Diversity and abundance of macrocrustaceans on coral reefs differing in level of degradation

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Coral reefs sustain abundant and diverse macrocrustaceans that perform multiple ecological roles, but coral reefs are undergoing massive degradation that may be driving changes in the species composition and abundance of reef-associated macrocrustaceans. To provide insight into this issue, we used non-destructive visual census techniques to compare the diversity and abundance of conspicuous macrocrustaceans (i.e., those >1 cm and visible without disturbance) between two shallow Caribbean coral reefs similar in size (~1.5 km in length) and close to each other, but one ("Limones") characterized by extensive stands of the branching coral *Acropora palmata*, and the other ("Bonanza") dominated by macroalgae and relic coral skeletons (i.e., degraded). We also assessed the structural complexity of each reef and the percent cover of various benthic community components. Given the type of growth of *A. palmata*, we expected to find a greater structural complexity, a higher cover of live coral, and a lower cover of macroalgae on Limones, and hence a more diverse and abundant macrocrustacean community on this reef compared with Bonanza. Overall, we identified 64 macrocrustacean species (62 Decapoda and two Stomatopoda). Contrary to our expectations, the structural complexity did not differ significantly between the back-reef zones of these reefs and the diversity and abundance of macrocrustaceans were higher on Bonanza than on Limones despite live coral cover being higher on Limones and macroalgal cover on Bonanza. However, the use of various types of microhabitats by macrocrustaceans differed substantially between reefs. On both reefs, the dominant species were the clinging crab *Mithraculus coryphe* and the hermit crab *Calcinus tibicen*, but the former was more abundant on Bonanza and the latter on Limones. *M. coryphe* occupied a diverse array of microhabitats but mostly coral rubble and relic skeletons, whereas *C. tibicen* was often, but not always, found associated with colonies of *Millepora* spp. A small commensal crab of *A. palmata*, *Domecia acanthophora*, was far more abundant on Limones, emerging as the main discriminant species between reefs. Our results suggest that local diversity and abundance of reef-

associated macrocrustaceans are partially modulated by habitat degradation, the diversity of microhabitat types and the establishment of different commensal associations rather than by structural complexity alone.

1 **Diversity and abundance of macrocrustaceans on coral reefs differing in level of**

2 **degradation**

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17 **ABSTRACT**

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19 roles, but coral reefs are undergoing massive degradation that may be driving changes in the

20 species composition and abundance of reef-associated macrocrustaceans. To provide insight into

21 this issue, we used non-destructive visual census techniques to compare the diversity and

22 abundance of conspicuous macrocrustaceans (i.e., those >1 cm and visible without disturbance)

23 between two shallow Caribbean coral reefs similar in size (~1.5 km in length) and close to each

24 other, but one ("Limones") characterized by extensive stands of the branching coral *Acropora*

25 *palmata*, and the other ("Bonanza") dominated by macroalgae and relic coral skeletons (i.e.,

26 degraded). We also assessed the structural complexity of each reef and the percent cover of

27 various benthic community components. Given the type of growth of *A. palmata*, we expected to

28 find a greater structural complexity, a higher cover of live coral, and a lower cover of macroalgae

29 on Limones, and hence a more diverse and abundant macrocrustacean community on this reef

30 compared with Bonanza. Overall, we identified 64 macrocrustacean species (62 Decapoda and

31 two Stomatopoda). Contrary to our expectations, the structural complexity did not differ

32 significantly between the back-reef zones of these reefs and the diversity and abundance of

33 macrocrustaceans were higher on Bonanza than on Limones despite live coral cover being higher

34 on Limones and macroalgal cover on Bonanza. However, the use of various types of

35 microhabitats by macrocrustaceans differed substantially between reefs. On both reefs, the

36 dominant species were the clinging crab *Mithraculus coryphe* and the hermit crab *Calcinus*

37 *tibicen*, but the former was more abundant on Bonanza and the latter on Limones. *M. coryphe*

38 occupied a diverse array of microhabitats but mostly coral rubble and relic skeletons, whereas *C.*

39 *tibicen* was often, but not always, found associated with colonies of *Millepora* spp. A small

40 commensal crab of *A. palmata*, *Domecia acanthophora*, was far more abundant on Limones,

41 emerging as the main discriminant species between reefs. Our results suggest that local diversity

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44 associations rather than by structural complexity alone.

