but
345 the time pattern of consumption varied according to species. The percentage of non-
346 consumed macroalgae showed that *A. spicifera* was preferentially consumed, and on the
347 fourth day none remained. After *A. spicifera*, *L. variegata* was preferentially consumed
348 although it was not completely consumed at the end of the experimentation. The highest
349 consumption of *L. variegata* occurred when *A. spicifera* was consumed completely. *H.*

opuntia was the least consumed, after 8 days the percentage of non-consumed macroalga was greater than 40%. In the analysis of the number of *E. viridis* associated with each macroalgae bush, there was significant interaction between ‘macroalgae species x time’ (Fig. 6b, Table 4cS), and the number of urchins showed a similar pattern. At the beginning, the number of urchins associated with each bush was higher for *A. spicifera*. On finishing it, the urchins moved towards *L. variegata*, then after consuming that they gathered around *H. opuntia*.

Analysis of the percentage of macroalgal increase in the cage experiment revealed significant interaction between ‘macroalgae species x herbivore’ (Fig 7, Table 5S). There were differences in macroalgal growth but it depended on the presence of herbivores. Pairwise analysis found significant differences between *L. variegata* and *H. opuntia* in caged samples. In caged samples, the growth of *H. opuntia* and *A. spicifera* was higher than *L. variegata* growth, although no significant differences were found between *A. spicifera* and the other macroalgae. In uncaged samples, all species were heavily consumed but *H. opuntia* not completely, unlike *L. variegata* and *A. spicifera*.

Discussion

Over recent decades, changes in the ecosystem include the mass die-off of *Diadema antillarum* (Lessios et al., 1988) and the progressive erosion of predator pressure by overfishing (Brown-Saracino et al., 2007; Paddack et al., 2009). These have modified the natural relative proportion of each sea-urchin species and their roles in the Caribbean coral reef system. Although *D. antillarum* has recovered slightly in some regions, their populations are still much lower than the previous massive die-off (Lessios, 2016). Based on its abundance, spatial distribution and ability to control the spread of macroalgae, we can confirm that *Echinometra viridis* plays a key role in the

375 current community organization on the disturbed Caribbean marginal coral reefs. It is
376 clearly the most abundant among the three sea-urchin species under consideration here,
377 with more than 10 indiv. $\cdot$ m⁻², ten times more than *E. lucunter* and 40 more than *D.*
378 *antillarum*. The predominance of *E. viridis* over other species has been noted in other
379 regions, e.g. Honduras (Bologna et al., 2012). The spread of *E. viridis* seems to be a
380 natural tendency in numerous places in the Caribbean, especially in the Mesoamerican
381 region (McClanahan et al., 1999), with a progressive increase in its populations
382 (McClanahan and Muthiga, 1998; Chiappone et al., 2002). The distribution of
383 populations of these three urchin species was heterogeneous throughout our studied
384 reefs as previously indicated (Guzman and Guevara 1998), displaying spatial
385 segregation patterns that suggest they exploit particular ecological niches and play
386 distinct roles in the reef system. *E. viridis* is particularly abundant on leeward reefs,
387 whereas *E. lucunter* is more abundant on exposed reefs and very scarce to leeward.
388 Although some sea-urchin populations can coexist, the difference in environmental
389 conditions between leeward and windward reefs leads to spatial segregation between
390 species (Cubit et al., 1986; McClanahan and Muthiga, 2001, Tuya et al., 2007). The *D.*
391 *antillarum* density was very low, perhaps for this reason no clear distribution pattern
392 was observed for it. However, its populations are frequently higher on leeward reefs
393 (Hernández et al., 2008). The use of quadrats instead of transects could also
394 underestimate the *D. antillarum* populations, although it was so rare that at many sites
395 not a single specimen could be spotted. Different levels of predation may have caused
396 the observed *E. viridis* density between the Western and Central regions.. The Western
397 region suffers from severe overfishing which has decimated predatory urchin species
398 (Guzman and Guevara 1998;Dominici-Arosamena and Wolf, 2005). Macroalgae were
399 particularly reduced in abundance when *E. viridis* populations were high. Likewise with

