Rapid relative increase of crustose coralline algae following herbivore exclusion in a reef of El Salvador

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The Eastern Tropical Pacific (ETP) is one of the most isolated and least studied regions in the world. This particularly applies to the coast of El Salvador, where the only reef between Guatemala and Nicaragua, called Los Cóbanos reef, is located. There is very little published information about the reef's biodiversity, and to our knowledge, no research on its ecology and responses to anthropogenic impacts, such as overfishing, has been conducted. The present study, therefore, described the benthic community of Los Cóbanos reef, El Salvador, using the Line-Point-Intercept-Transect method and investigated changes in the benthic community following the exclusion of piscine macroherbivores over a period of seven weeks. Results showed high benthic algae cover (up to 98 %), dominated by turf and green algae, and low coral cover (0 - 4 %). *Porites lobata* was the only hermatypic coral species found during the surveys. Surprisingly, crustose coralline algae (CCA) showed a remarkable total cover increase by 58 %, while turf algae cover decreased by 82 %, in experimental plots after seven weeks of piscine macroherbivore exclusion. These findings apparently contradict the results of most previous similar studies. While it was not possible to ascertain the exact mechanisms leading to these drastic community changes, the most likely explanation is grazing on turf by small grazing macroherbivores that had access to the cages during the experiment and clearing of CCA initially covered by epiphytes and sediments. A higher CCA cover would promote the succesful settlement by corals and prevent further erosion of the reef framework. Therefore it is crucial to better understand algal dynamics, herbivory, and implications of overfishing at Los Cóbanos to avoid further reef deterioration. This could be achieved through video surveys of the fish community, night-time observations of the macroinvertebrate community, exclusion experiments that also keep out herbivorous macroinvertebrates, and/or experimental assessments of turf algae/CCA interactions.

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18 Abstract

20 The Eastern Tropical Pacific (ETP) is one of the most isolated and least studied regions in the

21 world. This particularly applies to the coast of El Salvador, where the only reef between

22 Guatemala and Nicaragua, called Los Cóbanos reef, is located. There is very little published

23 information about the reef's biodiversity, and to our knowledge, no research on its ecology and

24 responses to anthropogenic impacts, such as overfishing, has been conducted. The present study,

25 therefore, described the benthic community of Los Cóbanos reef, El Salvador, using the Line-

26 Point-Intercept-Transect method and investigated changes in the benthic community following

27 the exclusion of piscine macroherbivores over a period of seven weeks. Results showed high

28 benthic algae cover (up to 98 %), dominated by turf and green algae, and low coral cover (0 - 4

29 %). *Porites lobata* was the only hermatypic coral species found during the surveys. Surprisingly,

30 crustose coralline algae (CCA) showed a remarkable total cover increase by 58 %, while turf

31 algae cover decreased by 82 %, in experimental plots after seven weeks of piscine

32 macroherbivore exclusion. These findings apparently contradict the results of most previous

33 similar studies. While it was not possible to ascertain the exact mechanisms leading to these

34 drastic community changes, the most likely explanation is grazing on turf by small grazing

35   macroherbivores that had access to the cages during the experiment and clearing of CCA initially

36   covered by epiphytes and sediments. A higher CCA cover would promote the succesful

37   settlement by corals and prevent further erosion of the reef framework. Therefore it is crucial to

38   better understand algal dynamics, herbivory, and implications of overfishing at Los Cóbanos to

39   avoid further reef deterioration. This could be achieved through video surveys of the fish

40   community, night-time observations of the macroinvertebrate community, exclusion experiments

41   that also keep out herbivorous macroinvertebrates, and/or experimental assessments of turf

42   algae/CCA interactions.

43

44   **Introduction**

45

46   Many tropical reefs around the world are undergoing changes in benthic community composition

47   (away from dominance by stony corals) as a result of the combined effect of anthropogenic

48   disturbances (Hoegh-Guldberg et al., 2018; Hughes et al., 2007; Pandolfi et al., 2005). Studies

49   show that by removing herbivores that consume macroalgae, overfishing may favor competitive

50   fleshy algae and turf over corals and other reef-building organisms (Burkepile and Hay, 2006;

51   Hughes et al., 2007; Smith et al., 2010). Reef herbivores directly affect the composition of reef

52   benthic communities by freeing benthic space from macroalgae and allowing, for example, coral

53   larval settlement (Lewis, 1986; Steneck,1995) and crustose coralline algae growth (CCA)

54   (Mumby, 2009). The latter plays a crucial role in coral reef ecosystems by facilitating the

55   settlement of coral larvae via chemical cues (Heyward and Negri, 1999; Ritson-Williams et al.,

56   2010), solidifying the reef framework (Adey, 1998; Weiss and Martindale, 2017), and preventing

57   bioerosion (Weiss and Martindale, 2017).

58

59   Several studies address the role that herbivorous fish and invertebrates play in the coral reefs of

60   the Caribbean Sea and the Indo-Pacific (e.g. Foster, 1987; Green and Bellwood, 2009; Hughes et

61   al., 2007; Lewis, 1986). The Caribbean Sea, for example, suffered a drastic decrease in coral

62   cover after mass mortality of the sea urchin, *Diadema antillarum*, preceded by overfishing of

63   herbivorous fishes on many Caribbean reefs (Jackson et al., 2014), while the Indo-Pacific is

64   characterized by a large number of diverse herbivorous fishes, showing higher functional

65   diversity among herbivorous fish than the Caribbean (Roff and Mumby, 2012).

