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

3

4 Carlos Sangil^{1,2*}, Hector M. Guzman³

5

6 ¹Department of Botany, Ecology and Plant Physiology, University of La Laguna,
7 Canary Islands, Spain

8 ²Department of Animal Biology, Soil Science and Geology, University of La Laguna,
9 Canary Islands, Spain

10 ³Smithsonian Tropical Research Institute, Smithsonian Institution, Panama City,
11 Panama

12

13

14 *Corresponding author: Department of Botany, Ecology and Plant Physiology,
15 University of La Laguna, 38071 La Laguna, Canary Islands, Spain. Tel.: +34 922 316
16 502. E-mail address: casangil@ull.es.

17

18

19 **Abstract**

20 Long-term changes in macroalgal cover, spatial variation between macroalgal
21 communities, and relationships with environmental variables and benthic groups were
22 assessed in coral reefs along the Caribbean coast of Panama. Sampling was conducted
23 in two regions: Western and Central. Data collected between 2000 and 2012 showed a
24 continuous increase in macroalgal abundance, although patterns differed according to
25 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.

Key words: coral reef macroalgae, community structure, time series, *Lobophora variegata*, *Halimeda opuntia*, *Echinometra viridis*

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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51 struggle for substrate (McCook et al., 2001). Macroalgae are also ecological engineers
52 and can reorganize the communities (Spalding and Jarvis, 2002; Lambo and Ormond,
53 2006).

54 Due to their key role in structuring the reefs, macroalgal studies are now more
55 relevant than ever. Conservation priorities therefore need to take account of temporary
56 changes within macroalgal communities, as well as factors that determine macroalgal
57 community spatial distribution and structure (Hughes et al., 2003; Tribollet and Vroom,
58 2007; Vroom and Timmers, 2009). Macroalgal research is already a core component of
59 most reef monitoring programs but these studies rarely, if ever, investigate the long-
60 term dynamics of macroalgae (e.g., Edmunds, 2002; Nugues and Bak, 2008), nor do
61 they often study the effect of multiple environmental variables on spatial variability
62 (Aguila-Ramirez et al., 2003; Vroom et al., 2005). On the other hand, short-term
63 changes such as seasonal variability have been well documented (Díaz-Pulido and
64 Garzón-Ferreira, 2002; Ateweberhan et al., 2006; Lefèvre and Bellwood, 2010). It is
65 important to identify the factors that determine macroalgal community structure on the
66 coral reefs because macroalgae affect coral recruitment and coral exclusion (McCook et
67 al., 2001; Mumby et al., 2005; Díaz-Pulido et al., 2010). Furthermore, the predominance
68 of one functional group of macroalgae may be indicative of the state of conservation of
69 a reef since its abundance is related with different successional stages (Díaz-Pulido and
70 McCook, 2002)

71 The coral reefs in the Caribbean are among the most disturbed and threatened in
72 the world (Gardner et al., 2003; Pandolfi et al., 2003; Mora, 2008). Since the 1980s
73 when monitoring programs began in Panama, the area occupied by scleractinian coral
74 species has reduced by 50-70% (Guzman, 2003). In the last thirty years, warming
75 events have contributed to the decline of these reefs due to anomalously high

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

76 temperatures and coral bleaching (Baker et al., 2008). Mass coral bleaching occurs
77 when the thermal tolerance of corals and their photosynthetic symbionts (zooxanthellae)
78 is exceeded. Episodes of elevated sea temperatures over the past involve loss of
79 zooxanthellae (Hoegh-Guldberg, 1999). The 2005 warming event alone resulted in
80 mortality of 40% of the coral colonies in Bocas del Toro (on the western Panama coast)
81 (Eakin et al., 2010). The number of herbivores exerting top-down control on macroalgae
82 has also fallen. In 1983, populations of the sea-urchin *Diadema antillarum*, a major
83 herbivore on these reefs, were reduced by more than 93% as a result of a mass mortality
84 event (Lessios et al., 1984). Decades later, *Diadema antillarum* has still not recovered
85 on most Caribbean reefs (Lessios, 2005). Only in some places (e.g., Jamaica, Costa Rica
86 or Puerto Rico) is recovery of their populations reported (Edmunds and Carpenter,
87 2001; Lessios, 2016). This has also contributed to greater community dominance by
88 macroalgae (Carpenter, 1990). Other anthropogenic factors have also accentuated the
89 rise in macroalgal dominance. Artisanal fisheries have decimated populations of reef
90 fish (Harper et al., 2014) and in the coastal zone and river basins the impact on the reefs
91 of sedimentation and enrichment by nutrients has increased, due to indiscriminate
92 deforestation and the construction and operation of the Panama Canal (Guzman, 2003;
93 Guzman et al., 2008; Cramer et al., 2013). Other factors include oil spills (Guzman et
94 al., 1991) and traditional coral mining by the Guna people (Guzman et al., 2003).

95 In our study we attempted to discover the current status of macroalgae on the
96 coral reefs around the Caribbean coast of Panama, as well as the pattern of change over
97 the last decade. In order to answer these questions we examined: (i) non-crustose
98 macroalgal cover in time-series data collected between 2000 and 2012; (ii) the spatial
99 variability of macroalgal communities in two different regions (western and central
100 Caribbean Panama) and at two different levels of wave exposure (windward and

101 leeward) and (iii) the structure and composition of macroalgal communities in relation
102 to the variables depth, selected oceanographic parameters, sand cover, benthic groups,
103 sea-urchins and herbivorous fish.

104

105 **Materials and methods**

106 **Data collection**

107 The study area is situated on the Caribbean coast of Panama at latitude 8.6–9.6N
108 longitude 82.5–77.3W. It spans 1,295 km of coastline between Costa Rica and
109 Colombia (Fig. 1). Here, reef corals are one of the main engineer species in the coastal
110 ecosystems, however the abundance of coral communities is highly variable spatially in
111 diversity and structure, depending on the wave exposure, turbidity, nutrients and
112 proximity to the mainland (D’Croz and Robertson, 1997; Guzman, 2003). In
113 comparison, coral reefs from the entrance to the Panama Canal to the limit with Guna
114 Yala region are the most affected by coastal and industrial development, being generally
115 poorly developed and of low diversity. In contrast, the most developed coral reefs in
116 western Panama are found on the leeward side of island systems in Bocas del Toro,
117 where hundreds of cays, islands, and islets are surrounded by fringing reefs (Guzman,
118 2003).

119

120 *Long-term change monitoring*

121 Coral reefs were sampled by snorkeling and scuba diving between the years 2000 and
122 2012 at 9 sites, 5 in the western Panama region (WPR) (sites 2, 6, 10, 13, 15), and 4 in
123 the central Panama region (CPR) (sites 18, 19, 25, 26) (Fig. 1). These sites were
124 sampled once per year in the same season September-October, except the CPR reefs,
125 which were not sampled in 2007 due to logistic restrictions. At each site, 3 to 5

126 permanent 30x1 m transects were marked out in water 0.5 to 10 m deep, parallel to the
127 coastline. Using this type of fixed transects offsets the methodological difficulties
128 arising from environmental heterogeneity in coral reefs, therefore permitting the
129 detection of relatively small changes over time. Percentage macroalgal cover within
130 each transect were measured *in situ* using thirty quadrats (100x100 cm, subdivided into
131 10x10 cm). Only non-crustose macroalgae were counted.

132

133 *Relationships with environmental variables and spatial variability*

134 Fieldwork was conducted by snorkeling and scuba-diving at 29 sites, 17 in WPR and 12
135 in CPR (Fig. 1). Each site was sampled once, between September 2013 and April 2014.
136 Samples were obtained from reefs between 0.5 and 10 m deep. Percentage species cover
137 was estimated using photographs of quadrats (50x50 cm, subdivided into 10x10 cm). At
138 each site, between 18 and 24 high resolution photographs of reef communities were
139 taken randomly with a Nikon D7000 camera with Nauticam D7000 housing and two
140 Sea&Sea YS100 strobes. The dominant seaweed species were identified *in situ* and
141 percentage cover was estimated using the visual scanning method (*sensu* Murray, 2001).
142 Some conspicuous species were collected for later laboratory identification.