400 *D. antillarum* and non-crustose macroalgae, but it was not so with *E. lucunter*. There is
401 an apparent negative relationship between *E. lucunter* and *L. variegata*. *L. variegata* is a
402 species on which the waves act adversely (pers. obs.); precisely the wave-exposed zones
403 are where populations of *E. lucunter* are most abundant. These field data showed *E.*
404 *viridis* influences macroalgal communities most significantly as herbivore, but only in
405 places where it is abundant, such as the leeward reefs. As on other coral reefs when sea-
406 urchin density is extremely high (Hay, 1997), this herbivore can remove the complete
407 macroalgal coverage demonstrating the important role it can play in the resilience of
408 some coral reefs. Like other *Echinometra* species that develop in exposed places
409 burrowing holes in the reef, *E. lucunter* may be a species that feeds preferentially on
410 macroalgal drifts. On windward reefs, drifts are the dominant food, and the urchins do
411 not have to leave their holes to feed (McClanahan and Muthiga, 2001). The opposite
412 happens on leeward reefs, where *E. viridis* has to graze actively even in daylight; this
413 indicates the low levels of predation it is subject to (McClanahan, 1999).

414 Many factors are involved in urchin species distribution on coral reefs, leading
415 to wide spatial variation and patchiness (Dumas et al., 2007; Brown-Saracino et al.,
416 2007; Iken et al., 2010). In fact all factors considered here, except microalgae and depth,
417 were related to both their distribution and abundance. Depth is a factor affecting sea
418 urchins distribution (Hernández et al., 2008); in particular *Echinometra* species, which
419 are mainly distributed in shallow waters (McClanahan and Muthiga, 2001). However,
420 the depth range studied here (0-10 m) was insufficient to create differences. . Among the
421 other factors influencing their distributions, wave exposure and sedimentation were the
422 most linked to variation in sea-urchin density, followed by the cover of other benthic
423 groups. Wave exposure is the main environmental variable that differentiates windward
424 from leeward reefs, and is known to influence echinoderm assemblages (Iken et al.,

2010). In areas exposed to heavy wave-action, urchin mobility is limited (Lewis and Wainwright, 1985), and they may be dislodged from the substratum by strong waves and deterred from grazing by constant wave-induced thallus motion of the algae (Kawamata et al., 2011). For this reason active species, such as *E. viridis* and *D. antillarum*, have problems in developing on windward reefs. The opposite happens with sedentary species, such as *E. lucunter*, that spend their entire lives in holes, not directly exposed to the waves. Similar effects are caused by sedimentation, since sea-urchins from rocky and coral reefs avoid sedimentary environments (Dumas et al., 2007). We observed that the rise in abundance of the three studied urchins was inversely related to the sand cover on coral reefs. Different phases of sea-urchin development e.g., recruitment and settlement, may be affected by sedimentation (Walker, 2007). Its effects are especially negative when combined with wave-action, causing an abrasive effect (Hernández et al., 2008). Furthermore, sedimentation also deters grazing because macroalgae covered by sediment are less palatable (Sangil et al., 2011). Changes in sea-urchin density between sites in the same area (e.g., the leeward reefs of a region) may be caused by different levels of sedimentation or wave exposure. For instance, the leeward reefs of the Western region have been transformed through deforestation patching (Seemann et al., 2014), causing varied levels of sedimentation. Normally, we observed that *E. viridis* density was low at sites where sedimentation was high. The physical structure of habitats is also a factor to consider in sea-urchin distribution (Dumas et al., 2007; Hernández et al., 2008), and the highest densities are usually linked to heterogeneous substrates with prominent three-dimensional structures (McClanahan 1999; Kawamata et al., 2011; Rogers and Lorenzen, 2016). Here, though it was one of the less influential factors, the density of *E. viridis* and *D. antillarum* was higher where the cover of foliose corals, soft corals and anemones was greater.

