Top-down control involved in (turf) algae-mediated coral damage in coastal reefs of Belize, Central America

Many coral reefs in the Caribbean experienced substantial changes in their benthic community composition during the last decades, resulting in a shift from scleractinian corals to other benthic invertebrate and algae dominance and consequent degradation of coral reefs, but knowledge about the related role of coral-algae contacts that may negatively affect corals is scarce. Therefore, benthic community composition, abundance of algae grazers, and the abundance and character of coral-algae contacts were assessed at 13 Belizean reef sites distributed along a distance gradient to the Belizean mainland (12-70 km): Mesoamerican Barrier Reef (inshore), Turneffe Atoll (inner and outer midshore), and Lighthouse Reef (offshore). In-situ surveys revealed significantly higher benthic cover by scleractinian corals at the remote Lighthouse Reef (26 – 29 %) when compared to the other sites (4 - 19 %). The abundance of herbivorous fish and the sea urchin Diadema antillarum significantly increased towards the offshore reef sites, while the occurrence of direct coral-algae contacts consequently increased significantly with decreasing distance to shore. About 60 % of these algae contacts were harmful (exhibiting coral tissue damage, pigmentation change, or overgrowth) for corals (mainly genera Orbicella and Agaricia), particularly when filamentous turf algae were involved. These findings provide support to the theory that a top-down control is involved in primarily (turf) algae-mediated coral damage in Belizean coastal coral reefs.

1   **Top-down control involved in (turf) algae-mediated coral damage in coastal reefs of Belize,**

2   **Central America**

3   Christian Wild[1*], Carin Jantzen[2], Stephan Georg Kremb[3]

4   [1]Coral Reef Ecology Group (CORE), Leibniz Center for Tropical Marine Ecology (ZMT),

5   Fahrenheitstr. 6, 28359 Bremen, Germany

6   [2]SECORE Media & Communication, Bremen, Germany

7   [3]King Abdullah University of Science and Technology, Thuwal, 23955 -6900, Kingdom of Saudi

8   Arabia

9   *corresponding author, E-mail: christian.wild@zmt-bremen.de

10   **ABSTRACT**

11   Many coral reefs in the Caribbean experienced substantial changes in their benthic community

12   composition during the last decades, resulting in a shift from scleractinian corals to other benthic

13   invertebrate and algae dominance and consequent degradation of coral reefs, but knowledge

14   about the related role of coral-algae contacts that may negatively affect corals is scarce.

15   Therefore, benthic community composition, abundance of algae grazers, and the abundance and

16   character of coral-algae contacts were assessed at 13 Belizean reef sites distributed along a

17   distance gradient to the Belizean mainland (12-70 km): Mesoamerican Barrier Reef (inshore),

18   Turneffe Atoll (inner and outer midshore), and Lighthouse Reef (offshore). In-situ surveys

19   revealed significantly higher benthic cover by scleractinian corals at the remote Lighthouse Reef

20   (26 – 29 %) when compared to the other sites (4 - 19 %). The abundance of herbivorous fish and

21   the sea urchin *Diadema antillarum* significantly increased towards the offshore reef sites, while

22   the occurrence of direct coral-algae contacts consequently increased significantly with decreasing

23   distance to shore. About 60 % of these algae contacts were harmful (exhibiting coral tissue

24   damage, pigmentation change, or overgrowth) for corals (mainly genera *Orbicella* and *Agaricia*),

25   particularly when filamentous turf algae were involved. These findings provide support to the

26   theory that a top-down control is involved in (turf) algae-mediated coral damage in Belizean

27   coastal coral reefs.

29   Keywords: coral reef ecology, phase shift, coral algae contacts, coastal influence

INTRODUCTION

31   Phase shifts from scleractinian corals to other invertebrates such as sponges (Maliao et al. 2008),

32   ascidians (Bak et al. 1996) or octocorals along with a strong increase in occurrence of benthic

33   algae and cyanobacteria (Hughes 1996; Gardner et al. 2003; Andrefouet and Guzman 2005) are

34 particularly reported from coral reefs in the Caribbean Sea (Hughes 1994; Gardner et al. 2003).

35 These reefs are highly affected by intense tourism, overfishing and coastal agriculture (Burke and

36 Maidens 2004), but also by a wide diversity of severe coral diseases (Goreau et al. 1998; Aronson

37 and Precht 2001; Patterson et al. 2001), and a previous pathogen-induced mass mortality of the

38 sea urchin *Diadema* spec. (Lessios et al. 1984), the formerly dominant herbivorous invertebrate

39 in Caribbean reefs.

40 In contrast, Caribbean coral reefs off Belize, Central America, have been described as pristine

41 and undisturbed compared to reef locations in the Northern Caribbean (Lapointe et al. 1997),

42 which was mainly attributed to low fishing pressure in Belize waters and a modest development

43 of coastal development for agriculture and tourist industry. However, McClanahan and Muthiga

44 (1998) and McClanahan et al. (1999) reported benthic community shifts from corals to fleshy

45 macroalgae at reef locations along the Belizean Barrier Reef and Glovers Atoll off Belize,

46 although fishing and inorganic nutrient concentrations were at relatively low levels. Thus, there is

47 obviously some debate about the degradation status of Belizean coral reefs and the particular role

48 of benthic algae that can damage corals if they are in direct contact to each other (Smith et al.

49 2006; Haas et al. 2010a).