45

INTRODUCTION

Habitat complexity is an important factor driving the abundance and diversity of associated species by facilitating niche separation and resource partitioning (Vytopil & Willis, 2001; Idjadi & Edmunds, 2006). Keystone structures (*sensu* Tews et al., 2004) are distinct spatial structures that create complex habitats that facilitate species' coexistence by offering food resources and shelter against predators and various environmental stressors (Bruno & Bertness, 2001; Kerry & Bellwood, 2015). In coral reefs, keystone structures are created by scleractinian corals, which provide great spatial complexity to the system and multiple shelters for other organisms in the form of crevices, holes, and branches.

The role of corals in maintaining abundant and diverse communities of reef invertebrates in well recognized. For example, Stella et al. (2011) identified 869 coral-associated invertebrate species, with arthropods (mostly crustaceans) as the major contributors to the overall diversity. Not only are reef macrocrustaceans (in particular Decapoda and Stomatopoda) highly diverse; they are also abundant and perform multiple ecological roles. They are part of numerous feeding guilds, acting as predators, parasites, herbivores, scavengers, and detritivores, as well as suspension and deposit feeders (Abele, 1976; Glynn & Enochs, 2011; Stella et al., 2011), and constitute a critical link between primary production and a wide array of higher order consumers, including reef fishes (Randall, 1967). Some macrocrustaceans defend live coral from potential predators (McKeon & Moore, 2014), maintain coral health by clearing sediments (Stewart et al., 2006), or eliminate parasites from reef fishes, many of which are of economic value (Becker & Grutter, 2004). Therefore, macrocrustaceans are a key component of coral reef ecosystems, making it necessary to understand the potential effects that coral reef degradation may have on their communities.

Coral reefs are undergoing massive degradation due to the effects of multiple stressors, including climate change induced-bleaching, increases in disease outbreaks and prevalence, eutrophication, and invasive or destructive fishing practices (Hughes et al., 2017). This is particularly true for Caribbean coral reefs, where declines in reef architectural complexity and phase shifts from coral to macroalgal dominance have been extensively documented (Gardner et al., 2003; Álvarez-Filip et al., 2009; Bruno et al., 2014; Jackson et al., 2014; Suchley, McField & Álvarez-Filip, 2016). Coral reef degradation is likely to have serious consequences for ecosystem functioning and services, as well as for reef biodiversity (Álvarez-Filip et al., 2009), and there is

77 support for this latter assumption in the case of reef fishes (e.g. Graham et al., 2011; Coker,

78 Wilson & Pratchett, 2014; Álvarez-Filip et al., 2015; Newman et al., 2015). However,

79 predictions for invertebrate taxa are less clear because different studies have reported contrasting

80 results (see Graham & Nash, 2013). For example, in Papua New Guinea, the density and

81 abundance of several macroinvertebrate groups, including motile crustaceans, decreased in reefs

82 with lower architectural complexity due to acidification compared with more complex reefs

83 (Fabricius et al., 2014). In the US Virgin Islands, diversity, but not abundance, of invertebrates

84 was positively related with topographic complexity, but not with coral diversity or live coral

85 cover (Idjadi & Edmunds, 2006). Invertebrate assemblages were more diverse and abundant on

86 dead than on live coral habitats in Panama (Nelson, Kuempel & Altieri, 2016), whereas habitat

87 complexity accounted for very little of the variability in invertebrates (including arthropods) on

88 Caribbean *Orbicella* reefs (Newman et al., 2015). These contrasting results suggest that many

89 reef-associated invertebrates do not necessarily benefit from the presence of live corals per se,

90 but from the complex 3-D framework of coral reefs, which can persist for years after the death of

91 corals.