450 The grazing experiments showed that *E. viridis* is an active consumer of
451 macroalgae, and those conducted in the laboratory suggest it is even more active than
452 the other two sea-urchins. Fresh macroalgae consumed by *E. viridis* per day was
453 statistically different from that by *D. antillarum* but only slightly higher (20%), but.
454 Compared to *E. lucunter*, *E. viridis*' consumption rate was three times higher. This
455 finding emphasizes that the latter is a strong competitor with *D. antillarum* for food
456 resources in Caribbean coral reefs, in their current state of conservation (absence of
457 predators that limit its activity) (*sensu* McClanahan, 1999). The grazing activity of *E.*
458 *lucunter* is lower, as in other species of the genus (McClanahan and Muthiga, 2001;
459 Hiratsuka and Uehara, 2007). This is linked to its life strategy and habitats; more
460 passive preferential feeding on macroalgal drifts (instead of an active search for food) is
461 enough to maintain populations (McClanahan and Muthiga, 2001). Sammarco (1982)
462 performed exclusion experiments, conversely finding more intense grazing by *D.*
463 *antillarum* than *E. viridis*. He showed the effects of *Diadema* grazing to be more
464 uniformly distributed, clearing macroalgae off the fenced space, while grazing by *E.*
465 *viridis* was very patchy. Perhaps the differences in his grazing results compared to ours
466 were due to calculations based on urchin densities and not on the relative weight of each
467 species, since an individual of *D. antillarum* weighs much more than an *E. viridis*.
468 Furthermore, the ratio between the grazing on each of the three macroalgae species was
469 not equal, although the three species of urchins showed equal grazing on them, i.e. there
470 was a similar preference for the three macroalgae studied. That is, there was no
471 statistical interaction between the factors sea-urchin and macroalgae. *Acanthophora*
472 *spicifera* was the most consumed, almost four times more than *L. variegata* and *H.*
473 *opuntia*; between these latter two there were no differences. These results indicate that
474 macroalgal species vary in palatability between the herbivores on coral reefs (Hay,

1991; Keeley et al., 2015). In our experiments, urchins consumed a greater quantity of *A. spicifera*, a palatable early-successional turf macroalga, avoiding the less palatable late-successional fleshy species such as *L. variegata* and *H. opuntia*. The latter algae exhibit chemical and structural defenses as strategies to deter herbivores. *L. variegata* has phlorotannins, common metabolites in other brown macroalgae, which have the potential to bind to digestive enzymes and plant nutrients, thus limiting assimilation efficiency in the grazer (Arnold et al., 1995; Iken, 2012). *H. opuntia* possesses both morphological and chemical defenses. Structural calcification hinders biting action by herbivores and reduces the nutritional value of the algae, while lipid-soluble compounds as in *L. variegata* deter reef herbivores (Hay 1997).

The food preference experiments, both in the field and the laboratory, like previous grazing experiments, showed that *E. viridis* is a generalist herbivore feeding on all the variety of macroalgae offered to it. This is a widespread character among herbivores but especially among sea-urchins, where their success derives from the ability to exploit different food resources (McClanahan and Muthiga, 2001; Iken, 2012). However, when several species of algae are offered at the same time, *E. viridis* presents food preferences. In the field it consumed twice as much *A. spicifera* than *L. variegata*, and four times as much than *H. opuntia*. Other urchin species also consume the most palatable algae first (Coppard and Campbell, 2007; Kawamata et al., 2011). Conversely, our results contrast with others (Hiratsuka and Uehara, 2007) who claim that some *Echinometra* spp. in the Pacific Ocean feed randomly. Our food preference experiment performed in tanks led to the same conclusions as these authors regarding the order of preference for macroalgae. Moreover, it showed that sea-urchin diet depends on the availability of food, as put forward by Laurence (1975). When it is abundant i.e., the relationship between food resources and sea-urchin density is high, they consume the