50 Many benthic algae (Hay et al. 1987; Schmitt et al. 1995) and cyanobacteria (Nagle and Paul

51 1998) species produce toxic secondary metabolites that act as agents against herbivory and anti-

52 fouling (Paul et al. 2001) and therefore may negatively affect corals. Additionally, abrasion-

53 mediated polyp retraction (River and Edmunds 2001) or high production of labile dissolved

54 organic matter (DOM) by reef algae, which can stimulate planktonic microbial metabolism with

55 ensuing O_2 deficiency (Haas et al. 2010a; Haas et al. 2010b; Wild et al. 2010), may also

56 negatively affect corals in direct contact with algae.

57 However, data about benthic community composition in combination with assessments of coral-

58 algae interactions in reefs off Belize have not been described in the scientific literature.

59   The focus of the present rapid assessment pilot study therefore was to estimate live coral and reef

60   algae cover along with grazer (sea urchin *Diadema antillarum* and herbivorous fish) abundance,

61   and to quantify and characterize coral-algae contacts at different reef locations in Belize. Main

62   objective of this study was to link abundance of herbivorous reef organisms with the occurrence

63   and character of coral-algae interactions.

64   **MATERIAL AND METHODS**

65   **Study site**

66   All surveys were carried out during a Belize expedition of the research and media vessel

67   *Aldebaran* between 12 and 23 March 2009. In total, 13 reef sites were investigated along a

68   distance gradient to the Belize mainland (12-70 km). Surveys were conducted at sites located

69   along the Mesoamerican Barrier Reef (inshore, n = 4), Turneffe Atoll (West side, i.e. inner

70   midshore, n = 5; East side, i.e. outer midshore, n = 2) and Lighthouse Reef (offshore, n = 2).

71   Locations were mapped with GPS, and distances to Belize City were determined (Fig. 1 and

72   Table 1).

73   **Benthic cover**

74   At each site, two surveys (I. and II.) were carried out independently in water depths of 5 – 8 m by

75   SCUBA divers. I. During each of these surveys, two 50 m line point intercept transects (LPI) with

76   measuring points every 50 cm (n = 202 data points) were conducted to assess benthic community

77   composition. Test transects were carried out prior to select appropriate categories for benthic

78   cover and were then defined as: all present scleractinian corals and benthic alga genera as well as

79   turf algae (which were defined as a dense conglomerate of various diminutive and filamentous

80   algae growing up to a height of about 1 cm), hydrozoan fire corals, octocorals (soft corals and

81   gorgonians), sponges and seagrasses. According to Nadon and Stirling (2006), the conducted

82   transect methodology provides best combination of efficiency and accuracy.

83   II. Herbivore abundance was measured in a 2 m wide and 50 m long belt, with the transect line in

84   the middle (resulting area = 100 m²). In this area, abundances of the sea urchin *D. antillarum*

85   were quantified along with numbers of key herbivorous fishes (parrot fishes, surgeon fishes and

86   chubs) in the water column up to 3 m above this area using the following categories: 1. few (n =

87   1-5), 2. few-occasional (n = 6-10), 3, occasional (n = 11-50), 4. occasional-many (n = 51-100), 5.

88   many (n > 101). Photo documentation was used to verify taxonomic identification and to avoid

89   any observer bias.

90   **Coral-algae contacts**

91   Along with benthic cover, coral-algae contacts were recorded at each site in one LPI transect. All

92   scleractinian corals were carefully inspected for the occurrence of coral-algae contact, i.e. the

93   presence of macro or turf algae in direct contact to the coral. Coral-algae contacts were recorded

94 with photos, taken directly above the contact area using Panasonic LUMIX DMC-TZ5 and

95 Canon PowerShot G10 digital cameras (resolution: 7 and 14 mega pixels, respectively).

96 Subsequently, digital image analysis was used to identify both groups of organisms to the genus

97 level and to evaluate the character of coral-alga contacts.

98 The following categories were used: I. no visible impact on corals (Fig. 2 a), II. overgrowth by

99 algae (i.e. parts of the algae overbearing the interface between coral and algae and entering the

100 coral zone) leading to reduced light availability or even coral tissue damage (Fig. 2 b, c), III.

101 coral tissue pigmentation decrease at the interface (Fig. 2 d); categories II. & III. were

102 considered as visibly harmful contact for corals.

103 **Statistical analyses**

104 Data were not normally distributed. Therefore, the two-sided Mann-Wilcox U-Test was

105 conducted for direct comparisons of parameters between the remote locations and the other sites,

106 both pooled for that purpose. All values are given as means ± SE. The non-parametric Spearman

107 correlation test was applied to relate shore distance to a) benthic cover (coral and algae), b)

108 abundance of coral-algae contacts and c) *D. antillarum* occurrence. To check for correlation of

109 herbivorous fish abundances and distance from shore, their frequency was set as rank order and

110 the non-parametric Spearman correlation test was likewise conducted.

111 **RESULTS**

112 **Benthic cover and grazer abundance**

113 Benthic cover by scleractinian corals was low (4 - 19 %) at all investigated coral reef locations

114 except at the remote Lighthouse Reef (26 – 29 %) where coral cover was significantly higher

115 compared to Turneffe Atoll and the Barrier Reef (two-sided U-test, p < 0.05) (Table 2 and Fig. 3).

116 Among the scleractinian corals, the genera *Agaricia* and *Orbicella* dominated (Table 2).

117 Specimens of the genus *Acropora*, namely *A. cervicornis*, were only observed at Lighthouse

118 Reef, and *A. palmata* was not found at any site. Scleractinian corals were the most abundant

119 benthic organisms only at the remote Lighthouse Reef. At eight other sites, algae dominated the

120 benthic community, and at the remaining three sites octocorals were dominant. Coral cover was

121 positively correlated with distance to shore (Table 3, non-parametric Spearman correlation, p <

122 0.05; Fig. 4).