143 Filamentous blue-green algae (cyanobacteria), small red filamentous species
144 (Ceramiales), green filamentous (Chlorophyta and Phaeophyceae), and crustose
145 coralline algae (CCA) (except *Neogoniolithon strictum* and *Peyssonnelia* spp.) were
146 treated as groups in later analyses due to the difficulty of identification *in situ*. Number
147 of species (species density) per unit area (Simpson, 1964), and Shannon–Wiener
148 diversity were calculated for each sample (Shannon and Weaver, 1949).

149

150 *Environmental variables and benthic groups*

151 Fifteen environmental variables and benthic groups were considered and associated with
152 each quadrat in the multivariate analysis: depth, temperature, productivity, wave
153 exposure, sand cover, branching coral, foliose corals, massive and encrusting corals,
154 soft corals and anemones, *Echinometra viridis*, *Echinometra lucunter*, *Diadema*
155 *antillarum*, surgeonfish, damselfish, parrotfish, and sea-chubs. Depth of each quadrat
156 was determined from a dive computer. We obtained mean values of sea surface
157 temperature and productivity (chlorophyll A concentration $\text{mg}\cdot\text{m}^{-3}$) from the Bio-
158 Oracle (a geospatial database over an eight year period 2003-2010) to characterize the
159 study sites (Tyberghein et al., 2012). Wave exposure was calculated from a
160 topographical wave-exposure index, derived at each site from the sum of the product of
161 the distance of each location to the nearest coast (km) x the wind intensity ($\text{m}\cdot\text{s}^{-1}$) in the
162 sixteen cardinal points (see Burrow et al., 2008). Distances were calculated using GIS.
163 Wind data for the Caribbean coast of Panama was obtained from the Smithsonian
164 Tropical Research Institute Databases (between 2004-2013) (www.stri.si.edu). Sand
165 cover was estimated using the percentage cover of sand in each quadrat. Percentage
166 cover of live corals was estimated from the quadrats and grouped into the following
167 categories: branching coral, foliose corals, massive and encrusting corals, and soft
168 corals and anemones (McCook et al., 2001). Table 1S shows the species in each group.
169 The sea urchins *Echinometra viridis*, *Echinometra lucunter*, and *Diadema antillarum*
170 were counted using the same quadrats. To estimate the abundance of herbivorous fishes
171 we used a stationary visual count method (Bortone et al., 1989). In this method the
172 observer takes a position at the center of a circle with a radius 5.6 m (100 m^2) and
173 records the number (abundance), and size (cm) of individuals of each species. Only
174 herbivorous species were recorded (Froese and Pauly, 2014). At each site, six replicate
175 surveys were performed the same day the macroalgae were sampled. In later analyses

176 the species were grouped into the following four herbivorous groups: surgeonfish,
177 damselfish, parrotfish, and sea-chubs. Table 2 shows the herbivore species sampled.
178 Fish biomass was estimated using species-specific size-biomass relationships (Froese
179 and Pauly, 2014).

180

181 **Data analysis**

182 *Long-term change monitoring*

183 Changes in non-crustose macroalgal cover were examined using a permutational
184 ANOVA based on the euclidean distances of the percentage cover of permanent
185 transects using 4,999 permutations (Anderson et al., 2008). The use of permutational
186 procedures to generate a correct distribution of each *pseudo-F* statistic solves the
187 problem of non-independence of the samples when repeated-measure analyses are used
188 (Anderson et al., 2008). The design of the analysis involved a three-way model in which
189 “time” (12 levels: from 2000 to 2012, excluding 2007), and “region” (2 levels: WPR,
190 CPR) were treated as fixed factors, while site (9 levels; see Fig. 1) was treated as a
191 random factor nested within “region”. Data from 2007 in WPR were included in the
192 description.

193

194 *Spatial variability*

195 Permutational multivariate analysis of variance (PERMANOVA) (Anderson et al.,
196 2008) was performed to study spatial variations in community structure. Resemblance
197 matrices were obtained using Bray-Curtis dissimilarity for the percentage cover of the
198 macroalgae dataset using 4,999 permutations. The analysis consisted of a three-way
199 model in which “region” (two levels: WPR, CPR) and “wave exposure” (two levels
200 according to the wave exposure index previously calculated: reef exposed to the open

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

201 ocean “windward”; reef sheltered from the waves “leeward”) were treated as fixed
202 factors. “Site” (29 levels) was treated as a random factor, nested within “region × wave
203 exposure.” Sums of squares type III (Anderson et al., 2008) were employed to account
204 for unbalanced design. Significant terms in the full model were examined using
205 appropriate *a posteriori* pairwise comparisons. The species that contributed most to
206 differences in significant terms were identified using similarity percentages (SIMPER)
207 (Clarke and Gorley, 2006).

208 Additionally, permutational analyses of variance (ANOVAs) were performed to
209 test spatial differences in total algal cover, species density, and diversity. The design
210 utilized a three-way analysis, similar to PERMANOVA, with “region” and “wave
211 exposure” as fixed factors and “site” as a random factor nested within “region × wave
212 exposure”. Significant terms were examined using appropriate *a posteriori* pairwise
213 comparisons. Data used for PERMANOVA, SIMPER, and ANOVAs were square-root
214 transformed.

216 *Relationships between seaweed communities and environmental variables and benthic* 217 *groups*

218 In order to demonstrate that variability in community structure can be explained by the
219 environmental variables and benthic groups considered, we applied a distance-based
220 linear model routine (DistLM) (Legendre and Anderson, 1999). The analysis, based on
221 similarity matrices, used the Bray–Curtis index for the dataset percentage cover of
222 macroalgae. The method used stepwise selection, an adjusted R^2 criterion and 9,999
223 permutations. Prior to the DistLM analysis, we used the draftsman plot method with the
224 corresponding Pearson correlation coefficients to explore the relationships between the
225 environmental variables (Clarke and Gorley, 2006). This test detects any possible

relationships between variables to discard strongly correlated variables. Following recommendations by Clarke and Gorley (2006), macrophyte cover was square-root transformed and the environmental variables and benthic groups were normalized. A distance-based redundancy analysis (dbRDA) was used to visualize the relationships between seaweed assemblages and environmental variables based on the multivariate regression model generated by the DistLM analysis (McArdle and Anderson, 2001). These analyses show the fifteen macroalgal species with the highest percentage cover on the studied coral reefs. Additionally, Spearman partial correlations were used to test the relationships between the abundance of these fifteen species and the variables that contributed most to the DistLM analysis.

Statistical analyses were performed using PRIMER-E® v.6 + PERMANOVA+ (www.primer-e.com; Clarke and Gorley, 2006) and SPSS 17 for Windows (SPSS, Chicago, IL, USA).

Results

Long-term change monitoring

The percentage cover of non-crustose macroalgae showed significant differences from the interaction “time x region” and “time x site (region)” (Table 1). During the study period, the macroalgal cover on CPR reefs was higher than on WPR reefs throughout the studied decade, although the increase was faster in WPR (Fig. 2a). In both regions a bloom in coverage was observed over time, especially from the year 2003 onwards, however these changes did not follow a common pattern. Similar patterns were observed at the level of “site” (Fig. 2b); most acute at sites 2, 6, and 15.

Composition of communities

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

251 A total of 105 taxa were identified in the coral reefs studied (see Table 3S). The mean
252 percentage cover ($\pm$ s.d.) of all macrophytes per quadrat was 37.95 ± 24.88 %. CCA were
253 the most abundant taxa, with a cover of 10.90 ± 10.37 % (28.71% of total cover),
254 followed by *Halimeda opuntia* (cover: 5.37 ± 10.73 ; contribution to total (ctt): 14.15%),
255 *Lobophora variegata* (cover: 4.86 ± 11.70 ; ctt: 12.81%), *Dictyopteris delicatula* (cover:
256 2.83 ± 6.97 ; ctt: 7.45%), *Caulerpa verticillata* (cover: 1.61 ± 8.89 ; ctt: 2.98%), *Amphiroa*
257 *fragilissima* (cover: 1.45 ± 4.22 ; ctt: 3.82%), *Dictyota menstrualis* (cover: 1.13 ± 3.54 ; ctt:
258 2.98%), and cyanophytes (cover: 1.11 ± 3.68 ; ctt: 2.98%). These eight species groups
259 contributed more than 75% of the total algae cover. The remaining species exhibited
260 low abundances, generally well below 1%.