more palatable macroalgae species first, and as occurred in our experiment where *Echinometra viridis* consumed all the *Acanthophora spicifera* first, afterwards *Lobophora variegata* and finally *Halimeda opuntia*. These findings may contribute to explaining spatial differences (patch dynamics) in the macroalgal communities of coral reefs, since in the final community structure there is a dependency between the density of the sea urchin and macroalgal species available. Regarding the cage experiment, when herbivores, mainly *E. viridis* (herbivorous fish were heavily overfished and other sea urchins were absent), were excluded for four months all macroalgae grew, and *A. spicifera* was the fastest growing species, although significant differences with other species were not found. In uncaged conditions, *E. viridis* decimated the macroalgae bushes; *A. spicifera* and *L. variegata* were completely consumed while *H. opuntia* persisted although with a much lower abundance than at the beginning of the experiment. *Lobophora variegata* and *H. opuntia* are the two most abundant non-crustose macroalgae on the studied reefs (Sangil and Guzman, in review). However, derived from the various experiments and distribution in the field, we conclude that *H. opuntia* is the species best adapted to *E. viridis* activity. This probably explains its wide distribution over the reefs, maybe a symptom of close coevolution with reef grazers. *Lobophora variegata* is also abundant but its distribution is particularly localized, not being as wide as *H. opuntia*.

Conclusions

In conclusion, *E. viridis* is an important herbivore on Caribbean coral reefs, very active and able to control the growth of macroalgae; although it presents food preferences that explain why some macroalgal species are more abundant on the reefs than others. Its activity is however not homogeneous, as it is limited to certain habitats

(leeward reefs with low sedimentation and high cover of live corals) and only able to control the macroalgae when its population density is high. This contributes in part to the high variability of reef systems in the Mesoamerican region, and that certain habitats are free of macroalgae. In the current situation, where other herbivores are decimated (e.g., *Diadema antillarum* by the mass die-off, and herbivore fish by overfishing), *E. viridis* plays an important role in maintaining the system in a reasonable state of conservation, as it can promote the establishment of new scleractinian coral species (Sammarco, 1982), and its density has been positively related to coral cover (Bologna et al., 2012). However, the lack of predators to keep its populations in an appropriate equilibrium may be negative for the ecosystem in the long-term, since this sea-urchin has a great capacity to bioerode the reefs' calcareous structures (Griffin et al., 2003; Brown-Saracino et al., 2007; Perry et al., 2014).

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Figure captions

Fig. 1. Location of the study area and sampling sites. Caribbean Western Panama region sites (1-17) and Caribbean Central Panama region (18-27).

Fig. 2. Mean number (density, $\text{indv.} \cdot 0.25 \text{ m}^{-2}$) (+ s.e.) of *Echinometra viridis* (a), *Echinometra lucunter* (b) and *Diadema antillarum* (c) and mean percentage of cover of non-crustose macroalgae (d), *Halimeda opuntia* (e) and *Lobophora variegata* (f) (+ s.e.) according to regions, wave exposure levels and sites.

Fig. 3. Distance-based redundancy analysis (dbRDA). Relationships between the ordination of samples based on species cover and variables considered (a). Direction of increasing density ($\text{indv.} \cdot 0.25 \text{ m}^{-2}$) (b). CCA = crustose coralline algae.

Fig. 4. Consumption rate ($\text{g consumed} \cdot \text{day}^{-1}$) (+ s.e.) by *Echinometra viridis*, *Echinometra lucunter* and *Diadema antillarum* (a). Weight (g) of *Lobophora variegata*, *Halimeda opuntia* and *Acanthophora spicifera* consumed per day (b). Including the summary of the ANOVAs (see main test in Table 3S).