123 Visible benthic sponge cover was relatively low with 2 - 12 %. Among the hydrozoans, only the

124 fire corals *Millepora* could be observed, but its contribution to benthic community was minor (≤

125 5 % benthic cover at all reef sites, if any present). The relative seafloor cover by benthic algae

126 was highly variable among sites (Table 2). Consequently, there were no significant differences in

127 algal cover between the three geographical groups of reef sites and no correlation along the

128 distance gradient to the Belizean mainland (Fig. 4). The calcareous green algal genus *Halimeda*

129 was the most abundant benthic algae at eight sites, but brown algae of the genus *Dictyota*,

130 filamentous turf algae consortia and fleshy red or brown algae (*Jania, Wrangelia, Padina,*

131 *Lobophora*) along with coralline red algae were also observed at all sites. Other green algae

132 (*Udotea, Rhipocephalus*) and segrasses (*Thalassia*) could be detected only at three stations along

133 the Barrier Reef and at Southwest Turneffe Atoll.

134 Herbivorous fish were most abundant (more than 100 individuals per 100 m² reef area) at the

135 remote Lighthouse Reef, where also the only specimens of *D. antillarum* could be observed. This

136 coincided with lowest algal cover at the mentioned sites compared to all others (2-sided U-test, p

137 < 0.05).

138 By contrast, all other sites exhibited low (less than 50 individuals per 100 m² reef area)

139 herbivorous fish abundances, and no *D. antillarum* was present. *D. antillarum* abundance was

140 significantly correlated with distance to shore, and herbivorous fish abundance showed a trend

141 for the same relationship (Table 3, non-parametric Spearman correlation, p < 0.01 and p = 0.056;

142 Fig. 4).

143 **Abundance and character of coral-algae contacts**

144 Corals were relatively often in direct contact with algae (10-78 % of all corals observed), with

145 significantly higher percentage of contact at sites of the Barrier Reef and the inner-midshore of

146 Turneffe Atoll (Table 2) compared to the more remote sites (2-sided U-test, p < 0.01). Coral-algae

147 contacts decreased with growing distance to shore (Table 3, non-parametric Spearman

148 correlation, p < 0.01). The percentages of contacts that were visibly harmful for the corals,

149 including coral tissue damage, coral pigmentation change and overgrowth by algae, exhibited no

150 correlation with distance to the mainland, and were very variable (0 - 100 %).

151 In total, 203 different coral-alga contacts were investigated and revealed that 18 % of these

152 contacts involved more than one coral or algal genus. Among corals, the genera *Orbicella* and

153 *Agaricia* were most often involved in contacts with algae (31 and 29 % respectively), whereas the

154 genera *Porites* and *Siderastrea* showed low relative involvement (10 % each). Filamentous turf

155 (30 %), fleshy red (24 %, particularly genus *Jania*), the brown alga *Dictyota* spp. (21 %) and the

156 green alga *Halimeda* spp. (19 %) together accounted for 94 % of all algae representatives

157 involved in contact with corals.

158 Analysis of visibly harmful contacts revealed that in average among all sites 50 % of the

159 scleractinian corals were overgrown by algae and 11 % revealed pigmentation change, whereas

160 about 39 % of all coral-algae contacts showed no visible effect on corals. Harmful contacts were

161 primarily caused by filamentous turf algae consortia (35 %) and to a minor extent by fleshy red

162 algae (30 %), the calcifying green algae *Halimeda* spp. (26 %) and the fleshy brown algae

163 *Dictyota* spp. (19 %). Contact with *Halimeda* did only result in coral tissue pigmentation

164 decrease, but not in tissue damage.

165 **DISCUSSION**

166 This study indicates negative impacts on benthic coral reef communities close to the Belize

167 mainland coast, manifested by rising coral-algae contact frequency and decreasing coral cover.

168 Main objective of the present study was to assess potential linkage between abundance of

169 herbivores and abundance along with character of coral-alga contacts. The results of the present

170 study indicate that there is a relationship between those two variables in Belizean reefs. This

171 indicates that a top-down control is involved in (turf) algae-mediated coral damage in coastal

172 reefs of Belize. We can however not rule out a potential bottom-up co-effect of coastal

173 eutrophication, but unfortunately we were not able to measure inorganic nutrient concentrations

174 parallely on this expedition.

175 A crucial top down factor on reef degradation is the presence of herbivores, namely fish and sea

176 urchins (Hughes 1994, Lapointe 1997), and in the present study the abundance of herbivorous

177 fish and *D. antillarum* decreased with decreasing distance to shore. Therefore, grazing of algae

178 by both benthic and pelagic herbivores likely contributes in shaping benthic community

179 composition in the investigated reefs. Coral-algae contact abundance, as an indicator for

180 degradation of coral reefs, showed negative correlation with herbivorous fish abundance,

181 suggesting that a top-down scenario is involved in the algae-mediated degradation of Belizean

182 reefs.

183 Even though the low number of Belizean fishers does apparently not target herbivorous fish

184 (McClanahan and Muthiga 1998), herbivorous fish abundance was significantly higher in the

185 remote reef sites (Lighthouse Long Caye, Lighthouse Long Caye West and Turneffe NW). The

186 study by Williams et al. (2001) demonstrated that the presence of corals, i.e. their 3D-structure,

187 attracts herbivorous fish. Coral reef decline, when linked to low abundances of grazing fish, may

188 thus be a vicious cycle, which intensifies itself. Additionally, spatial heterogeneity in herbivore

189 abundance and therefore grazing intensity may contribute to regional diversity among and within

190 tropical reef habitats (Lewis 1986), and fishes do likely play a major role in structuring coral reef

191 macrophyte communities (Morrison 1988; Reinthal and Macintyre 1994).