66

67 On the contrary, little research has been conducted on coral reefs of the Eastern Tropical Pacific

68 (ETP), which is one of the most isolated ocean regions in the world (Cortés, 2017; Glynn and

69 Ault, 2000). The reefs in the region are exposed to extreme environmental conditions, such as

70 high CO_2 concentrations, low aragonite saturation, high levels of nutrients, high tidal amplitudes,

71 and extreme fluctuations in seawater temperature caused by the El Niño-Southern Oscillation

72 (Bennett, 1966; Cortés, 1997; Guzmán and Cortés, 1993; Kessler, 2006). Moreover, there is little

73 research on how herbivores structure benthic communities in the ETP. Only a few studies have

74 investigated the role of consumers through exclusion experiments in the region (e.g. Menge et

75 al., 1986; Vinueza et al. 2006; Vinueza et al. 2014; Roth et al., 2015).

76

77 Los Cóbanos reef, located in El Salvador, is the only known reef in the country with hermatypic

78 coral species. Los Cóbanos lies within the so-called "Pacific Central American Faunal Gap

79 (PCAFG)", which is the coastal stretch between Guatemala and northwestern Nicaragua (Cortés

80 et al., 2017). Los Cóbanos reef, together with the recently discovered reef at the coast of

81 Nicaragua, are the only two sites within the PCAFG that have been found to host significant

82 coral communities (Alvarado et al., 2010; Reyes-Bonilla and Barraza, 2003).

83

84 There is little information about Los Cóbanos reef. Reyes-Bonilla and Barraza (2003) reported

85 eight reef -building coral species belonging to the genera *Porites*, *Pocillopora*, and *Pavona*.

86 Unpublished management reports and surveys document that the reef is dominated by algae (~77

87 %) (Segovia-Prado and Navarrete-Calero, 2007), with 81 algae species reported (Arrivillaga et

88 al., 2010), and that hard coral cover is extremely low (~4 %) (Segovia-Prado, 2016). According

89 to Reyes-Bonilla and Barraza (2003), the fish abundance on the reef is low, but generally,

90 information about the fish community at Los Cóbanos is scarce. Fish play a crucial role in coral

91 reef systems by, for example, controlling macroalgae which compete with corals for space

92 (Bellwood et al., 2004; Mumby, 2015). Overfishing in coral reefs can increase overgrowth of

93 algae and/or other benthic organisms and lead to phase shifts from coral dominance to degraded

94 ecosystems (Bellwood et al., 2004; Loh et al., 2015; Pandolfi et al., 2005). Currently, the

95 literature states that around 137,000 kg of fish are being caught at Los Cóbanos (Arrivillaga et

96 al., 2010). Although several studies (e.g. Molina and Vásquez-Jandres, 2006; Segovia-Prado and

97   Navarrete-Calero 2007) state that Los Cóbanos reef is overfished, to our knowledge, no research
98   has been conducted investigating how the piscine community affects benthic community
99   composition at Los Cóbanos reef. This study aimed to address those knowledge gaps by, firstly,
100 describing the current benthic community state of Los Cóbanos reef, and secondly, assessing the
101 effect of piscine macroherbivore exclusion on the benthic community using an *in-situ* exclusion
102 experiment, simulating overfishing. We hypothesized that the reef would exhibit high algae and
103 low coral cover (H1), and that by excluding piscine macroherbivores, macroalgae would
104 overgrow *P. lobata* colonies as suggested by previous studies (Hughes et al., 2007; Roth et al.,
105 2015; Thacker et al., 2001) (H2).

106

107 **Materials & Methods**

108

109 **Study site**
110 The study was carried out on Los Cóbanos reef (13°31'25.6"N 89°48'24.6"W), El Salvador, from
111 March to May 2018. The reef lies within the nature reserve "Complejo Los Cóbanos", 11 km
112 east of the city Acajutla (Fig. 1). The Ministry of Environment and Natural Resources of El
113 Salvador (MARN, initials in Spanish) approved the fieldwork for this study inside the nature
114 reserve. Los Cóbanos reef consists of a heterogeneous basalt shore with a tidal variation of ~3 m
115 (Segovia-Prado, 2016). Colonies of the hermatypic coral species *Porites lobata* grow inter- and
116 subtidally, covering only 2 – 7 % of the benthos. The region is characterized by two seasons: a
117 dry (December to May) and a rainy (June to November) season. The benthic community at Los
118 Cóbanos is exposed to sedimentation impacts during the raining season, when river runoff brings
119 sediments and nutrients to the reef, significantly increasing water turbidity.

120

121 **Benthic community survey**
122 The benthic community was evaluated using the Line-Point-Intercept-Transect method via
123 snorkelling, as described by English et al. (1997). In April 2018, seven 50 m long transects were
124 placed parallel to the coastline at 2-3 m water depth, with at least 25 m between individual
125 transects. During low tide, for a total of 100 points per transect (one every 0.5 m), the benthic
126 organism underneath each point was identified *in situ* to genus level, except for turf and crustose
127 coralline algae (CCA) that could not be identified to this level and were classified generically. If

128   no organism was found on that point, non-living structures were categorized as: 'sand', 'rock' or

129   '*Pocillopora* sp. skeleton'. The relative benthic cover of each category was calculated using the

130   resulting 100 points per transect.