261 262 *Spatial variability*

263 Analyses of the total species composition set showed a significant interaction between
264 the factors “region x wave exposure” and significant differences within the factor “site
265 (region x wave exposure)” (Table 2a). *A posteriori* tests for “region x wave exposure”
266 and pairs of levels of the factor “region” found differences between the windward reefs
267 of WPR and CPR. For pairs of levels of the factor “wave exposure” the test found
268 differences between windward and leeward reefs in both regions (Table 2b). Mean
269 percentage cover of species per region and per level of wave exposure have been
270 recorded in the Table 3S. According to the SIMPER procedure (Table 2c), the
271 differences between WPR and CPR on the windward reefs were most marked for CCA,
272 *H. opuntia*, *Dictyopteris delicatula*, *Dictyota mertensii*, and *Sargassum polyceratum*.
273 The differences between windward and leeward reefs of WPR were due to differences
274 in the percentage cover of *Dictyopteris delicatula*, CCA, *Lobophora variegata*, *Dictyota*
275 *mertensii*, and *Halimeda opuntia*. Between the windward and leeward reefs of CPR, the

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

276 differences were due to percentage cover of *Halimeda opuntia*, *Lobophora variegata*,
277 CCA, *Dictyopteris delicatula*, and filamentous Ceramiales. The differences in the factor
278 “site (region x wave exposure)” showed high local variability in community structure.
279 Mean percentage cover of some species varied between sites (see Table 4S).

280 The percentage of total macroalgal cover differed significantly with the factor
281 ‘wave exposure,’ and also “site (region x wave exposure)” (Table 3a). The cover on
282 windward reefs was higher ($48.37 \pm 23.68\%$) than on leeward reefs ($30.96 \pm 23.19\%$) (Fig.
283 3a). Differences were also found in cover between sites within the same region and
284 within the same level of wave exposure (Fig. 3b). Species density and diversity showed
285 significant differences in the interaction “region x wave exposure” (Table 3b, c). Both
286 species density and diversity, used as *a posteriori* analyses for pairs of levels of the
287 factor “region”, found differences between windward reefs of WPR and CPR. Analyses
288 of pairs of levels of the factor “wave exposure” found differences between windward
289 and leeward reefs in both regions (Table 3b, c). Species density and diversity were
290 highest on windward reefs of WPR, followed by leeward reefs of CPR, whereas they
291 were lowest on the leeward reefs of WPR and the windward reefs of CPR (Fig. 4a, c).
292 Mean species density and diversity per site (Fig. 4b, d) also showed differences for the
293 factor “site (region x wave exposure)”.

294

295 *Relationships between macroalgal communities and environmental variables and* 296 *benthic groups*

297 There was a high correlation ($R > 0.5$) between temperature and wave exposure, and
298 temperature and productivity. For this reason, temperature was excluded from the
299 multivariate analyses. DistLM analysis showed there was significant variation between
300 community structure and all the environmental variables and benthic groups except

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

301 depth (Table 4). The marginal test (Table 4a) examined the significant variation
302 between algal community and each separate environmental variable in turn. Macroalgal
303 community variation was explained by each variable as follows: wave exposure
304 (5.38%), productivity (3.75%), *Echinometra viridis* (3.45%), sand cover (2.88%),
305 branching corals (1.80%), *Echinometra lucunter* (1.59%), massive and encrusting corals
306 (1.39%), sea-chubs (1.12%), surgeonfish (1.05%), damselfish (1.05%), *Diadema*
307 *antillarum* (0.95%), parrotfish (0.87%), soft corals and anemones (0.86), and foliose
308 corals (0.85%). The values for each of these environmental variables differed slightly in
309 the sequential test (Table 4b), which tested the effect of all variables together. In the
310 sequential test, wave exposure (5.38%), *Echinometra viridis* (3.50%), and sand cover
311 (3.22%) were the dominant variables affecting macroalgal community variability,
312 followed by productivity (1.90%), branching corals (1.88%), massive and encrusting
313 corals (1.20%), foliose corals (0.94%), surgeonfish (0.86%), damselfish (0.71%), sea
314 chubs (0.65%), parrotfish (0.56%), *Diadema antillarum* (0.43%), *Echinometra lucunter*
315 (0.38%), and soft corals and anemones (0.32%). Together these fourteen variables
316 explained 21.64% of the total variability in the macroalgal community.

317 In the dbRDA analysis (Fig. 5a) wave exposure and *Echinometra lucunter* were
318 positively correlated with the first axis, whereas productivity was negatively correlated
319 with the first axis. Sand cover was correlated positively with the second axis, and sea
320 chubs were negatively correlated with the second axis. Surgeonfish, damselfish, and
321 parrotfish were partially positively correlated with the first axis and negatively
322 correlated with the second. *Echinometra viridis*, massive and encrusting corals, foliose
323 corals, and soft corals and anemones were partially negatively correlated with the first
324 axis and positively correlated with the second. When algal abundance data were
325 overlaid (Fig. 5b) it was seen that *Dictyopteris delicatula* and *Dictyota ciliolata*

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

326 increased in percentage with positive values on the first axis. *Caulerpa fastigiata*
327 increased in cover with negative values of the first axis. Percentage cover of CCA,
328 *Lobophora variegata*, filamentous Ceramiales, *Dictyota menstrualis*, and cyanophytes
329 increased with negative values on the second axis. *Amphiroa fragilissima*, *Caulerpa*
330 *verticillata*, and *Bryothamnion seaforthii* showed partial correlation with positive values
331 on both axes. Percentage cover of *Halimeda opuntia*, *Dictyota mertensii* and *Sargassum*
332 *polyceriatum* showed partial correlation with the positive values of the first axis and the
333 negative values of the second axis. *Dictyota bartayresiana* abundance showed partial
334 negative correlation on both axes.

335 The Spermann's correlations (Table 5) found significant positive relationships
336 between wave exposure and CCA, *Halimeda opuntia*, *Dictyopteris delicatula*, *Dictyota*
337 *ciliolata*, *Dictyota mertensii*, and *Sargassum polyceriatum*. The relationship was
338 negative between wave exposure and *Lobophora variegata*, filamentous Ceramiales
339 *Dictyota bartayresiana*, and *Caulerpa fastigiata*. The number of *Echinometra viridis*
340 per quadrat was negatively related to *Halimeda opuntia*, *Lobophora variegata*,
341 *Dictyopteris delicatula*, *Amphiroa fragilissima*, *Dictyota menstrualis*, *Dictyota ciliolata*,
342 *Sargassum polyceriatum*, filamentous Ceramiales, and *Caulerpa fastigiata*. There was
343 a significant positive relationship between sand cover and *Caulerpa verticillata*,
344 *Amphiroa fragillissima*, *Bryothamnion seaforthii*, and *Caulerpa fastigita*; the
345 relationship was negative between sedimentation and CCA, *Halimeda opuntia*,
346 *Lobophora variegata*, *Dictyota mertensii*, *Sargassum polyceriatum*, and filamentous
347 Ceramiales.