192 In the Caribbean, supplementary to herbivorous fish, *D. antillarum* and other sea urchins control

193 benthic algae populations (Aronson et al. 2000, Aronson and Precht 2001, (McManus and

194 Polsenberg 2004). McClanahan and Muthiga (1998) reported that population density of *D.*

195 *antillarum* in Belizean reefs was less than 1 individual per 1000 m^2 14 years after the die off in

196 1983-84. The present study showed that *D. antillarum* now occurs in actual numbers of 20 to 30

197 individuals per 1000 m^2 at some reef locations off Belize, i.e. at least one order of magnitude

198 higher population density compared to about 10 years ago. These findings are supported by

199 observations of *D. antillarum* at other reef locations along the Barrier Reef and Turneffe Atoll

200 (M. McField, Smithsonian Institution Belize, pers. comm.) and is in agreement with other studies,

201 who reported recovery of *D. antillarum* in reefs around Jamaica (Edmunds and Carpenter 2001)

202 and St. Croix (Miller et al. 2003). The findings of the present study however indicate that

203 combined herbivory by fishes and sea urchins was not sufficient in order to prevent a large

204 number of coral-algae contacts particularly at reef sites close to the Belizean mainland.

205 The observed coral-algae contacts can be the cause for manifold threats triggered directly or

206 indirectly by algae in contact with corals. Overgrowth of coral tissue, tissue damage, and

207 pigmentation decrease occurred most often in contact with turf algae. Considerable tissue damage

208   caused by the turfing filamentous red alga *Corallophila huysmansii* on the branching

209   scleractinian coral *Porites cylindrica* was also observed by Jompa and McCook (2003a), which

210   may be related to allelochemical mechanisms. The delicate filaments of turf algae are likely be

211   able to colonise and kill coral tissue by direct chemical effects as suggested by Jompa and

212   McCook (2003b). This assumption is supported by results from Titlyanov et al. (2007), who

213   demonstrated that the cyanobacterium *Lyngbya bouillonii*, often associated with algae turf, acts as

214   a poison against scleractinian corals and is able to kill live coral tissue. Turf algae can also trap

215   organic matter by their delicate branches (Stewart 1989), which was frequently observed in the

216   present study. Thus, while overgrowing coral colonies, turf algae may form dense algal-sediment

217   mats causing a localized smothering and shading of coral colonies (Nugues and Roberts 2003).

218   This increases energy expenditure for cleaning mechanisms and leads to a reduced energy

219   acquisition due to shading of photosynthetically active parts of the coral (Potts 1977).

220   Additionally, the proximity of macroalgae may further lead to the alteration of water flow, not

221   only causing a change in the rate of sedimentation (Eckman and Duggins 1991), but also an

222   alteration in the rate of gas exchange (Hurd and Stevens 1997) and an inhibition of particle

223   capture rates of corals (Morrow and Carpenter 2008). The combination of light reduction through

224   shading, reduced gas exchange, a decrease in nutrient supply through the inhibition of particle

225   capture rates and increased energy expenditure for cleaning mechanisms may weaken the

226   competitive ability of corals. Weakened or dead coral tissue may then be more easily overgrown

227   by more persistent secondary settlers such as fleshy red or brown algal species tightening the

228   algal predominance following the first invasion of the relatively short-lived turf algal

229   assemblages. The result of the present study that comparably less coral tissue damage was

230   observed in direct contact with calcifying green algae of the genus *Halimeda* may be explained

231   by the morphology of these algae that in contrast to turf and fleshy red algae do not exhibit such

232   delicate filaments. However, Nugues et al. (2004) reported that pigment decrease of corals in

233 contact with *Halimeda* may be explained by the role of this particular alga in introducing white

234 plague disease to reef corals. This is confirmed by the finding of the present study that most

235 pigment decrease of coral tissue was associated with *Halimeda* contacts.

236 In summary, the observed negative correlation between abundance of coral-algae contacts and

237 occurrence of herbivores may thus be a further piece of a puzzle supplementing recent studies

238 (Stevenson et al. 2007; Sandin et al. 2008) that found negative correlation between coastal

239 pressures (overuse of resources, but also eutrophication that was not assessed in the present

240 study) and coral reef health.

241 **ACKNOWLEDGEMENTS**

242 We thank Dr. M. Mc Field and E. M. Zetsche for background information about Belize coral reefs

243 and their valuable advice prior to this study. S. Bendixen, S. Duewel, A. Wittenzellner, and

244 particularly captain F. Schweikert, are acknowledged for their help during the ALDEBARAN

245 cruise, and A. Haas and S. Becker are acknowledged for their help during data analysis and figure

246 preparation.