131

132   **Experimental cage set-up**

133   The experimental design followed the Before-After Control-Impact/Treatment (BACI) design

134   (Stewart-Oaten et al., 1986). Four 70 x 70 x 50 cm^3 cages constructed from 2.5 x 2.5 cm^2

135   galvanized wire mesh (as used by Smith et al., 2001) were deployed on the reef with at least 2 m

136   distance from each other. Each cage enclosed one *Porites lobata* colony of a diameter of 8 - 12

137   cm and surrounding algae. Even though *P. lobata* only covered up to 4 % of the benthos, it was

138   targeted in the experiment to assess how simulated overfishing affects coral-algae interactions.

139   Four more plots with a similar benthic community composition to the enclosed ones were

140   selected as controls (70 x 70 cm^2). The experiment ran for seven weeks, from April to May 2018.

141   Each week the cages were cleaned using a plastic washing brush to avoid algae growth. The

142   plots were inspected for small fish, snails, crustaceans and echinoderms every week during the

143   cleaning. None were observed in the enclosed plots. Also, the control plots were carefully

144   inspected weekly, but no macroinvertebrates were observed at any time. The cover of the

145   different algae functional groups in the enclosed and control plots was estimated *in situ* using

146   quadrats that indicated the cage limits (70 x 70 cm^2) to the nearest 1 % at the beginning and the

147   end of the experiment. The same categories used during the benthic surveys were identified in

148   the exclusion experiment. Only the uppermost benthic community layers were analyzed. The

149   cover of *P. lobata* was estimated by comparing the projected area of the colony (calculated by

150   measuring the length and width of the colony at the beginning and end of the experiment) to the

151   total selected cage and control area (0.49 m^2). All surveys were conducted by the first author.

152

153   Due to logistical constraints, it was not possible to include semi-closed cages to assess potential

154   physical effects of the cages in this experiment. CCA often perform better under lower light

155   availability than other algae (Van den Hoek et al., 1978, Vásquez-Elizono and Enríquez 2017),

156   while algal turfs increase their net primary productivity with increased water flow (Carpenter et

157   al., 1991; Carpenter and Williams, 2007). The cage structure could have reduced light

158   availability and water flow within the enclosed plots, benefiting CCA. In order to quantify the

159   potential effects of the cages on water flow and light attenuation, gypsum cards and HOBO light

160   sensors were placed inside and outside cages with the same design as those used in the

161   experiments, at the experimental sites for 24 h in April 2019. The gypsum cards were weighed

162   before and after 24 h exposure to obtain an aggregate measure of water flow over that period.

163   The HOBO light sensors measured light intensity within and outside the cages in lum/ft $^{-2}$ every

164   30 seconds.

165

166   **Data analysis**

167   The mean relative cover of each functional group identified in the benthic community survey

168   was calculated using the relative cover of all transects. To compare the community composition

169   of the control and enclosed plots at the beginning and end of the experiment, Bray – Curtis

170   Dissimilarity was calculated on untransformed data, and a PERMANOVA test was conducted

171   using PRIMER 7. For the pair-wise comparisons, Monte Carlo P-values were obtained using

172   PRIMER 7 due to the small number of permutations resulting from the PERMANOVA test, as

173   suggested by Anderson et al. (2008). All additional tests were conducted in the statistics program

174   R version 3.5.1 (R Core Team, 2018). Differences in coral, CCA, and turf benthic cover were

175   tested with repeated measures ANOVA (rmANOVA from the ez package, Lawrence, 2016). In

176   order to test the weight difference of the gypsum cards after the 24 h exposure, a t-test (from the

177   stats package) was conducted. To test for potential differences in the measured light intensities, a

178   Wilcoxon Rank Sum test (stats package) was used, as normality and sphericity assumptions were

179   not met. An Anderson-Darling-Test (ADGofTest package) was used to test for data normality

180   and Levene's-test (from the car package) was used to test sphericity assumptions. The jitter

181   function (from ggplot2 package, Wickham et al., 2019) was used to add random variation to the

182   non-metric multidimensional scaling (nMDS) plot and reveal the points with the same

183   community assemblage that were overlapping.

184

185   # Results

186

187   **Benthic community survey**

188   The benthic community composition of Los Cóbanos reef was dominated by algae. Different

189   types of algae comprised 72 – 98 % of the benthic community. Turf algae were the most

190   dominant algae group, with a mean benthic cover of 26.6 ± 8.8 (SD) %, followed by green algae

191   with 22.8 ± 21.2 (SD) % (Table 1). Only one hermatypic coral species was found alive (*Porites*

192   *lobata*), which had a benthic cover of 2.0 ± 2.8 (SD) %. Calcium carbonate skeletons of the

193   branching coral genus *Pocillopora* were widely observed. Mobile benthic macroinvertebrates

194   were not observed within the transects; however, the nudibranchs *Elysia diomedea* and

195   *Glossodoris sedan* and the echinoderms *Ophiocoma aethiops*, *Echinometra vanbrunti,* and

196   *Holothuria (Halodeima) kefersteinii* were observed on the reef during the benthic surveys

197   (Supplementary Materials, Table S1).