348

349 Discussion

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

350 Along the Caribbean Panama coast the coral reef ecosystem is in decline
351 (Guzman, 2003). Meanwhile, the abundance of non-crustose macroalgae has been
352 gradually increasing, as seen in the trend in our data between the years 2000 and 2012.
353 Macroalgae are now the main benthic organisms on the reefs along this coast, and in
354 some areas percentage cover of macroalgae may even exceed 60%, surpassing the cover
355 of scleractinian coral species (Guzman et al., 2008). The increase in macroalgal
356 abundance coincides with other signs of degradation common to most of the world's
357 coral reefs (Hughes et al., 2003; Pandolfi et al., 2003) and in diverse areas of the
358 Caribbean, e.g., Virgin Islands and Curaçao (Edmunds, 2002; Nugues and Bak, 2008).
359 We also found a significant increase over time in both WPR and CPR, as well as at the
360 sites within each region. However, over the time-frame of the study (12 years), the
361 patterns of change found between regions and sites show that Caribbean Panama reefs
362 have differed in their temporal dynamics. These different observed trajectories cannot be
363 attributed to a single factor but rather to synergies between them. Indeed the scientific
364 debate is reaching the conclusion that decline of the reefs is a response to the interaction
365 between local and global disturbance (Knowlton and Jackson, 2008). Global variables
366 (warming, acidification) have already changed and will continue to affect the coral
367 reefs, favoring a phase shift from scleractinian corals to non-crustose macroalgae
368 (Anthony et al., 2011). In addition, local and regional factors like sedimentation,
369 nutrient input, diseases and overfishing, multiply the changes in community structure
370 (Pandolfi et al., 2005), causing profound changes at locations where human activities
371 are greater. In our study, the CPR and WPR have differed in their percentages of non-
372 crustose macroalgae cover, and in the speed these have increased over time. The cover
373 of non-crustose macroalgae was higher in CPR, probably due to two factors: First, all
374 data from this region belong to exposed sites, we will discuss below the effect of waves

on the development of macroalgae. Second, in the past and present, the studied localities are also within a disturbed area. Previous to our study (before 2000), impacts such as oil spills and increased leaching of nutrients and sedimentation deriving from coastal development and Panama Canal activities, had heavily transformed the reef ecosystem in the area (Guzman et al., 1991; Guzman et al., 2008). Unfortunately there are no previous data on macroalgal cover to aid in accurately assessing the direct impact of the past activities. However, the continual spread of macroalgae in this region indicates such impacts have accelerated it. In fact, the highest and fastest increase in macroalgal abundance was detected in the WPR, with a severe outbreak after 2002, although the macroalgal cover never reached the values of CPR. Macroalgal spread and sudden shifts in abundance like those observed here tend to occur immediately after a specific disturbance, such as a coral bleaching event (Diaz-Pulido and McCook, 2002), a drastic reduction in the population of herbivores (Nugues and Bak, 2008), or an extreme climate event (Edmonds, 2002), chronic coastal runoff or sedimentation (Fabricius, 2005). However, the 2002 bloom we observed around WPR does not seem to be directly related to a mass coral mortality because the documented bleaching events in this region occurred before 2002 (Eakin et al., 2010). Neither were any mass mortalities of herbivores recorded in 2002, or any extreme climate events. Rather than being caused by a single event, the increase in macroalgal abundance in the region may be the result of a cascade of disturbances (Cheal et al., 2010). In the past decade the Bocas del Toro area, which lies within the WPR, has been cleared of much of its jungle habitat. This deforestation has led to greater nutrient runoff into coastal waters, an effect which has been further amplified by tourism and growth of the human population and their activities, e.g., fishing (Guzman and Guevara, 1998; Seemann et al., 2014). Some sites, where the highest significant increases in macroalgae have occurred, are close to

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

400 more populated areas (e.g., site 2 and 6). However, other reefs had low macroalgal
401 cover throughout the entire period studied (e.g., site 10). These small-scale differences
402 may have also originated from individual site disturbances, each of which affect only a
403 specific location (Edmunds, 2002).

404 Most macroalgal community cover (> 75% of the total macroalgal cover) was
405 comprised of a small number of different taxa: CCA, *Halimeda opuntia*, *Lobophora*
406 *variegata*, *Dictyopteris delicatula*, *Caulerpa verticillata*, *Amphiroa fragilissima*,
407 *Dictyota menstrualis*, and cyanophytes. These eight taxa are documented as being the
408 most common and dominant species throughout the Caribbean (Williams and Polunin,
409 2001; Beach et al., 2003) and frequently inhabit areas where scleractinian corals have
410 subsided (Lapointe, 1997; Nugues and Bak, 2008). These species are characterized by
411 deterring herbivores, since they have chemical and/or structural defences such as
412 calcification (Hay, 1997). Though dominated by a few species, the macroalgal
413 community structure in our study region was a complex mosaic, featuring small patches
414 of many different algae. This variability in algal colonization (Fig. 6) results from
415 different successional stages (Díaz-Pulido and McCook, 2002; McManus and
416 Polsenberg, 2004), and the interaction of multiple factors (Bonaldo and Bellwood,
417 2010). Multivariate analyses of all the datasets and univariate analyses of total cover,
418 species density and diversity, also show a high spatial variability. Such spatial variation
419 in macroalgal community structure is a common characteristic within coral reefs (Díaz-
420 Pulido and McCook, 2002; Vroom et al., 2005); and wave exposure is one of the main
421 disturbances involved in these changes (Kilar and McLachlan, 1989), as confirmed in
422 our study. The multivariate analysis of all data sets found that differences in wave
423 exposure levels between windward and leeward were related to differences in cover of
424 the main species. However, unlike the leeward reefs that were similar between the two

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

425 regions, windward areas resulted different due, we suggest, to sedimentation. This
426 added factor was higher on the heavily disturbed windward reefs of CPR. Within each
427 region and level of wave exposure, community structure was also highly variable
428 between sites. Local changes may be caused by different levels of wave exposure and
429 sedimentation within each area (windward *vs.* leeward) and region, or by urchin density,
430 which was especially variable between sites. Note that when considering a wide area,
431 the studied variables may have a wider range of values (Bauman et al., 2013). Total
432 cover was higher on windward reefs than leeward reefs in both studied regions. It
433 additionally varied between sites exposed to the same level of wave action. On
434 windward reefs, macroalgae tend to be naturally more dominant than corals, regardless
435 of anthropogenic interference or climate events (Purcell and Bellwood, 2001, Costa et
436 al., 2002). Species density and diversity showed a similar pattern to the multivariate
437 analysis of all data sets. Windward reefs differed from leeward reefs, but also the
438 windward reefs differed between the two regions. The number and diversity of species
439 were higher on the windward reefs of WPR, but on the windward reefs of CPR the
440 values of species density and diversity were similar to the values of the leeward reefs in
441 both areas. Wave action generally prevents the monopolization of a few species and
442 favors heterogeneous communities (Cheroske et al., 2000). Here, the effect of the waves
443 was not observed clearly, likely due to interaction with sedimentation.
444 All environmental variables considered (except depth), whether individually or
445 integrated into a multiple regression, showed a significant influence on community
446 structure. Depth is an important factor in macroalgal community structure on coral
447 reefs, mainly due to light attenuation, water movement, and herbivore pressure
448 differences (Hoek and Breeman, 1978). However, we hypothesize that the depth range
449 studied was not enough to change community structure. Wave exposure, herbivore

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

450 density (*Echinometra. viridis*), and sedimentation (estimated indirectly as sand cover of
451 the quadrats) were the variables that best explain community variability. These three
452 factors are widely documented as being the main drivers of changes in macroalgal
453 communities and coral reef ecosystems (Fabricius and De'ath, 2001; Diaz-Pulido and
454 McCook, 2002; McManus and Polsenberg, 2004). Productivity was also important,
455 whereas cover of live corals (branching corals, massive and encrusting corals, foliose
456 corals, and soft corals) and the abundance of other herbivores, fish (surgeonfish,
457 damselfish, sea-chubs, and parrotfish) and sea-urchins (*Diadema antillarum* and
458 *Echinometra lucunter*), had limited influence. Water turbulence can influence
459 community structure in a range of ways; it can prevent the settlement of algal
460 propagules, affect herbivore density and feeding rates, cause movement of sediment, or
461 improve the rate of nutrient uptake by macroalgae (Hurd, 2000). All these effects
462 depend on the velocity of the seawater. According to dbRDA analysis and Spearman's
463 correlations: CCA, *Halimeda. opuntia*, *Dictyopteris delicatula*, *Dictyota* (*D. ciliolata*,
464 *D. mertensii*), and *Sargassum polyceriatum* were found in higher abundance on
465 windward reefs. *Lobophora variegata*, filamentous Ceramiales, *Dictyota bartayresiana*,
466 and *Caulerpa fastigiata* were more abundant on leeward reefs. We found that
467 productivity was negatively correlated with wave exposure level, which was unexpected
468 because wave action usually prevents stratification of water masses and raises up
469 nutrients and re-suspends sediment from deep water (Hurd, 2000). However, our
470 analyses did include data from leeward sites around Bocas del Toro where runoff from
471 the land adds significant nutrient input (Seemann et al., 2014). The sea-urchin
472 *Echinometra viridis* was the herbivore that influenced macroalgal communities most
473 significantly. After the mass mortality of *Diadema antillarum* in 1983 (Lessios et al.,
474 1984; Lessios, 2005), *Echinometra viridis* became the key herbivore on many