247 **FUNDING STATEMENT**

248 This research was funded by German Research Foundation (DFG) grant Wi 2677/2-1 to C.W and

249 ALDEBARAN Förderverein für Meeresforschung und Umweltjournalismus e.V.

250 **LITERATURE CITED**

251 Eckman JE, Duggins DO (1991) Life and death beneath macrophyte canopies: effects of
252   understory kelps on growth rates and survival of marine benthic suspension feeders. .
253   Oecologia 87: 473-487
254 Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover
255   and increases abundance of juvenile corals on a Carribean reef. Proc Nat Acad Sci 98:
256   5067-5071
257 Haas AF, al-Zibdah M, Wild C (2010a) Seasonal in-situ monitoring of coral-algae interaction
258   stability in fringing reefs of the Northern Red Sea Coral Reefs 29: 93-103
259 Haas AF, Naumann MS, Struck U, Mayr C, el-Zibdah M, Wild C (2010b) Organic matter release
260   by coral reef associated benthic algae in the Northern Red Sea. J Exp Mar Biol Ecol 389:
261   53-60
262 Hay ME, Fenical W, Gustafson K (1987) Chemical defence against diverse coral-reef herbivores.
263   Ecology 68: 1581-1591
264 Hurd CL, Stevens CL (1997) Flow simulation around single- and multiple-bladed seaweeds with
265   various morphologies. J Phycol 33: 360-367
266 Jompa J, McCook L (2003a) Contrasting effects of turf algae on corals: massive *Porites* spp. are
267   unaffected by mixed-species turfs, but killed by the red algae *Anotrichium tenue*. Mar
268   Ecol Prog Ser 258: 79-86
269 Jompa J, McCook LJ (2003b) Coral-algal competition: macroalgae with different properties have
270   different effects on corals. Mar Ecol Prog Ser 258: 87-95
271 Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef
272   community. Ecol Monogr 56: 183-200
273 McClanahan TR, Muthiga NA (1998) An ecological phase shift in a remote coral atoll of Belize
274   over 25 years. Env Conserv 25: 122-130
275 McManus JW, Polsenberg JF (2004) Coral–algal phase shifts on coral reefs: ecological and
276   environmental aspects. Prog Oceanogr 60: 263-279
277 Miller RJ, Adams AJ, Ogden NB, Ogden CJ, Ebersole JP (2003) *Diadema antillarum* 17 years
278   after mass mortality: is recovery beginning on St. Croix? Coral Reefs 22: 181-187
279 Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper reef algal
280   communities. Ecology 69: 1367-1382
281 Morrow KM, Carpenter RC (2008) Macroalgal morphology mediates particle capture by the
282   corallimorpharian *Corynactis californica*. Mar Biol 155: 273-280
283 Nadon MO, Stirling G (2006) Field and simulation analyses of visual methods for sampling coral
284   cover. Coral Reefs 25: 177-185
285 Nagle DG, Paul VJ (1998) Chemical defense of a marine cyanobacterial bloom. J Exp Mar Biol
286   Ecol 255: 29-38
287 Nugues MM, Roberts CM (2003) Coral mortality and interaction with algae in relation to
288   sedimentation. Coral Reefs 22: 507-516
289 Nugues MM, Smith GW, van Hooidonk RJ, Seabra MI, Bak RPM (2004) Algal contact as a
290   trigger for coral disease. Ecol Let 7: 919-923
291 Paul VJ, ruz-Rivera, Thacker RW (2001) Chemical mediation of macroalgal–herbivore
292   interactions: ecological and evolutionary perspectives. . In: McClintock JB, Baker BJ
293   (eds) Marine Chemical Ecology. CRC Press, Boca Raton, FL, pp 227-265
294 Potts DC (1977) Suppression of coral populations by filamentous algae within damselfish
295   territories. J Exp Mar Biol Ecol 28: 207-216
296 Reinthal PN, Macintyre IG (1994) Spatial and temporal variations in grazing pressure by
297   herbivorous fishes: Tobacco reef, Belize. Atoll Res Bull 425: 1-11
298 River GF, Edmunds PJ (2001) Mechanisms of interaction between macroalgae and scleractinians
299   on a coral reef in Jamaica. J Exp Mar Biol Ecol 261: 159-172

300 Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T,
301   Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder
302   RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of
303   coral reefs in the Northern Line Islands. PloS One 3: e1548
304 Schmitt TM, Hay ME, Lindquist N (1995) Constraints on chemically mediated coevolution:
305   multiple functions foe seaweed secondary metabolites. Ecology 76: 107-123
306 Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M,
307   Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced
308   coral mortality. Ecology Letters 9: 835-845
309 Stevenson C, Katz LS, Micheli F, Block B, Heiman KW, Perle C, Weng K, Dunbar R, Witting J
310   (2007) High apex predator biomass on remote Pacific islands. Coral Reefs 26: 47-51
311 Stewart JG (1989) Establishment, persistence and dominance of Corallina (Rhodophyta) in algal
312   turf. J Phycol 25: 436-446
313 Titlyanov EA, Yakovleva IM, Titlyanova TV (2007) Interaction between benthic algae (*Lyngbya*
314   *bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. J
315   Exp Mar Biol Ecol 342: 282-291
316 Wild C, Niggl W, Naumann MS, Haas AF (2010) Organic matter release by Red Sea coral reef
317   organisms - potential effects on microbial activity and in-situ O_2 availability. Mar Ecol
318   Prog Ser 411: 61-71

319 **FIGURE LEGENDS**

320 Figure 1. Summary of transect sites. The numbers next to dots refer to order of station names

321 (Table 1), along a distance gradient to shore; distance groups: inshore (site 1-4), inner midshore

322 (site 5-8, 13), outer midshore (site 9-10), offshore (site 11-12).

Figure 2. Exemplary photographs of coral-algae contacts observed during the transect surveys; (a) no visible harmful impact of *Halimeda* sp. on *Orbicella* sp., (b) overgrowth of *Agaricia agaricites* by the brown alga *Dictyota*, (c) overgrowth of *Orbicella* sp. by filamentous algae, (d) or pigment change of *Siderastrea* sp. next to red algae.