198

199   **Fish herbivore exclusion**

200   No significant effect of cage structures was observed on either light intensity (Wilcoxon Rank

201   Sum test, p = 0.520) or water flow (t-test, t $_{(2.08)}$ = -1.21, p = 0.343), indicating that the physical

202   structure of the cages did not affect light or water flow.

203

204   There was a significant interaction effect of treatment and time on the benthic community

205   composition (PERMANOVA, P(perms) = 0.001, perms = 996). The benthic community

206   composition in the enclosed and control plots only differed significantly at the end of the

207   experiment (PERMANOVA, P(perms) = 0.027, perms = 35, P(MC) = 0.007) (Fig. 2,

208   Supplementary Materials, Tables S2 and S3). The benthic community composition in the

209   enclosed (PERMANOVA, P(perms) = 0.030, perms = 35, P(MC) = 0.001) and control

210   (PERMANOVA, P(perms) = 0.028, perms = 35, P(MC) = 0.003) plots changed significantly

211   between the beginning and the end of the experiment. Crustose coralline algae cover increased

212   by a total 57.5 % (from 0 to 57.5 ± 9.6 (SD) %) in the enclosed plots and 21.5 % (from 1 ± 1.4

213   (SD) % to 22.5 ± 8.66 (SD) %) in the control plots, while the turf algae benthic cover decreased

214   by 81 % (from 83.8 ± 4.7 (SD) % to 2 ± 2.3 (SD) %) in the enclosed plots and 63 % (from 79.75

215   ± 4.3 (SD) % to 16.5 ± 7 (SD) %) in the controls (Fig. 3). There was a significant interactive

216   effect of treatment and time on both the CCA (rmANOVA, F $_{(1,6)}$ = 27.47, p = 0.003) and turf

217   algae benthic cover (rmANOVA, F $_{(1,6)}$ = 14.69, p = 0.009).

218

219   **Discussion**

220

Benthic community survey

222   This study aimed to describe the current state of the benthic community of Los Cóbanos reef, El

223   Salvador, and to investigate the effect of piscine macroherbivore exclusion on benthic

224   community composition. As expected (H1), the survey results show that the reef was dominated

225   by algae (mostly turf and green algae) and that the coral cover was extremely low. Compared to

226   the coral diversity described for the same reef by Reyes-Bonilla and Barraza (2003), the number

227   of living hermatypic coral species present decreased from five to one in less than two decades.

228   Past unpublished surveys conducted at Los Cóbanos yielded similar results; however, the

229   reported algae cover was slightly lower two years prior the present study (~72 %) (Herrera

230   2017). Yearly surveys conducted by J. Segovia using permanent transects reported a coral cover

231   decrease from 6 % to 2 % between 2014 and 2016. Segovia et al. (2019) and Segovia (2020),

232   using haphazardly deployed transects, documented a *P. lobata* cover of 2 % in 2019 and 2020, in

233   line with the value observed in this study for 2018. In contrast to the present study, the benthic

234   community in Los Cóbanos has been mainly surveyed using 30-meter long transects at three

235   different distances from the shore and a 1 m^2 quadrat (Segovia-Prado, 2016; Segovia et al., 2019;

236   Segovia, 2020). Regardless of the difference in the monitoring methodology, the results of the

237   different surveys yield very similar results, indicating a clear decrease of hard coral cover over

238   time up to 2016, mainly attributed to El Niño events in 2014 and 2016 (Segovia et al., 2019).

239   Moreover, according to personal communication with fishers from the local community, 20 - 30

240   years ago, *Pocillopora* sp. cover in the shallow parts of the reef was high. According to the

241   fishers, the only way to access the reef was during high tide with the help of boats, suggesting a

242   much higher coral cover and a higher hard coral diversity than the present one. A vast number of

243   calcium carbonate skeletons, some of them still attached to the substrate, belonging to the coral

244   genus *Pocillopora* were observed during the surveys, indicating this genus comprised a

245   significant component of the shallow benthic community in the recent past.

246

247   Studies of other reefs in the ETP showed a higher hard coral species richness (2-3 coral species)

248   than at Los Cóbanos (Guzmán and Cortés, 1993; Reyes-Bonilla et al., 2010; Stuhldreier et al.

249   2015). Turf algae also seem to dominate other ETP reefs (Cortés et al., 2017; Stuhldreier et al.,

250   2015). Yet, these reefs display a lower algae diversity, with only two or three macroalgae genera

251   dominating the reef benthos (Stuhldreier et al., 2015), compared to nine different genera found at
252   Los Cóbanos.