Caribbean reefs. In our study, the mean density of *Echinometra viridis* was 10.24
indv. $\cdot$ m⁻², while *Echinometra lucunter* and *Diadema antillarum* showed lower densities,
1.20 and 0.24 indv. $\cdot$ m⁻² respectively. dbRDA analyses showed that macroalgal
abundance was negatively correlated to *Echinometra viridis* density. Spearman's test
also revealed a negative correlation between urchin density and the cover of *Halimeda*
opuntia, *Lobophora variegata*, *Dictyoteris delicatula*, *Amphiroa fragilissima*, *Dictyota*
menstrualis, *Dictyota ciliolata*, *Sargassum polyceriatum*, filamentous Ceramiales, and
Caulerpa fastigiata. There was no relationship found between macroalgal cover and
CCA and cyanophyte abundance. Wave action is known to be an important force
limiting urchin grazing and population density, and promoting segregation of
populations (Hernández et al., 2008). In reefs along the Caribbean coast of Panama,
Echinometra species showed clear spatial segregation, *Echinometra viridis* was most
abundant on leeward reefs, where its populations reached maximum values per site of
53.76 indv. $\cdot$ m⁻². On windward reefs they were scarce, at some sites too few to count.
Contrary to this, *Echinometra lucunter* was most abundant on windward reefs, reaching
maximum values per site of 12.01 indv. $\cdot$ m⁻², but it was not found on leeward reefs. Due
to their effects on grazing pressure, these differences in urchin density and distribution
explain some of the differences in abundance of macroalgal communities between
windward and leeward reefs. We observed that high *Echinometra viridis* densities
appeared to control the abundance of non-crustose macroalgae, whereas *Echinometra*
lucunter seemed to have less influence. *Diadema antillatum* was only abundant (up to
1.32 indv. $\cdot$ m⁻²) at some sites of the leeward reefs of the CPR, although macroalgae were
scarce at this density. The role of fish in controlling macroalgae has been widely
discussed, but both field and experimental evidence suggest that sea-urchins have a
greater influence (McClanahan et al., 1996). In our study, fish (parrotfish, surgeonfish,

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

500 damselfish, and sea-chubs) were most abundant on the windward reefs and the grazing
501 pressure they exerted was not significant enough to drastically reduce the cover of non-
502 crustose macroalgae; the same is also documented for other reefs (Newman et al. 2006).
503 It has been suggested that the fish act selectively, choosing to graze on the most
504 palatable algal species (Burkepile and Hay, 2008; Williams and Polunin, 2001).
505 Sedimentation has been associated with the increase of macroalgal abundance on coral
506 reefs. However, it has negative effects on the growth of many macroalgae (McCook et
507 al., 1999). It is directly involved in various phases of macroalgal development including
508 growth, reproduction, settlement, and recruitment (Umar et al., 1998). Indeed,
509 sedimentation has previously been associated with reorganization of macroalgal
510 communities (Fabricius and De'ath, 2001). In our analysis, we found that the cover of
511 *Amphiroa fragilissima*, *Caulerpa verticillata*, *Bryothamnion seaforthii*, and *Caulerpa*
512 *fastigiata* increased with increased sedimentation. In contrast, the percentage cover of
513 *CCA*, *Halimeda opuntia*, *Lobophora variegata*, *Dictyota mertensii*, *Sargassum*
514 *polyceriatum*, and *Dictyota bartayresiana* decreased with greater sedimentation.
515 Sediment build-up therefore seems to impact macroalgal abundance indirectly by
516 inhibiting competitors (e.g., other sessile organisms such as corals) and herbivores (both
517 urchins and fish). It also reduces the abundance of herbivores, particularly urchins, and
518 thereby relieves grazing pressure on macroalgae (Sangil et al., 2011). Moreover,
519 sediment coverage can lower the nutritional value of macroalgae, by making it less
520 palatable for herbivores (Bonaldo and Bellwood, 2010). In fact we found that the key
521 herbivore, *Echinometra viridis*, was always significantly lower in abundance at highly
522 sedimented sites. When corals are in a healthy state, they are able to exclude macroalgae
523 from patches of substrate (McCook et al., 2001). We found that coral abundance was
524 inversely related to macroalgae cover, although the percentage cover of live corals was

not the main variable explaining the structure of algal communities. However, we commonly found macroalgae and corals coexisting on reefs, e.g., *Halimeda opuntia* and *Lobophora variegata* grew close to coral but mainly fixed to adjacent branches of dead coral fragments.

529

530 **Conclusion**

Macroalgae have expanded, and it is expected to continue expanding over the reefs of the Caribbean coast of Panama. Currently, they are the dominant benthic group in many places, exceeding the cover of scleractinian coral species, and in a few decades they could significantly decimate many coral colonies. In the macroalgal spatio-temporal dynamics, various synergies (global changes and local factors) are involved. Some of these interactions are still poorly understood. For this reason, long-term studies are needed to predict the future structure of coral reef communities. Macroalgal cover is higher on windward reefs, where the lowest herbivory favours their development. In contrast, on some leeward reefs high densities of the sea urchin *Echinometra viridis* prevent the macroalgal growth. Relationships between *Echinometra viridis* and macroalgae need to be thoroughly explored because this can contribute to create different patches of colonization and successional stages of communities, contributing to the resilience of some coral reefs in the Caribbean.

544

545 **Acknowledgments**

Long-term data was produced by the Panama Coral Reef Monitoring Network, a program supported by the Smithsonian Tropical Research Institute, Smithsonian Institution. Special thanks to Carlos Guevara and Marta Rodríguez for field work

support and comments and initial review of this manuscript. C. Sangil benefited from a postdoctoral fellowship from the Dr. Manuel Morales Foundation.

551

552 **References**

- 553 Águila-Ramírez, R.N., Casas-Valdez, M., Ortega-García, S., Núñez-García, S., López,
554 R.A., Cruz-Ayala, M.B., 2003. Spatial and seasonal variation of macroalgal biomass in
555 Laguna Ojo de Liebre, Baja California Sur, México. *Hydrobiologia* 501, 207–14.
- 556 Anderson, M.J., Gorley, R.N., Clark, K.R., 2008. *Permanova + for Primer: Guide to*
557 *Software and Statistical Methods*. Primer-E Ltd, United Kingdom.
- 558 Anthony, K.R.N., Maynard, J.A., Díaz-Pulido, G., Mumby, P.J., Marshall, P.A., Cao,
559 L., Hoegh-Guldberg, O., 2011. Ocean acidification and warming will lower coral reef
560 resilience. *Global Change Biol.* 17, 1798-1808.
- 561 Aronson, R.B., Precht, W.F., 2001. White-band disease and the changing face of
562 Caribbean coral reefs. *Hydrobiologia* 460, 25–38.
- 563 Aronson, R.B., Precht, W.F., 2006. Conservation, precaution, and Caribbean reefs.
564 *Coral Reefs* 25, 441–450.
- 565 Ateweberhan, M., Bruggemann, J.H., Breeman, A.M., 2006. Effects of extreme
566 seasonality on community structure and functional group dynamics of coral reef algae in
567 the southern Red Sea (Eritrea). *Coral Reefs* 25, 391–406.
- 568 Baker, A.C., Glynn, P.W., Riegl, B., 2008. Climate change and coral reef bleaching: an
569 ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar.*
570 *Coast. Shelf S.* 80, 435-471.
- 571 Bauman, A.G., Feary, D.A., Heron, S.F., Pratchett, M.S., Burt J.A., 2013. Multiple
572 environmental factors influence the spatial distribution and structure of reef
573 communities in the northeastern Arabian Peninsula. *Mar. Pollut. Bull.* 72, 302–312.