323   Figure 3. Benthic cover of scleractinian corals and algae along with their contact frequency and
324   *D. antillarum* abundances (per 100 m^{-2} seafloor area) at the three reef complexes (Barrier Reef,
325   inshore; Turneffe Atoll, midshore; Lighthouse Reef, offshore) in increasing distance to shore.
326   Values are means ± SE.

327   Figure 4. Benthic cover of corals and algae, including herbivorous fishes (in ranks) and number
328   of coral-algae contacts in relation to shore distance (measured as relative distance to population
329   centre Belize City).

Table 1

Table 1. Location and characteristics of sampling sites.

Table 1. Location and characteristics of sampling sites.

Site	Category	Distance (km)	Longitude	Latitude	Water depth (m)
1	inshore	17	17 ° 22.411 N	88 ° 4.714 W	5
2	inshore	19	17 ° 21.115 N	88 ° 1.730 W	6
3	inshore	19	17 ° 19.499 N	88 ° 2.951 W	7
4	inshore	12	17 ° 29.706 N	88 ° 02.550 W	8
5	inner midshore	32	17 ° 19.541 N	87 ° 57.547 W	6
6	inner midshore	34	17 ° 17.871 N	87 ° 57.685 W	5
7	inner midshore	39	17 ° 13.441 N	87 ° 56.632 W	5
8	inner midshore	37	17 ° 15.213 N	87 ° 57.406 W	5
9	outer midshore	47	17 ° 15.733 N	87 ° 49.147 W	6
10	outer midshore	47	17 ° 16.704 N	87 ° 48.394 W	6
11	offshore	70	17 ° 13.562 N	87 ° 36.104 W	6
12	offshore	70	17 ° 12.891'N	87 ° 36.475'W	6
13	inner midshore	40	17 ° 32.642'N	87 ° 49.581'W	7

Table 2

Table 2. Benthic cover and major organisms at the sites of investigation. "Coral-algae contact (%)" is the relative proportion of corals in direct contact with benthic algae. "Visibly harmful (%)" illustrates which of these interactions resulted in coral overgrowth or pigmentation change (see Fig. 2b-d). Herbivorous fish (parrot fishes, surgeon fishes and chubs) abundance in the water column up to 3 m above the surveyed 100 m² area was estimated using the following categories: few (n = 1-5), few-occasional (n = 6-10), occasional (n = 11-50), occasional-many (n = 51-100), many (n > 101). "N.a." indicates that values are not available.

Table 2. Benthic cover and major organisms at the sites of investigation. "Coral-algae contact (%)" is the relative proportion of corals in direct contact with benthic algae. "Visibly harmful (%)" illustrates which of these interactions resulted in coral overgrowth or pigmentation change (see Fig. 2b-d). Herbivorous fish (parrot fishes, surgeon fishes and chubs) abundance in the water column up to 3 m above the surveyed 100 m² area was estimated using the following categories: few (n = 1-5), few-occasional (n = 6-10), occasional (n = 11-50), occasional-many (n = 51-100), many (n > 101). "N.a." indicates that values are not available.

Site	Coral cover (%)	Dominant corals	Algae cover (%)	Dominant algae	Coral-algae contact (%)	Visibly harmful (%)	Octocoral (%)	Fire coral (%)	Sponge (%)	*D. antillarum* (n 100 m⁻²)	Herbivorous fish abundance
1	5	*Agaricia*	20	*Halimeda*	67	n.a.	16	0	12	0	few
2	19	*Montastrea*	14	*Halimeda*	41	47	30	4	2	0	few
3	4	*Montastrea*	39	*Halimeda*	44	44	10	2	6	0	occasional
4	15	*Montastrea*		*Dictyota*	78	33	14	0	2	0	occasional
5	4	*Montastrea*		*Halimeda*	67	33	8	2	5	0	few-occasional
6	7	*Agaricia*	12	*Halimeda*	50	0	13	5	6	0	occasional
7	6	*Agaricia*	45	*Rhipocephalus*	50	100	2	1	3	0	occasional
8	10	*Siderastrea*	7	*Halimeda*	41	43	7	3	8	0	occasional
9	19	*Siderastrea*	28	*Dictyota*	22	33	16	2	4	0	occasional
10	13	*Porites*	27	*Halimeda*	35	33	12	5	4	0	few
11	29	*Agaricia*	14	*Halimeda*	40	50	17	4	7	1	many
12	26	*Agaricia*	13	*Dictyota*	21	41	5	2	4	2	many
13	5	*Porites*	9	*Dictyota*	10	n.a.	15	1	11	3	occasional-many

Table 3

Table 3. Correlation of measured parameters with distance to shore.

Table 3. Correlation of measured parameters with distance to shore.