253

254   Cortés et al. (2017) state that the increasing temperature and length of El Niño events,
255   sedimentation, and local human activities have caused reef degradation in the region. The coral
256   cover of Los Cóbanos reef decreased drastically in the last decades. Two oil spills in El Salvador
257   in 1993 together with extreme El Niño events may have caused the disappearance of most of the
258   coral community of Los Cóbanos (Cortés et al., 2017; Molina, 1996; Alvarado, 2012; Segovia et
259   al., 2019). Currently, the reef is exposed to high nutrient input from the local human population,
260   intense fishing, and sedimentation (Herrera, 2017, unpublished; Reyes-Bonilla and Barraza,
261   2003). The hard coral population is limited to a small area at 0-15 m water depth extending for
262   about 7,000 m along the coastline between Punta Remedios and Acajutla (Fig. 1) (pers. obs. J
263   Segovia). The results of this study, together with the aforementioned literature, suggest that Los
264   Cóbanos reef may have undergone a shift from a reef with high coral cover towards a rather
265   algae-dominated reef, as described by Pandolfi et al. (2005) for other regions of the world, at
266   least in the first 600 meters from the coast. Bellwood et al. (2004) defined coral reefs as "three-
267   dimensional shallow-water structures dominated by scleractinian corals". The low coral cover
268   and high algae cover and diversity underline that Los Cóbanos is no longer a coral reef but rather
269   an algal-dominated reef. Concordantly, recent literature refers to Los Cóbanos reef as rather a
270   rocky reef featuring hard coral and algal communities (Herrera, 2017, unpublished; Segovia,
271   2017). There is, however, no historical monitoring data that verifies the assumption that Los
272   Cóbanos reef was indeed a coral reef in the past. Core drilling and examination of the underlying
273   matrix might be able to resolve this question.

274

275   **Herbivore exclusion**

276

277   Unexpectedly, CCA cover increased in both enclosed (by a total of ca. 58 %) and control areas
278   (ca. 21 %), while turf algae decreased in both treatments (enclosed ca. 82 %, control ca. 63 %) at
279   a remarkable speed. As CCA are among the slowest-growing marine algae, it is unlikely that this
280   result reflects actual growth of CCA. Rather, at least some CCA may have been covered by turf-
281   forming fouling epiphytes, the removal of which would have led to an apparent short-term

282   increase in CCA. CCA are often considered as subordinate in their capacity to compete for space

283   and are often overgrown or shaded by turf or macroalgae (Dethier et al., 1994; Littler and Littler,

284   1980). In some cases, this overgrowth even provides protection to CCA from harmful

285   environmental conditions (Figueiredo et al., 2000). However, our results cannot confirm this, as

286   only the uppermost layer of the benthic community was analyzed at the beginning and end of the

287   experiment. No observations were made on whether CCA could indeed be found living under the

288   turf algae. The exclusion of large piscine herbivores through caging had a significant effect on

289   the benthic community composition. Surprisingly, there was a significantly higher apparent

290   increase in CCA cover in the enclosed areas, whereas turf algae decreased more in the absence of

291   piscine macroherbivores (Fig. 3). This is remarkable, as most literature indicates that herbivore

292   exclusion causes an increase of macro- and turf algae (e.g. Hughes et al., 2007; Roth et al., 2015;

293   Thacker et al., 2001; Zaneveld et al., 2016). No effect of the cage structures on the current

294   regime or light availability was detected through the 24 h measurements, meaning that the

295   stronger observed benthic community changes in the enclosed plots were presumably caused by

296   biotic factors. Nevertheless, the extent to which these results can be transferred to the seven-

297   week experimental period is limited. High frequency data loggers were used to monitor light

298   changes over a 24 h period on a day that was representative for the study period during the dry

299   season. However, these measurements may not be representative for the study transition period

300   from the dry to rainy season. Our study thus is not able to directly determine the biotic and

301   abiotic processes behind the phenomenon observed at Los Cóbanos. Therefore, potential

302   explanations for these counterintuitive results are discussed in the following paragraphs.

303

304   *Low light and high nutrient availability*

305   The experiment at Los Cóbanos reef was conducted from April to the end of May, the transition

306   months from the dry to the rainy season. During these months, there were several rainfalls which

307   drastically decreased the underwater visibility through sediment input, and possibly increased the

308   nutrient concentration via river runoff. Low light availability has been reported to negatively

309   affect turf algae growth (Russel 2007). Fricke et al. (2011) attributed the decrease of turf biomass

310   to the depth-related decrease in light quantity. The change in the light conditions could have

311   reduced the turf algae uncovering the CCA beneath it. However, little is known about the

312   response of turf algal communities to changes in abiotic factors and further experiments would

313   be needed to test this (Fricke et al. 2014). On the other side, CCA tolerate lower light availability

314   (Van den Hoek et al., 1978, Vásquez-Elizono and Enríquez 2017) and have been reported to be

315   nutrient-limited (Smith et al. 2001). The sudden high nutrient input may have allowed CCA to

316   survive the sudden change in light availability, contrary to the turf algae. Similar seasonal

317   observations were made by Menge et al. (1986) at a rocky shore in Panama where the cover of

318   coralline crust increased during the rainy season and decreased during the dry season. The

319   change in abiotic conditions due to seasonal changes at the study site may have driven the

320   unexpected turf algae decrease and apparent CCA increase in the enclosed and control plots.