Fig. 5. Food preferences: Mean percentage of macroalgae consumed (+ s.e.) by *Echinometra viridis* in the field. Including the summary of the ANOVAs (see main test in Table 4aS).

768 **Fig. 6.** Food preferences: Mean percentage of macroalgae left unconsumed ($\pm$ s.e.) by
769 *Echinometra viridis* in the laboratory(a). Mean number of *Echinometra viridis*
770 associated with each bush of macroalgae during the laboratoryexperiment (b). Including
771 the summary of the ANOVAs (see main test in Table 4b,cS).

772

773 **Fig. 7.** Mean percentage of increase (+ s.e.) in each macroalga bush in the cage
774 experiment. Including the summary of the ANOVAs (see main test in Table 5S).

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Fig. 1

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Table 1. Results of distance-based permutational three-way ANOVAs and pairwise analyses comparing mean density of *Echinometra viridis*, *Echinometra lucunter* and *Diadema antillarum*, and mean cover of *Halimeda opuntia* and *Lobophora variegata* using ‘region’ (two levels: Western Panama vs Central Panama), and ‘wave exposure’ (two levels: windward vs leeward) as fixed factors, and ‘site’ (29 levels) as random factor nested in the interaction ‘zone x wave exposure’. RE = region, WE = wave exposure, S = site.

Sea urchins

[illegible]

Macroalgae

[illegible]

Table 2. Results of DistLM (distance-based linear model routine). (a) Marginal test. Test for relationships between individual environmental variables and sea urchin density. (b) Sequential test. Test for relationships between environmental variables and species cover considering all environmental variables integrated in a multiple regression model.

(a) Marginal test				
Variable	<i>Pseudo-F</i>	<i>p</i>	Prop.	
Depth	0.906	0.245	1.49	
Wave exposure	95.096	0.0001	13.50	
Sedimentation	10.563	0.0008	1.71	
Branching corals	28.183	0.0001	4.43	
Foliose corals	7.375	0.0055	1.20	
Massive and encrusting corals	3.870	0.0368	0.63	
Soft corals and anemones	25.391	0.0001	4.01	
Crustose coralline algae	11.250	0.0003	1.82	
Microalgae	0.632	0.461	0.10	
Filamentous algae	12.551	0.0006	2.02	
Foliose corticated algae	39.616	0.0001	6.12	
Corticated algae	4.501	0.026	0.73	
Geniculate coralline algae	13.945	0.0002	2.24	
Erect calcified algae	9.043	0.0015	1.47	
Leathery algae	12.151	0.0011	1.96	

(b) Sequential test				
Variable	Pseudo-F	<i>p</i>	Prop.	Cumul.
Wave exposure	95.096	0.0001	13.52	13.52
Sedimentation	35.330	0.0001	4.57	18.09
Foliose corticated algae	25.070	0.0001	3.43	21.52
Soft corals and anemones	13.886	0.0002	1.76	23.28
Geniculate coralline algae	11.750	0.0004	1.44	24.72
Filamentous algae	10.788	0.001	1.35	26.07
Erect calcified algae	10.931	0.0005	1.32	27.40
Foliose corticated algae	5.744	0.010	0.68	28.08
Crustose coralline algae	5.129	0.015	0.61	28.69

Table 3. Spearman's correlations *Echinometra viridis*, *Echinometra lucunter* and *Diadema antillarum* density (indv. · 0.25 m⁻²) and the cover percentage of non-crustose macroalgae, *Halimeda opuntia*, *Lobophora variegata* and *Acanthophora spicifera*. *** = p < 0.001, ** = p < 0.01.

Species	Non-crustose macroalgae	<i>H. opuntia</i>	<i>L. variegata</i>	<i>A. spicifera</i>
<i>E. viridis</i>	- 0.479***	-0.130**	-0.140**	0.053
<i>E. lucunter</i>	0.123**	0.135**	-0.153***	-0.024
<i>D. antillarum</i>	-0.128**	-0.007	-0.030	-0.030