92   One of the most structurally complex Caribbean corals is the branching coral *Acropora*

93 *palmata.* This species, once dominant in the region, form thick stands that provide an intricate

94 network of crevices on shallow-water reefs (< 5 m). The populations of this species have

95 sustained extensive mortality since the early 1980s, substantially reducing coral cover, increasing

96 substratum for algal growth, and drastically reducing reef complexity (Aronson & Precht, 2001;

97 Alvarez-Filip et al., 2009; Jackson et al., 2014). Currently, *Acropora*-dominated reefs are rare.

98 For example, a recent assessment in 107 sites along the Mesoamerican Reef (MAR) revealed that

99 *A. palmata* was present (mostly at low cover values) in only 20% of the sites, and that only one

100 site (Limones reef), located in the northernmost Mexican portion of the MAR, exhibited

101 extensive stands of *A. palmata* resulting in a high (>35%) cover of this branching coral

102 (Rodríguez-Martínez et al., 2014). Therefore, assessing the composition and structure of the

103 ecological condition on these *Acropora*-dominated reefs is crucial to elucidate how reef

104 degradation is modifying the ecological relationships on coral reefs.

105   The aims of the present study were twofold: to obtain a list of species of conspicuous

106 macrocrustaceans associated to shallow Caribbean reef habitats, and to compare the diversity and

107 abundance of these macrocrustaceans between Limones reef and another reef (Bonanza), similar

108 in size to Limones but highly degraded, to elucidate the potential effects of coral reef degradation

109 on this type of invertebrates. We predicted that the diversity and abundance of macrocrustaceans

110 would be higher in Limones because the presence of extensive stands of live *A. palmata* would

111 presumably conger a greater structural complexity and provide a broad diversity of microhabitats

112 potentially used by reef-associated species (Roberts & Ormond, 1987; Garpe et al., 2006).

113

114 **MATERIALS AND METHODS**

115 **Study site**

116   The study was conducted at the Puerto Morelos Reef National Park (PMRNP; Fig. 1a), a

117 marine protected area located on the NE coast of the Yucatan Peninsula, Mexico. The PMRNP is

118 an extended fringing reef system composed of a series of reef units that differ in size and

119 structural complexity (Lozano-Álvarez et al., 2017; Morillo-Velarde et al., in press). Coral cover

120 tends to be greater on the back-reef and crest zones than on the low-relief fore-reef, which

121 descends gradually into an extensive sand platform at 20-25m (Jordán-Dahlgren, 1993). Two of

122 these reef units are "Limones" (centered at 20˚59.1' N, 86˚47.9' W) and "Bonanza" (centered at

123 20˚57.6' N, 86˚48.9' W) (Fig. 1). Both reefs are similar in length, depth and distance from the

124 coast, but differ in their level of degradation. As noted before, Limones is an exceptional site due

125 to its abundant and generally healthy populations of *Acropora palmata*, which provide reef

126 structure and essential fish habitat (Rodriguez-Martínez et al., 2014; Morillo-Velarde et al., in

127 press). In contrast, Bonanza, which in 1985 had 33% cover of live coral and 4% cover of algae

128 (Jordán-Dahlgren, 1993), currently exhibits extensive areas of relic *Acropora* skeletons (Fig. 1)

129 and a predominance of erect macroalgae (Morillo-Velarde et al., in press). Based on a number of

130 broad- and local-scale resilience indicators, including coral cover, Ladd & Collado-Vides (2013)

131 categorized Limones as a high-resilience site and Bonanza as a low-resilience site. Fishing

132 activities are banned on both reefs since 1996. Bonanza is open to visitation, whereas tourist

133 activities are not allowed in Limones since 2014 given the high ecological value of Limones

134 (Rodríguez-Martínez et al., 2014).

135

136 **Macrocrustacean surveys**

137   Sampling by divers remains the most efficient way to find reef-associated species when

138 they are large enough to be seen (Knowlton et al., 2010; Giraldes, Coelho Filho & Coelho,

139   2012). Therefore, we used SCUBA diving to conduct quantitative surveys of conspicuous

140   macrocrustaceans (herein defined as motile crustaceans larger than ~1 cm) via belt transects,

141   with a permit issued by Comisión Nacional de Acuacultua y Pesca (PPF/DGOPA-259/14). On

142   each reef, we haphazardly laid thirty 25-m transects on the back reef zone along the length of the

143   reef. We recorded all macrocrustaceans observed within 1 m to the right and 1 m to the left of the

144   transect line (i.e., an area of 50 m² per transect), both over the substrata and under coral rubble.