321

322   *Exclusion of piscine macroherbivores*

323   In this study, the apparent CCA cover increase within the cages relative to the controls could

324   have been caused by the exclusion of fauna that either feeds on turf algae or benefits its growth

325   through, for example, farming behavior. Underwater visual fish censuses were conducted at Los

326   Cóbanos during the study period; however, the results showed great variability. For this reason,

327   the results were not used in this study. Nonetheless, the highly territorial turf algae farming fish

328   species *Stegastes acapulcoensis* (Dominici-Arosemena and Wolff, 2008; Robertson and Allen,

329   2015) was found in high numbers in the census transects. As the presence of damselfishes can

330   favor the growth of turf algae over CCA in algae dominated reefs (Doropoulos et al., 2013), the

331   exclusion of *S. acapulcoensis* may have been to the detriment of turf algae, contributing to their

332   strong decrease. A further explanation could be the exclusion of detritivores, such as surgeonfish

333   that remove sediments and detritus from turf algae (Purcell and Bellwood, 1993; Tebbett et al.,

334   2017). This could have benefited CCA in a similar way to observations by Kendrick (1991), who

335   carried out a study in the Galapagos archipelago and found that, after 51 days of

336   experimentation, algal turf cover and recruitment decreased in treatments with a high rate of

337   sedimentation favoring crustose coralline algae. This way, the exclusion of a key non-identified

338   detritivore could have magnified the effect of sediment deposition on turf algae, without

339   detrimental effects on CCA.

340

341   *Grazing activity of macroinvertebrates*

342   A more probable explanation for the observed rapid decrease of turf algae and concomitant

343   increase in CCA within the enclosed areas appears to be the grazing activity of smaller

344   macroinvertebrates such as snails, sea urchins, or crabs. Following exclusion of larger fishes,

345   invertebrate micrograzers have been shown to lead to shifts in community composition and

346   reduced algal biomass (Brawley and Adey, 1981; Zeller, 1988). The deployed cages could have

347   provided an accessible predator-free habitat for small benthic grazers. Rather than leading to a

348   reduction in grazing, exclusion of fishes may thus have increased consumption of turf algae and

349   other fouling epiphytes, uncovering previously hidden CCA. Although no macroinvertebrates

350   were observed in or around the cages during the study, many macroinvertebrates are active at

351   night, when the cages would have offered refuge from mesopredators. The sea urchin

352   *Echinometra vanbrunti,* for example, was observed hidden between rocks during the benthic

353   surveys in the reef. Furthermore, the weekly examinations were made in short periods during

354   extreme low tides, when small invertebrates sought shelter from rising water temperatures and

355   increased wave activity in crevices, tide pools or deeper parts of the reef. Additionally, no

356   nocturnal observations were made that could verify the nocturnal grazing activity of sea urchins

357   (Nelson and Vance 1979; Mills et al., 2000). In exclusion experiments conducted on rocky

358   shores in Galápagos and the Bay of Panama, when small grazers such as gastropods, crabs, and

359   small fishes were not excluded, the CCA cover increased after 16 and 8 weeks, respectively

360   (Menge et al., 1986; Vinueza et al., 2006). The CCA cover in the exclusion experiment on the

361   Panamanian rocky shores was highest when only large fish were excluded from the areas (Menge

362   et al., 1986), similar to the design in the present study.

363

364   This study's results suggest that biotic factors do affect the benthic community composition at

365   Los Cóbanos. Even though CCA can suppress macroalgae in other ETP reefs (Smith et al., 2001;

366   Vermeij et al., 2011), this experiment does not provide evidence that CCA could effectively

367   outcompete turf algae, and that the observed increases were the result of actual CCA growth. If

368   that were the case, growth of CCA in this study would have, by far, exceeded the CCA growth

369   rates reported everywhere else in the tropics (e.g. Adey and Vassar, 1975; Villas Boas et al.,

370   2005; Tamega and Figueiredo, 2019). A more likely explanation for the apparent rapid increase

371   of CCA cover is the loss of turf algae and other fouling epiphytes growing on CCA as a result of

372   the grazing activity of small macroinvertebrates, thereby uncovering the CCA living underneath.

373   CCA can survive overgrowth by filamentous turfs over long periods of time (Kendrick 1991;

374   Airoldi, 2000). Lapointe (1997) proposed that high nutrient availability and high grazing activity

375   lead to CCA benthic dominance. Against expectations, simulated overfishing benefited

376   calcifying algae (H2). Our results, however, highlight the potential importance of

377   macroinvertebrates as grazers whose population seems to be controlled by piscine mesopredators

378   at Los Cóbanos. Macroinvertebrates composed less than 1 % of the benthic community in the

379   reef. The underwater visual fish census also revealed a large number of piscine mesopredators at

380   Los Cóbanos, such as the wrasses *Halichoeres dispilus*, *H. notospilus,* and *Thalassoma*

381   *lucasanums* that feed on benthic invertebrates such as small crabs, snails and sea urchins

382   (Gomon 1995). The high number of mesopredators is possibly the result of overfishing of top

383   predators such as sharks, barracudas, and large groupers, allowing mesopredators to proliferate

384   (Hixon 2015; Prugh et al., 2009). Future fishing management strategies at Los Cóbanos could

385   focus on controlling the population of mesopredators by, for example, reducing the fishing

386   intensity on top predators.