Benthic cover		Significance level	p	Rsp
Corals	(%)	(*)	0.046	0.508
Algae	(%)	-	0.274	-0.328
Coral-algae-contact	(%)	**	0.001	-0.810
Octocorallia	(%)	-	0.656	-0.137
Fire corals	(%)	-	0.19	0.388
Sponges	(%)	-	0.814	0.072
D. antillarum abundance	(individuals 100 m^{-2})	*	0.028	0.606
Herbivorous fish	(ranks)	*	0.045	0.564

Figure 1

Figure 1

Figure 1. Summary of transect sites. The numbers next to dots refer to order of station names (Table 1), along a distance gradient to shore; distance groups: inshore (site 1-4), inner midshore (site 5-8, 13), outer midshore (site 9-10), offshore (site 11-12).
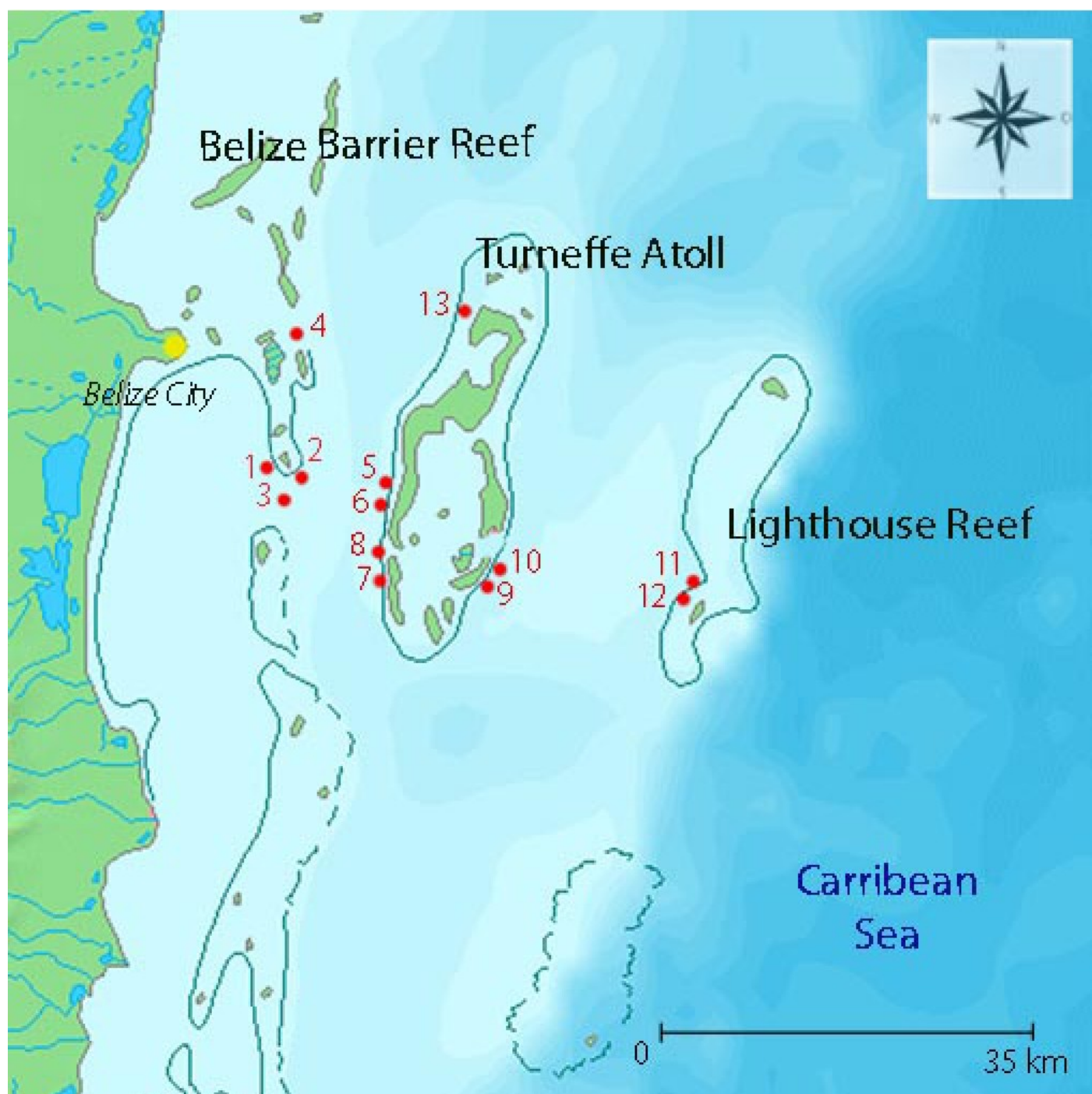
Figure 2