145   Individuals were identified *in situ* to the lowest possible taxonomic level by two trained divers.

146   Only a few individuals that could not be identified *in situ* were collected in zip-lock bags and

147   taken to the laboratory for their identification. Also recorded was the type of microhabitat in

148   which each specimen was observed. These microhabitats included *Acropora palmata*, *Agaricia*

149   *agaricites*, other live corals, *Millepora* spp., dead coral skeletons, coral rubble, gorgonians,

150   algae, anemones, and sand. Despite their relatively large size, many macrocrustaceans hide

151   deeply in holes and crevices in coral reefs during the day but forage over the reef substrata at

152   night, therefore, to obtain a species list as complete as possible, we further conducted qualitative

153   surveys on each reef by recording all specimens observed during three separate nocturnal 1-h

154   dives.

155

156   **Structural complexity and benthic community**

157   We assessed the current ecological condition of the back-reef zones of Limones and

158   Bonanza by using two metrics of structural complexity and estimating the percent cover of

159   different components of the benthic community. Structural complexity was assessed with the

160   Habitat Assessment Score (HAS; Gratwicke & Speight, 2005) and the rugosity index (Risk,

161   1972; Álvarez-Filip et al., 2009), and benthic community composition was obtained with the

162   point intercept method (Hill & Wilkinson, 2004).

163   HAS provides an overall structural complexity value by visually evaluating six variables

164   of the local topography (rugosity, variety of growth forms, height, refuge size categories,

165   percentage of live cover and percentage of hard substratum). Each variable is assigned a score

166   between 1 and 5 (from smallest or lowest to largest or highest), and the sum of the individual

167   scores is the HAS. Therefore, a score of 6 would represent the least complex habitats and a score

168   of 30 would represent the most complex habitats. HAS values were obtained in three 4 m²

169   quadrats positioned at the beginning, middle, and end of each of nine transects per reef, and the

170   three values were averaged to obtain the transect-level HAS.

171   The rugosity index is the ratio of the length of a chain molded to the reef surface to the

172   linear distance between its start and end points. A perfectly flat surface would have a rugosity

173   index of one, with larger numbers indicating more complex surfaces. The rugosity index and the

174   percent cover of components of the benthic community components were obtained from 10-m

175   transects marked every 10 cm (100 point per transect), laid parallel to the coast (21 in Bonanza

176   and 24 in Limones). Briefly, a diver recorded which of the following benthic components was

177   found under each mark: live hard corals, calcareous macroalgae, fleshy macroalgae, coralline

178   algae, algal turf, cyanobacterial mat, other invertebrates (e.g. zoanthids, *Millepora*, *Cliona*),

179   other components (e.g. sand, seagrass).

180

181   **Data analysis**

182   **Structural complexity and benthic community**

183   HAS values were compared between reefs with a simple ANOVA because the data met

184   the assumptions of normality and homogeneity of variances, as previously checked with Shapiro-

185   Wilk and Levene tests, respectively. In contrast, the rugosity values did not meet these

186   assumptions and were compared between reefs with a Mann-Whitney U test. A significance level

187   of 95% was used in all cases. All analyses were performed in PAST v2.17c. The percent data on

188   the benthic community structure were logit-transformed (Warton & Hui, 2011) and subjected to

189   a principal component analysis (PCA). Then, the data for each benthic component was compared

190   between reefs with a Student's *t*-test.