387

388   ## Conclusions

389   It is most likely that the combination of grazing macroinvertebrates, increased nutrient

390   concentration and turbidity as a result of seasonal river run-off, and potential effects of the cages,

391   tipped the balance from turf algae to CCA. This phenomenon has been observed in other ETP

392   reefs (Menge et al., 1986; Vinueza et al., 2006). However, due to the methodological limitations

393   of the experiment, this study could not determine the drivers of the unexpected apparent increase

394   in CCA cover observed at Los Cóbanos. Therefore, further experiments assessing the interaction

395   between CCA and turf algae under different abiotic conditions at Los Cóbanos should be

396   conducted. In addition, targeted studies of the fish and macroinvertebrate communities, their role

397   in structuring the benthic community, and their trophodynamics are needed for a better

398   understanding of the ecology of Los Cóbanos reef. Understanding the processes affecting the

399   persistence of an important benthic component such as CCA is crucial first to understand the

400   failed recovery of stony corals as in Los Cóbanos reef and secondly to take accurate management

401   measures to avoid further deterioration.

402

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404

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407

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642
643

Relative cover of the benthic community surveyed at Los Cóbanos reef using the Line
Point Intercept method

	Genus/Group	Mean cover ± SD
Chlorophyta	*Codium* sp.	7.9 ± 12.7
	Halimeda sp.	14.9 ± 8.5
Phaeophyta	*Padina* sp.	5.4 ± 4.0
	Ralfsia sp.	1.6 ± 1.9
	Colpomenia sp.	0.3 ± 0.5
	Dictyota sp.	8.6 ± 6.4
Rhodophyta	*Galaxaura* sp.	2.7 ± 2.7
	Ceramium sp.	3.5 ± 2.9
	Acanthophora sp.	3.3 ± 8.6
	CCA	10.0 ± 3.1
	Rodoliths	0.7 ± 0.8
Turf	-	26.6 ± 8.8
Cnidaria	*Porites lobata*	2.0 ± 2.8
Rock	-	2.0 ± 1.4
Sand	-	9.3 ± 8.5
Skeleton	*Pocillopora* sp.	7.5 ± 2.1

Figure 1

Pacific coast of El Salvador

Square indicates Los Cóbanos reef where the monitoring and experimental set-up took place.

Red dots: survey area. Map generated with QGIS2.18.13 (http://**qgis**.org)
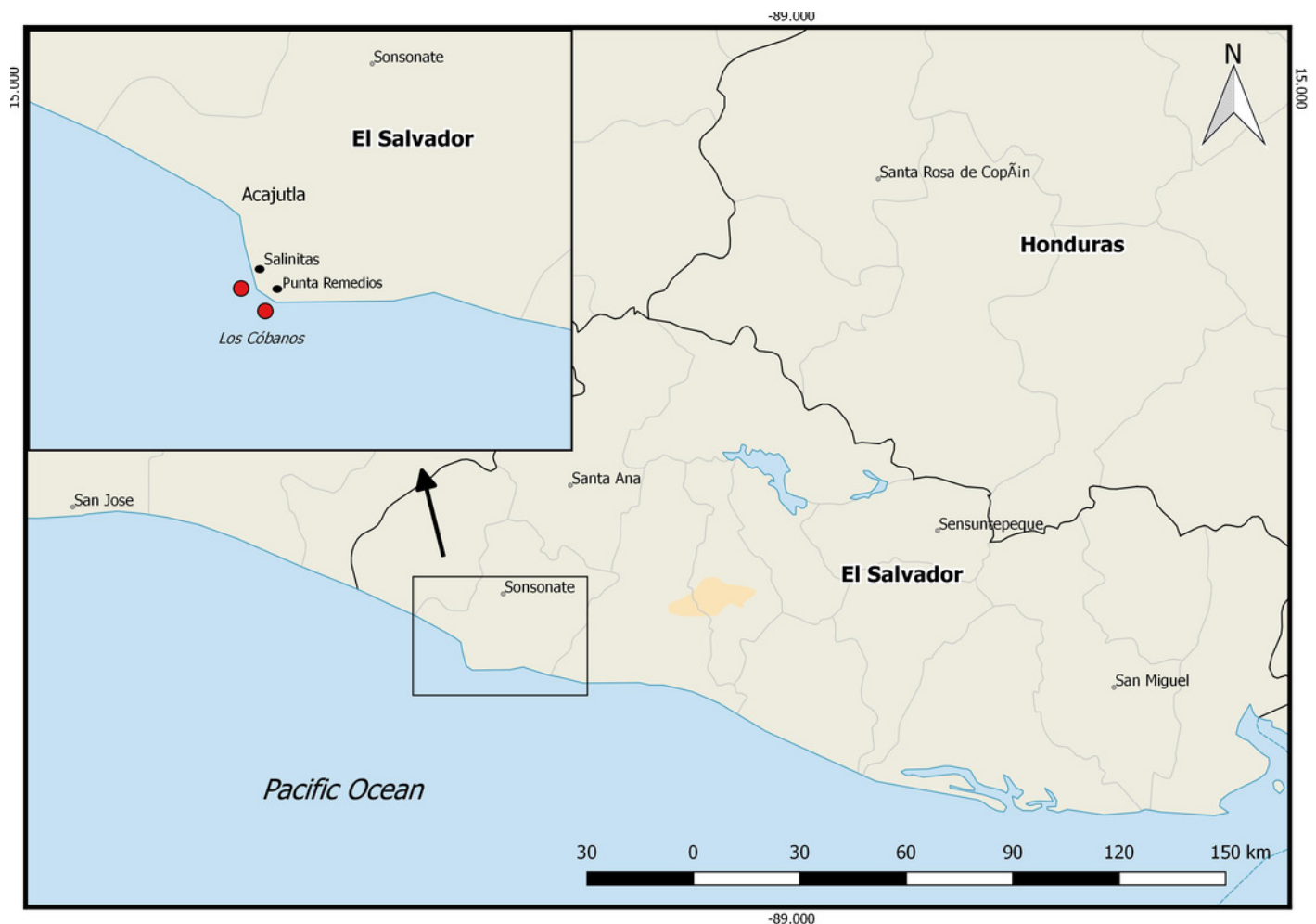
Figure 2