574 Beach, K., Walters, L., Borgeas, H., Smith, C., Coyer, J., Vroom, P., 2003. The impact
 575 of *Dictyota* spp. on *Halimeda* populations of Conch Reef, Florida Keys. J. Exp. Mar.
 576 Biol. Ecol. 297, 141-159.
 577 Bellwood, D.R., Hughes, T.P., Folke, C., Nyström, M., 2004. Confronting the coral reef
 578 crisis. Nature 429, 827-833.
 579 Bonaldo RM, Bellwood DR (2010) Spatial variation in the effects of grazing on
 580 epilithic algal turfs on the Great Barrier Reef Australia. Coral Reefs, 30: 381-390.
 581 Bortone, S.A., Kimmel, J.J., Bundrick, C.M., 1989. A comparison of three methods for
 582 visually assessing reef fish communities: time and area compensated. Ne. Gulf S. 10,
 583 85-96.
 584 Burkepile, D.E., Hay, M.E., 2008. Herbivore species richness and feeding
 585 complementarity affect community structure and function on a coral reef. PNAS 105,
 586 16201–16206.
 587 Burrows, M.T., Harvey, R., Robb, L., 2008. Wave exposure indices from digital
 588 coastlines and the prediction of rocky shore community structure. Mar. Ecol. Prog. Ser.
 589 353, 1–12.
 590 Carpenter, R.C., 1990. Mass mortality of *Diadema antillarum* I. Long-term effects on
 591 sea urchin population-dynamics and coral reef algal communities. Mar. Biol. 104, 67–
 592 77.
 593 Carpenter, K.E., Abrar, M., Aeby, G., et al., 2008 One-third of reef-building corals face
 594 elevated extinction risk from climate change and local impacts. Science 321, 560-563.
 595 Cheal, A.J., Emslie, M.J., Sweatman, H., MacNeil, A.M., Jonker, M., Cripps, E.,
 596 Schaffelke, B., 2010. Coral–macroalgal phase shifts or reef resilience: links with
 597 diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral
 598 Reefs 29, 1005–1015.

599 Cheroske, A.C., Willialms, S.L., Carpenter, R., 2000. Effects of physical and biological
600 disturbances on algal turfs in Kaneohe Bay, Hawaii. *J. Exp. Mar. Biol. Ecol.* 248, 1-34.
601 Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E,
602 Plymouth.
603 Costa, O.S., Attrill, M.J., Pedrini, A.G., De Paula, J.C., 2002. Spatial and seasonal
604 distribution of seaweeds on coral reefs from Southern Bahia, Brazil. *Bot. Mar.* 45, 346-
605 355.
606 Crabbe, M.J., 2008. Climate change, global warming and coral reefs: modeling the
607 effects of temperature. *Comput. Biol Chem.* 32, 31-34.
608 Cramer, K.L., 2013. History of human occupation and environmental change in
609 Western and Central Caribbean Panama. *B. Mar. Sci* 89, 955-982.
610 D'Croz, L., Robertson, D.R., 1997. Coastal oceanographic conditions affecting coral
611 reefs on both sides of the Isthmus of Panama. *Proc. 8th Intl. Coral Reef Symp.* 2, 2053-
612 2058.
613 Diaz-Pulido, G., Garzón-Ferreira, J., 2002. Seasonality in algal assemblages on
614 upwelling-influenced coral reefs in the Colombian Caribbean. *Bot. Mar.* 45, 284-292.
615 Diaz-Pulido, G., Harii, S., McCook, L.J., Hoegh-Guldberg, O., 2010. The impact of
616 benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29, 203-208.
617 Diaz-Pulido, G., McCook, L.J., 2002 The fate of bleached corals: patterns and dynamics
618 of algal recruitment. *Mar. Ecol. Prog. Ser.* 232, 115-128.
619 Eakin, C.M., Morgan, J.A., Heron, S.F., Smith, T.B., 63 others, 2010. Caribbean corals
620 in crisis: record thermal stress, bleaching, and mortality in 2005. *PlosOne* 11, ee13969.
621 Edmunds, P.J., 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands.
622 *Coral Reefs* 21, 357-367.

623 Edmunds, P.J., Carpenter, R.C., 2001. Recovery of *Diadema antillarum* reduces
 624 macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. PNAS
 625 98, 5067-5071.
 626 Fabricius, K., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs:
 627 review and synthesis. Mar. Pollut. Bull. 50, 125-146.
 628 Fabricius, K., De'ath, G., 2001. Environmental factors associated with the spatial
 629 distribution of crustose coralline algae on the Great Barrier Reef. Coral Reefs, 19: 303-
 630 309.
 631 Fong, P., Paul, V.J., 2011. Coral reef algae. In: Dubinsky, Z., Stambler, N. (Eds.), Coral
 632 Reefs: an ecosystem in transition. Dordrecht: Springer, Netherlands, pp. 241-272.
 633 Froese, R., Pauly, D., 2015. FishBase World Wide Electronic Publication. www.
 634 fishbase.org (accessed 1.12.15).
 635 Gardner, T.A., Côte', I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term
 636 region-wide declines in Caribbean corals. Science 301, 958–960.
 637 Guzman, H.M., 2003. Caribbean coral reefs of Panama: present status and future
 638 perspectives. In: Cortes J (eds.) Latin American Coral Reefs, Elsevier Science, pp. 241-
 639 274.
 640 Guzman, H.M., Cipriani, R., Jackson, J.B.C., 2008. Historical decline in coral reef
 641 growth after the Panama Canal. Ambio 37, 343-346.
 642 Guzman, H.M., Guevara, C.A., 1998. Arrecifes coralinos de Bocas del Toro, Panamá II:
 643 Distribución y estado de conservación de los arrecifes de las islas de Bastimentos,
 644 Solarte, Carenero y Colón. Rev. Biol. Trop. 46, 601-623.
 645 Guzman, H.M., Guevara, C.A., Castillo, A., 2003. Natural disturbances and mining of
 646 Panamanian coral reefs by indigenous people. Conserv. Biol. 17, 1396–1401.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

647 Guzman, H.M., Jackson, J.B.C., Weil, E., 1991. Short-term ecological consequences of
648 a major oil spill on Panamanian subtidal reef corals. *Coral Reefs* 10, 1–12.

649 Harper, S., Guzman, H.M., Zyllich, K., Zeller, D., 2014. Reconstructing Panama’s total
650 fisheries catches from 1950-2010: highlighting data deficiencies and management
651 needs. *Mar. Fish. Rev.* 76, 51-65.

652 Hay, M.E., 1997. The ecology and evolution of seaweed-herbivore interactions on coral
653 reefs. *Coral Reefs* 16, 67-76.

654 Hernández, J.C., Clemente, S., Sangil, C., Brito, A., 2008. The key role of *Diadema* aff.
655 *antillarum* (Echinoidea: Diadematidae) throughout the Canary Islands (eastern
656 subtropical Atlantic) in controlling macroalgae assemblages: an spatio-temporal
657 approach. *Mar. Environ. Res.* 66, 259-270.

658 Hoeg-Guldberg, O., 1999. Climate change, coral bleaching and the future of the
659 world’s coral reefs. *Mar. Freshwater Res.* 50, 839-866.

660 Hoek, C.V.D., Breeman, A.M., 1978. The distribution of algae, corals and gorgonians in
661 relation to depth, light attenuation, water movement and grazing pressure in the fringing
662 coral reef of Curaçao, Netherlands Antilles. *Aquat. Bot.* 5, 1-46.

663 Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., et al., 2003. Climate change,
664 human impacts, and the resilience of coral reefs. *Science* 301, 929–933.