191

192   **Characterization of the macrocrustacean community**

193   Quantifying biodiversity is problematic because there is no single "best" index. However,

194   simple indices (i.e., those that measure species richness) can be slightly preferable when the

195   primary goal is to detect effects of external factors on diversity, whereas compound indices (i.e.,

196   those that combine measures of richness and abundance) can be preferable when the primary

197   goal is to differentiate sites by their level of diversity (Magurran & Dornelas, 2010; Morris et al.,

198   2014). Given the aims of the present study, we used both types of indices for the

199   macrocrustaceans from each reef. These indices included species richness (S, number of species),

200   Simpson's dominance ($D = \sum (n_i/N)^2$, where n_i is number of individuals of the ith species and N

201 is total number of individuals), Shannon-Wiener's diversity ($H' = -\sum_{i=1}^{s} p_i \log_2 p_i$, where H' is

202 the information contained in the sample (bits/individual) and $p_i = n_i/N$), and Pielou's evenness (J'

203 $= H'/\log S$). The ecological indices were compared between reefs with ANOVAs. Species

204 accumulation and rarefaction curves were computed using EstimateS v9.1.0 (Gotelli & Colwell,

205 2001).

206   The community composition of macrocrustaceans was analyzed using non-parametric

207 techniques with PRIMER 6 v6.1.9 (PRIMER-E Ltd). Differences in the taxonomic composition

208 between Limones and Bonanza were analyzed by non-metric multidimensional scaling (MDS)

209 on fourth-root transformed data, using the Bray-Curtis similarity measure (Clarke, 1993). The

210 statistical significance of the observed differences in the macrocrustacean assemblages between

211 reefs was further tested with a one-way analysis of similarity (ANOSIM). This test provides an

212 R-value indicative of the degree of difference between samples as well as a p-value for the

213 significance of that difference. R values close to 0 are indicative of little difference while values

214 close to 1 are indicative of a large difference in sample composition (Clarke & Warwick, 2001).

215 Finally, we did a similarity percentage analysis (SIMPER, Clarke, 1993) to identify those species

216 responsible for the observed differences in community composition between both reefs. For each

217 of the 10 most abundant species, we also compared the density, standardized as individuals (ind.)

218 50 m^{-2}, between reefs with individual Student's t tests.

219

220 **RESULTS**

221 **Structural complexity and benthic community components**

222   The back-reef zones of Limones and Bonanza did not differ significantly in either mean

223 HAS values (mean ± 95% confidence interval: Limones: 18.3 ± 2.07, Bonanza: 18.0 ± 1.50)

224 (ANOVA, F = 0.066, df = 1, 16, p = 0.801) or rugosity index (Limones: 1.33 [1.13-2.21]. median

225 [interquartile range]; Bonanza: 1.24 [1.07-1.38]) (Mann-Whitney U test, U = 182, z = 1.764, n_1 =

226 25, n_2 = 25, p = 0.078). However, the percent cover of various components of the benthic

227 community did differ between reefs (Fig. 2). In particular, live coral cover was much higher on

228 Limones, whereas the cover of fleshy macroalgae, calcareous macroalgae, and cyanobacterial

229 mats were significantly higher on Bonanza (Fig. 2). In the PCA, the first two components

230 explained 63% of the total variance (Fig. 3). The first component explained 40.2% of the

231   variance and was positively correlated with fleshy macroalgae (loading: 0.640) and negatively

232   correlated with live hard coral (-0.685). The second component explained 22.8% of the variance

233   and was strongly positively correlated with turf algae (0.728) and negatively correlated with live

234   hard coral (-0.449) (Fig. 3). Most transects on Limones differed from those on Bonanza along the

235   first component.

236

237   **The macrocrustacean assemblage**

238   In all, we registered 64 species of macrocrustaceans (Table 1), including seven that were

239   only observed during the nocturnal dives (i.e., not quantified). These species were

240   representatives of the Infraorders Brachyura (33 species), Caridea (11), Anomura (10), Achelata

241   (5), Axiidea (2), and Stenopodidea (1); the Superfamily Penaeoidea (1), and the stomatopod

242   family Gonodactyloidea (2 species). Twelve species, mostly rare (i.e., with <3 individuals), were

243   only identified to the superfamily or family level. The most diverse superfamily was Majoidea,

244   with 22 species. The number of species was higher on Bonanza than on Limones (44 vs 33

245   species), as was the abundance (2800 vs 2067 individuals) (Table 1).