Benthic communities before and after exlosure experiment

Non-metric multidimensional scaling (nMDS) plot of control and enclosed (cage) benthic community composition before and after 7 weeks of experiment using Bray-Curtis similarity. Dashed circles: 60 % similarity, continuous circles 40 % similarity. Random variation added using the jitter function to reveal points overlapping (ggplot2 package, Wickham et al., 2019).
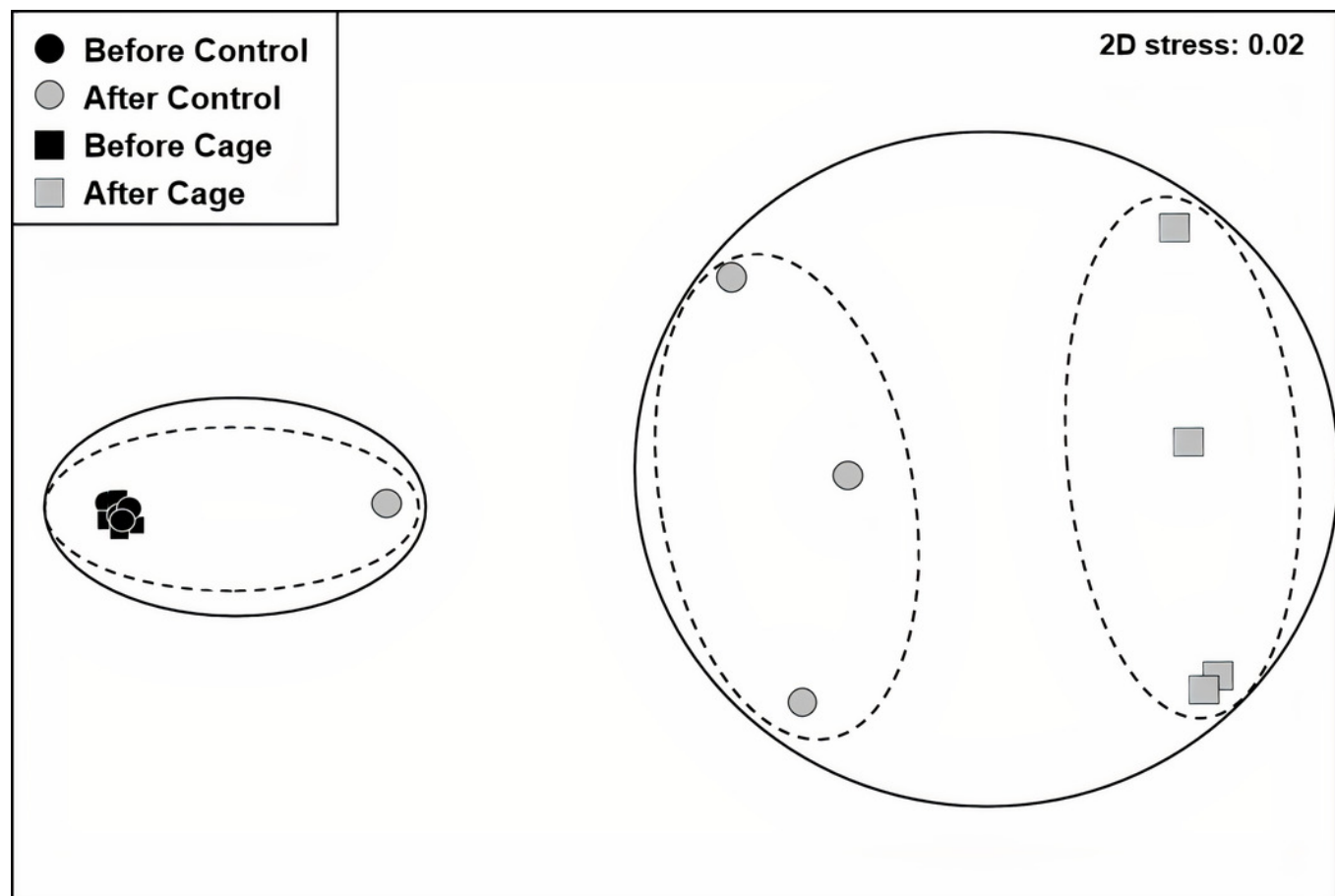
Figure 3

Crustose coralline and turf algae cover in the enclosed and control plots before and after the experiment

a) CCA cover before and after the experiment b) Turf algae cover before and after the experiment (Supplementary Materials, Table S2)