665 Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. *J.*
666 *Phycol.* 36, 453–472.

667 Kilar, J.A., McLachlan J., 1989. Effects of wave exposure on the community structure
668 of a plant-dominated, fringing-reef platform: intermediate disturbance and disturbance-
669 mediated competition. *Mar. Ecol. Prog. Ser.* 54, 265-276.

670 Knowlton, N., 2001. The future of coral reefs. *PNAS* 98, 5419-5425.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

671 Knowlton, N., Jackson, J.B.C., 2008. Shifting baselines, local impacts and global
672 change on coral reefs. Plos Biol. 6, 215-220.

673 Lambo, A.C., Ormond, R.F.G., 2006. Continued post-beaching decline and changed
674 benthic community of a Kenyan coral reef. Mar. Pollut. Bull. 52, 1617-1624.

675 Lapointe, B.E., 1997. Nutrient thresholds for bottom-up control of macroalgal blooms
676 on coral reefs in Jamaica and southeast Florida. Limnol. Oceanogr. 42, 1119-1131.

677 Lefebvre, C.D., Bellwood, D.R., 2010. Seasonality and dynamics in coral reef
678 macroalgae: variation in condition and susceptibility to herbivory. Mar. Biol. 157, 955-
679 965.

680 Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing
681 multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1-
682 24.

683 Lessios, H.A., 2005. *Diadema antillarum* populations in Panama twenty years following
684 mass mortality. Coral Reefs 24, 125-127.

685 Lessios, H.A., 2016. The great *Diadema antillarum* die-off, 30 years later. Annu. Rev.
686 Mar. Sci. 8, 1-17.

687 Lessios, H.A., Cubit, J.D., Robertson, D.R., Shulman, M.J., Parker, M.R., Garrity, S.D.,
688 Levings, S.C., 1984. Mass mortality of *Diadema antillarum* on the Caribbean coast of
689 Panama. Coral Reefs 3, 173-182.

690 McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a
691 comment on distance-based redundancy analysis. Ecology 82, 290-297.

692 McClanahan, T.R., Kamakura, A.T., Muthiga, N.A., Yebio, M.G., Obura, D., 1996.
693 Effect of sea urchin reductions on algae, coral and fish populations. Conserv. Biol. 10,
694 136-154.

695 McClanahan, T., Karnauskas, M., 2011. Relationships between cover, current strength,
 696 herbivory, and a fisheries closure in Glovers Reef Atoll, Belize. *Coral Reefs* 30, 9-19.
 697 McCook, L., 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific
 698 issues and management consequences for the Great Barrier Reef. *Coral Reefs*, 18, 357-
 699 367.
 700 McCook, L., Jompa, J., Díaz-Pulido, G., 2001. Competition between corals and algae
 701 on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400-417.
 702 McManus, J.W., Polsenberg, J., 2004. Coral–algal phase shifts on coral reefs: ecological
 703 and environmental aspects. *Progr. Oceanogr.* 60, 263–279.
 704 Mora, C., 2008. A clear human footprint in the coral reefs of the Caribbean. *P. Roy.
 705 Soc. B-Biol. Sci.* 275, 767–773.
 706 Mumby, P.J., Foster, N.L., Fahy, E.A.G., 2005 Patch dynamics of coral reef macroalgae
 707 under chronic and acute disturbance. *Coral Reefs* 24, 681–692.
 708 Murray, S.N., 2001. Quantifying abundance: density and cover. In: Murray NS,
 709 Ambrose, R.F., Dethier, M.N. (Eds.) *Methods for Performing Monitoring, Impact, and
 710 Ecological Studies on Rocky Shores*. Coastal Research Center, Marine Science Institute,
 711 University of California, Santa Barbara, California, pp. 123–154.
 712 Newman, M.J.H., Paredes, G.A., Sala, E., Jackson, J.B.C., 2006. Structure of Caribbean
 713 coral reef communities across a large gradient of fish biomass. *Ecol. Lett.* 9, 1216–
 714 1227.
 715 Nugues, M.M., Bak, R.P.M., 2008. Long-term dynamics of the brown macroalga
 716 *Lobophora variegata* on deep reefs in Curaçao. *Coral Reefs* 27, 389–393.
 717 Pandolfi, J.M., Bradbury, R.H., Sala, E., et al., 2003. Global trajectories of the long-
 718 term decline of coral reef ecosystems. *Science* 301, 955-958.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

719 Pandolfi, J.M., Jackson, J.B.C, Baron, N., Bradbury, R.H., et al., 2005. Are US coral
720 reefs on the slippery slope to slime? *Science* 307, 1725-1726.

721 Purcell, S.W., Bellwood, D.R., 2001. Spatial patterns of epilithic algal and detrital
722 resources on a windward coral reef. *Coral Reef* 20, 117-125.

723 Sangil, C., Sansón M., Afonso-Carrillo, J., 2011. Spatial variation patterns of subtidal
724 seaweed assemblages along a subtropical oceanic archipelago: thermal gradient vs
725 herbivore pressure. *Estuar. Coast. Shelf S.* 94, 322-333.

726 Seemann, J., González, C.T., Bolaños, R.C., Berry, K., Heiss, G.A., Struck, U.,
727 Leinfelder, R.R., 2014. Assessing the ecological effects of human impacts on coral reefs
728 in Bocas del Toro, Panama. *Environ. Monit. Assess.* 186, 1747-1763.

729 Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communications*.
730 University of Illinois Press, Illinois.

731 Simpson, G.G., 1964. Species density of North America recent mammals. *Syst. Zool.*
732 13, 57–73.

733 Spalding, M.D., Jarvis, G.E., 2002. The impact of the 1998 coral mortality on reef fish
734 communities in the Seychelles. *Mar. Pollut. Bull.* 44, 309-321.

735 Tribollet, A.D., Vroom, P.S., 2007. Temporal and spatial comparison of the relative
736 abundance of macroalgae across the Mariana Archipelago between 2003 and 2005.
737 *Phycologia* 46, 187-197.

738 Tyberghein, L., Verbruggen, H., Pauly, K., Troupin., C., Mineur, F., De Clerk, O.,
739 2012. Bio-ORACLE: a global environmental dataset for marine species distribution
740 modelling. *Global Ecol. Biogeogr.* 21, 272–281.

741 Umar, M.J., McCook, L.J., Price, I.R., 1998. Effects of sediment deposition on the
742 seaweed a fringing coral reef. *Coral Reefs* 17,169-177.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65

743 Vroom, P.S., Page, K.N., Peyton, K.A., Kukea-Shultz, J.K., 2005. Spatial heterogeneity
744 of benthic community assemblages with an emphasis on reef algae at French Frigate
745 Shoals, North-western Hawai'ian Islands. Coral Reefs 24, 574–81.
746 Vroom, P.S., Timmers, M.A.V., 2009. Spatial and temporal comparison of algal
747 biodiversity and benthic cover at Garden Pinnacles, northwestern Hawai'ian Islands. J.
748 Phycol. 45, 337–347.
749 Williams, I.D., Polunin, N.V.C., 2001. Large-scale associations between macroalgal
750 cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19, 358-
751 366.
752
753
754

Graphical Abstract (for review)

The map displays the geographical distribution of the Western and Central Panama biogeographic realms. The map includes latitude and longitude coordinates, a north arrow, and a 100 km scale bar. Two regions are highlighted with boxes and labels: 'Western Panama' and 'Central Panama'.

Table 1. Results of distance-based permutational three-way ANOVA comparing non – crustose macroalgae cover using ‘time’ (12 levels: from 2000 to 2012, excluding 2007), and ‘region’ (2 levels: Western Panama, Central Panama) as fixed factors, and ‘site’ (9 levels) as random factor nested in ‘region’. T= time, R= region, S= site.