246   On both reefs, the number of species increased with the number of transects

247   (accumulation curves, Fig. 4), but more steeply on Bonanza than on Limones. Rarefaction curves

248   did not reach an asymptote for either reef, suggesting that the species richness of conspicuous

249   macrocrustaceans on these reefs is even higher. All ecological indices differed significantly

250   between reefs (Table 2), with Bonanza exhibiting higher levels of S ($F_{1, 58}$= 9.07, p = 0.004), H'

251   ($F_{1, 58}$= 17.97, p < 0.001), and J' ($F_{1, 58}$ = 10.09, p = 0.002), and Limones exhibiting a higher D

252   ($F_{1, 58}$ = 18.60, p < 0.001).

253   Macrocrustacean assemblages differed significantly between reefs (ANOSIM, R = 0.279,

254   p < 0.001) but with some overlap (Fig. 5), suggesting a similar abundance of some species on

255   both reefs. Indeed, SIMPER revealed that the clinging crab *Mithraculus coryphe* and the hermit

256   crab *Calcinus tibicen* were the most abundant species on both reefs, accounting for 71.4% and

257   62.2% of the similarities observed in Limones and Bonanza, respectively (Table 3). Within

258   Limones, the composition of macrocrustaceans exhibited an average similarity among transects

259   of 48.1%, mainly due to three species: *C. tibicen*, *M. coryphe* and *Domecia acanthophora*, with

260   *C. tibicen* as the major contributor (45.2%). Within Bonanza, the average similarity among

261   transects was 46.9%, with *M. coryphe* emerging as the main contributor (33.1%), followed by *C.*

262 *tibicen* (29.1%) and *Neogonodactylus oerstedii* (8.8%). On Limones, six species accounted for

263 90% of the observed similarity, whereas on Bonanza, this same percentage was accounted for by

264 eight species (Table 3). The crustacean assemblages of Limones and Bonanza exhibited a mean

265 dissimilarity of 58.5%, with *D. acanthophora* as the main contributor to this dissimilarity (8.1%),

266 followed by *M. coryphe* (6.6%) and *Pagurus brevidactylus* (6.4%).

267 Despite wide variability among transects, the density of some of the 10 most abundant

268 species differed significantly between reefs (Fig. 6). This was the case for *D. acanthophora*,

269 which had a significantly higher density on Limones (12.6 ± 7.8 ind. 50 m^{-2}, mean ± 95% CI,

270 than on Bonanza (1.5 ± 1.9 ind. 50 m^{-2}), and for *M. coryphe*, which exhibited a higher density on

271 Bonanza (33.9 ± 14.4 ind. 50 m^{-2}) than on Limones (9.7 ± 3.6 ind. 50 m^{-2}), as was also the case

272 for *M. sculptus* and *N. oerstedii* (Fig. 6). In contrast, the density of *C. tibicen* did not differ

273 significantly between reefs (Limones: 38.1 ± 10.2 ind. 50 m^{-2}; Bonanza: 33.4 ± 10.1 ind. 50 m^{-2}).

274 Two of the most abundant species were recorded on Limones only (*Petrolisthes galathinus*,

275 *Paguristes cadenati*) and one was recorded on Bonanza only (*Paguristes tortugae*) (Fig. 6).

276

277 **Microhabitats used by macrocrustaceans**

278 On Limones, the types of microhabitats more commonly occupied by macrocrustaceans

279 were, on descending order, *Millepora* spp., *A. palmata*, coral rubble, dead coral skeletons, and

280 *Agaricia agaricites*, and on Bonanza, coral rubble, dead coral skeletons, macroalgae, *A.*

281 *agaricites*, and *Millepora* spp. (Fig. 7). Some of these microhabitats constitute components of the

282 benthic community and hence their percent cover was estimated. For example, the average

283 percent cover of *A. palmata* and *Millepora* spp. was higher on Limones (29% and 3.6%,

284 respectively) than on Bonanza (3.5% and 1.9%, respectively). In contrast, the percent cover of

285 fleshy and calcareous macroalgae was higher on Bonanza (32.1% and 15.4%, respectively) than

286 on Limones (19.7% and 5.2%, respectively). However, other types of microhabitat (e.g., coral

287 rubble, relic coral skeletons, gorgonian, sand) were not quantified because they are not

288 components of the benthic community.