Figure 2

Figure 2. Exemplary photographs of coral-algae contacts observed during the transect surveys; (a) no visible harmful impact of Halimeda sp. on Orbicella sp., (b) overgrowth of Agaricia agaricites by the brown alga Dictyota, (c) overgrowth of Orbicella sp. by filamentous algae, (d) or pigment change of Siderastrea sp. next to red algae.
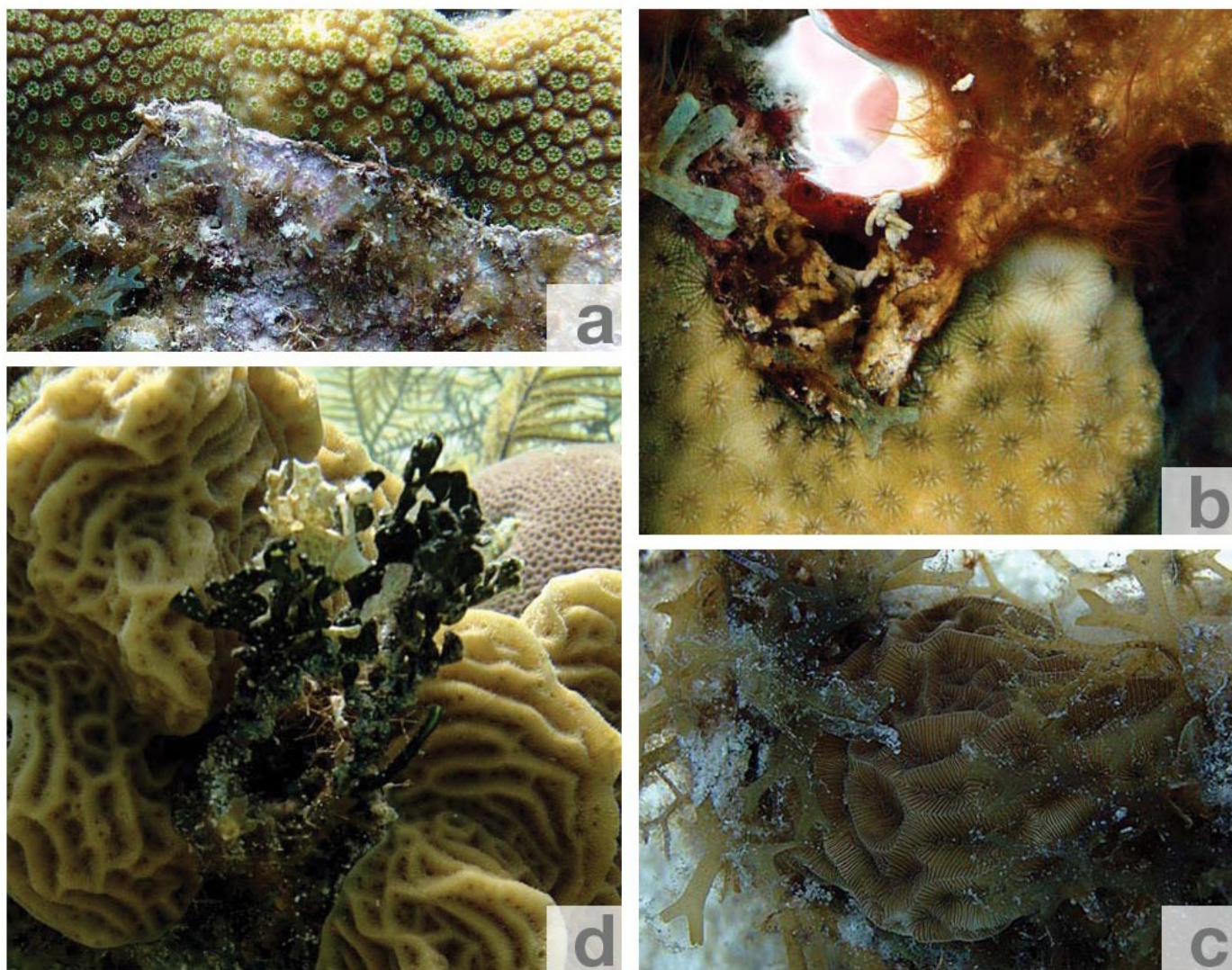
Figure 3

Figure 3. Benthic cover of scleractinian corals and algae along with their contact frequency and D. antillarum abundances (per 100 m-2 seafloor area) at the three reef complexes (Barrier Reef, inshore; Turneffe Atoll, midshore; Lighthouse Reef, offshore) in increasing distance to shore. Values are means ± SE.
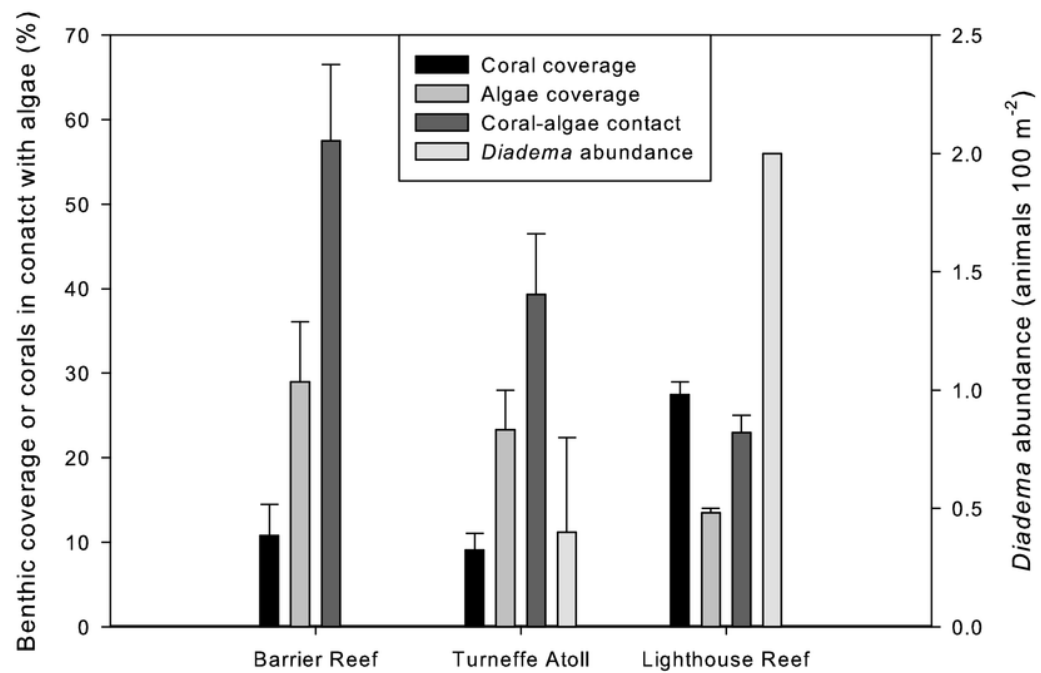
Figure 4

Figure 4

Figure 4. Benthic cover of corals and algae, including herbivorous fishes (in ranks) and number of coral-algae contacts in relation to shore distance (measured as relative distance to population centre Belize City).