ANOVA analysis				
Source of variation	df	MS	Pseudo-F	<i>P (perm)</i>
T	11	34.775	8.351	0.002
R	1	892.13	14.545	0.006
S (R)	7	65.588	23.351	0.0002
T x R	11	10.932	2.625	0.006
T x S (R)	77	4.288	1.526	0.008
Res	288	2.808		
Total	395			

Table 2. Results of distance-based permutational three-way PERMANOVA comparing macrophyte community structure using ‘region’ (two levels: Western Panama and Central Panama), and ‘wave exposure’ (two levels: windward and leeward) as fixed factors, and ‘site’ (29 levels) as random factor nested in the interaction ‘region x wave exposure’ (a). Results of pairwise analyses for ‘region x wave exposure’ interactions (b). SIMPER procedure shows species that most contribute to the differences in the interactions (c). R= region, W= wave exposure, S= site

(a) PERMANOVA analysis				
Source of variation	df	MS	Pseudo-F	P (perm)
R	1	49645	2.353	0.027
W	1	1.0836E5	5.137	0.0002
R x W	1	71336	3.382	0.0044
S (R x W)	25	22215	15.982	0.0002
Res	581	1390		
Total	609			
(b) Pairwise analyses				
For pairs of levels of factor ‘region’			t	P (perm)
windward	Western vs Central		1.870	0.012
leeward	Western vs Central		1.364	0.099
For pairs of levels of factor ‘wave exposure’			t	P (perm)
Western Panama	windward vs leeward		1.918	0.004
Central Panama	exposed vs sheltered		2.250	0.002
(c) SIMPER				
	Dissimilarity (%)			
Species	Exposed regions Western vs Central	Western Panama windward vs leeward	Central Panama windward vs leeward	
Crustose coralline algae	10.39	9.52	12.19	
Halimeda opuntia	9.89	5.94	13.61	
Dictyopteris delicatula	9.11	9.66	9.68	
Dictyota mertensii	5.65	6.15		
Sargassum polyceratum	5.38	5.88		
Cyanophytes	5.17	5.85	2.81	
Amphiroa fragilissima	4.62	5.36	4.83	
Dictyota ciliolata	4.43		5.37	
Lobophora variegata	4.39	6.94	12.84	
Dictyota menstrualis	3.88	4.03	5.31	
Bryothamnion seaforthii	3.35	3.78		
Caulerpa verticillata	3.16		4.03	
Filamentous Ceramiales	3.06	3.44	6.99	
Jania adhaerens	2.62	2.64		
Amphiroa hancockii		2.62		
Amphiroa tribulus		2.09		
Green filaments		1.92		

Table 3. Results of distance-based permutational three-way ANOVAs and pairwise analyses comparing mean of total cover (a), species density (number of species per sample) (b), and mean diversity (based on Shannon-Wiener index) (c) using ‘region’ (two levels: Western Panama and Central Panama), and ‘wave exposure’ (two levels: windward and leeward) as fixed factors, and ‘site’ (29 levels) as random factor nested in the interaction ‘region x wave exposure’. R= region, W= wave exposure, S= site.

(a) Total cover

ANOVA analysis				
Source of variation	df	MS	Pseudo-F	<i>P</i> (perm)
R	1	18803	2.704	0.120
W	1	64176	9.230	0.007
R x W	1	18585	2.673	0.120
S (R x W)	25	7337.6	35.542	0.0002
Res	581	206.45		
Total	609			

(b) Species density

ANOVA analysis				
Source	df	MS	Pseudo-F	<i>P</i> (perm)
R	1	14.161	4.639	0.039
W	1	13.553	4.440	0.046
R x W	1	69.931	22.909	0.0004
S (R x W)	25	3.216	18.326	0.0002
Res	581	0.175		
Total	609			

Pairwise analyses

For pairs of levels of factor ‘region’		t	<i>P</i> (perm)
windward regions	Western vs Central	1.870	0.012
leeward regions	Western vs Central	1.364	0.099
For pairs of levels of factor ‘wave exposure’		t	<i>P</i> (perm)
Western Panama	windward vs leeward	1.918	0.004
Central Panama	windward vs leeward	2.250	0.002

(c) Diversity

ANOVA analysis				
Source	df	MS	Pseudo-F	<i>P</i> (perm)
R	1	1.37E-02	1.99E-02	0.886
W	1	3.862	5.632	0.027
R x W	1	11.582	16.888	0.0002
S (R x W)	25	0.721	10.910	0.0002
Res	581	6.61E-02		
Total	609			

Pairwise analyses

For pairs of levels of factor ‘region’		t	<i>P</i> (perm)
windward regions	Western vs Central	3.894	0.001
leeward regions	Western vs Central	1.861	0.096
For pairs of levels of factor ‘wave exposure’		t	<i>P</i> (perm)
Western Panama	windward vs leeward	3.708	0.012
Central Panama	windward vs leeward	2.877	0.010

Table 4. Results of DistLM (distance-based linear model routine). (a) Marginal test. Test for relationships between individual environmental variables and species cover. (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	Pseudo-F	<i>p</i>	Prop.	
Depth	0.671	0.799	0.10	
Productivity	23.709	0.0001	3.75	
Wave exposure	34.539	0.0001	5.38	
Sand cover	18.025	0.0001	2.88	
Branching corals	11.147	0.0001	1.80	
Foliose corals	5.265	0.0001	0.85	
Massive and encrusting corals	8.550	0.0001	1.39	
Soft corals and anemones	5.288	0.0001	0.86	
<i>Echinometra viridis</i>	21.732	0.0001	3.45	
<i>Echinometra lucunter</i>	9.820	0.0001	1.59	
<i>Diadema antillarum</i>	2.408	0.015	0.95	
Surgeonfish	6.432	0.0001	1.05	
Damselfish	6.469	0.0001	1.05	
Parrotfish	5.392	0.0001	0.87	
Sea chubs	6.862	0.0001	1.12	

(b) Sequential test				
Variable	Pseudo-F	<i>p</i>	Prop.	Cumul.
Wave exposure	34.539	0.0001	5.38	5.38
<i>Echinometra viridis</i>	21.642	0.0001	3.50	8.88
Sand cover	21.406	0.0001	3.22	11.75
Productivity	13.313	0.0001	1.90	13.65
Branching corals	13.454	0.0001	1.88	15.53
Massive and encrusting corals	8.723	0.0001	1.20	16.73
Foliose corals	6.918	0.0001	0.94	17.68
Surgeonfish	6.460	0.0001	0.86	18.39
Damselfish	5.288	0.0001	0.71	19.27
Sea chubs	4.926	0.0002	0.65	19.92
Parrotfish	4.242	0.0003	0.56	20.49
<i>Diadema antillarum</i>	3.299	0.002	0.43	20.93
<i>Echinometra lucunter</i>	2.950	0.004	0.38	21.31
Soft corals and anemones	2.498	0.01	0.32	21.64

Table 5

Table 5. Spearman’s correlations between the cover of the fifteen most abundant macrophytes and the three main environmental variables according to the DistLM analysis. ** = p <0.01, * = p <0.05.

Variables	Species							
	C. coralline algae	H. opuntia	L. variegata	D. delicatula	C. verticillata	A. fragilissima	D. menstrualis	Cyanophytes
Wave exposure	0.284**	0.146**	-0.167**	0.476**	-0.022	0.026	-0.041	-0.054
<i>Echinometra viridis</i>	0.027	-0.100*	-0.141**	-0.172**	-0.079	-0.111**	-0.123**	-0.053
Sand cover	-0.352**	-0.156**	-0.208**	0.002	0.287**	0.118**	-0.030	-0.058
	D. ciliolata	D. mertensii	S. polyceriatium	F. Ceramiales	B. seaforthii	D. bartayresiana	C. fastigiata	
Wave exposure	0.362**	0.155**	0.179**	-0.134**	-0.025	-0.137**	-0.184**	
<i>Echinometra viridis</i>	-0.114**	-0.074	-0.092*	-0.118**	-0.043	-0.033	-0.100*	
Sand cover	0.056	-0.134**	-0.118**	-0.188**	0.165**	-0.158**	0.133**	

Figure 1

Fig. 1

Figure 2

Fig. 2

Figure 3

Fig. 3

Figure 4

Fig. 4

Figure 5

Fig. 5

Fig. 6