289

290 **DISCUSSION**

291 Contrary to our expectations, Bonanza supported a more diverse and abundant

292 macrocrustacean community than Limones, and this occurred despite the structural complexity

293   of the back-reef zone not varying significantly between both reefs, as suggested by their similar

294   rugosity indices and HAS scores. However, the two reefs differed in the percent cover of distinct

295   benthic community components, and the types of microhabitats used by macrocrustaceans

296   differed substantially between reefs.

297   Live coral cover (mostly *Acropora palmata*) was much greater on Limones than on

298   Bonanza, whereas the opposite occurred for fleshy and calcareous macroalgae, and

299   cyanobacterial mats. These results support previous studies concluding that Bonanza has

300   sustained substantial degradation over the past few decades, whereas Limones is an exceptional

301   site due to its healthy populations of *Acropora palmata* (Rodríguez-Martínez et al., 2014).

302   Previously, Morillo-Velarde et al. (in press) found a significant difference in rugosity between

303   Limones and Bonanza, but these authors measured this variable in only eight transects over the

304   central part of each reef, where development of *A. palmata* on Limones appears to be greater.

305   The similarity in structural complexity between the back-reef zones of these reefs that we found

306   could be partially explained by the presence of extensive areas of dead coral skeletons on

307   Bonanza as opposed to the extensive stands of live *A. palmata* on Limones. These results are

308   consistent with studies suggesting that live coral cover is not necessarily a key factor determining

309   the level of structural complexity as long as the reef structure persists (Lindahl, Ohmann &

310   Schelten, 2001; Nelson, Kuempel & Altieri, 2016), i.e., that the relic skeletons (i.e. those left

311   behind after the coral tissue dies) and the structural diversity they create can be important factors

312   determining the diversity and structure of invertebrate communities (Idjadi & Edmunds, 2016).

313   However, in addition to relic skeletons, different types of benthic components can provide

314   different types of microhabitats for invertebrates such as crustaceans.

315   Despite the limitations of our visual census method, which was restricted to conspicuous

316   taxa and especially excluded small cryptofauna, we found that the macrocrustacean species

317   richness of Limones and Bonanza was high, as previously reported for other Caribbean reef

318   systems (Reed et al., 1982; Martínez Iglesias & García Raso, 1999; Briones-Fourzán & Lozano-

319   Álvarez, 2002). However, given that many crustaceans hide deeply in reef crevices or under

320   sediments during the day and only emerge at night to forage (Glynn & Enochs, 2011), a more

321   exhaustive sampling would undoubtedly increase the number of macrocrustacean species

322   recorded in these reefs (e.g. Alpheidae and Thalassinidae) as indicated by the rarefaction curves

323   (see Fig. 4).

324   Most of the species that we observed on both reefs were facultative coral-dwelling

325   crustaceans, i.e., species that are not considered to be fundamentally dependent upon abundant

326   live coral for their local persistence (Stella et al., 2011). Although there was some overlap in the

327   macrocrustacean community composition between reefs, most diversity indices were higher on

328   Bonanza except for the dominance index, which was higher on Limones. These results likely

329   reflect a greater heterogeneity of microhabitats on Bonanza, which is characterized by the

330   abundance of relic coral skeletons, coral rubble, and fleshy and calcareous macroalgae (Morillo-

331   Velarde et al., in press; the present study), than on Limones, which is characterized by extensive

332   stands of *A. palmata* (Rodríguez-Martínez et al., 2014). The latter would also explain why

333   *Domecia acanthophora*, a small commensal crab of *Acropora* spp. (Patton, 1967), was the main

334   contributor to the dissimilarity between reefs. This species is considered an obligate coral-

335   dwelling crab (Patton, 1967), i.e., a species having strong reliance on live corals for food, habitat,

336   and/or recruitment (Stella et al., 2011). On the other hand, fleshy and calcareous macroalgae,

337   which were more abundant on Bonanza, offer high quality microhabitats to grazing species (Roff

338   et al., 2013) such as majoid crabs of the genera *Mithraculus*, *Mithrax*, *Omalacantha*, and

339   *Maguimithrax*, which use their modified, spooned-shaped chelae to feed on these algae (Coen,

340   1988; Stachowicz & Hay, 1996; Butler & Mojica, 2012). Consequently, majoids were among the

341   most abundant macrocrustaceans on Bonanza, particularly *M. coryphe*, which on this reef was

342   often found in coral rubble overgrown by macroalgae.

343   The diogenid *Calcinus tibicen* had a similar abundance as *M. coryphe* on Bonanza, but

344   was the dominant species on Limones. This small hermit crab, which is an omnivorous

345   detritivore (Hazlett, 1981), has also been reported as abundant on shallow coral reefs in Panama

346   (Abele, 1976), Cuba (Martínez Iglesias & García Raso, 1999), the Virgin Islands (Brown &

347   Edmunds, 2013), and Brazil (Giraldes, Coelho Filho & Coelho, 2012). Brown & Edmunds

348   (2013) discovered that *C. tibicen* can live commensally on hydrozoans of the genus *Millepora*

349   ("fire corals"). Fire corals were more abundant on Limones than on Bonanza, and many of the

350   individuals of *C. tibicen* that we observed were dwelling on *Millepora* colonies. However, the

351   overall abundance of fire corals was low and we also found *C. tibicen* on virtually all types of

352   microhabitats except for anemones and sand, consistent with Brown & Edmunds' (2013)

353   conclusion that the association with fire corals is facultative for this crab. In particular, *C. tibicen*

354 was observed in high numbers on relic coral skeletons and coral rubble on both reefs, but

355 especially on Bonanza, where these types of microhabitats abounded.

356   Our results would appear to confirm that, rather than structural complexity, the variety of

357 microhabitats (i.e., small-scale habitat structure, Dumas et al., 2013) is an important factor

358 driving the diversity and abundance of reef-associated crustaceans (Abele, 1976; Head et al.,

359 2015; Giraldes et al., 2017), as is the diversity of mutualistic relationships that these animals can

360 establish with other taxa (e.g., Patton, 1994; Briones-Fourzán et al., 2012; Brown & Edmunds,

361 2013). However, this does not mean that reef-associated crustaceans will benefit from coral reef

362 degradation over the long term, because changes in the abundance and species diversity could

363 eventually result in ecosystem shifts through alteration of local food webs and species

364 interactions (Prezlawski et al., 2008). For example, *A. palmata* provides habitat for many

365 species, but is very vulnerable to bleaching and diseases (Aronson & Precht, 2001; Stella et al.,

366 2011). In Australia, coral colonies displaying a significant reduction in live tissue cover due to

367 partial mortality exhibited an increase in the abundance and richness of small invertebrate

368 species, suggesting that as coral cover is reduced, new microhabitats arise within the colony,

369 allowing other species to occupy new niches (Stella, Jones & Pratchett, 2010). Thus, dead *A.*

370 *palmata* may become important for macrocrustaceans for which the relic coral skeletons and

371 coral rubble are preferred microhabitats. Kramer, Bellwood & Bellwood (2014) already

372 highlighted the importance of dead coral and coral rubble as key microhabitats for reef-dwelling

373 decapod crustaceans, as did Nelson, Kuempel & Altieri (2016) for other invertebrates. In

374 addition to providing refuge, relic skeletons and coral rubble are typically overgrown with

375 macroalgae, increasing their microhabitat value for various herbivorous species. Similarly, dead

376 coral colonies have been long known to be an important microhabitat for many species of small

377 cryptic crustaceans (e.g., Coles, 1980; Enochs, 2012). However, long-term coral loss may dictate

378 the availability of these microhabitats (Head et al., 2015; Lozano-Álvarez et al., 2017), because

379 degraded coral reefs continue to erode over time (Perry et al., 2012).

380   Specialist species are more vulnerable to disturbances and hence would be expected to be

381 more profoundly affected by coral reef degradation (Munday, 2004; Álvarez-Filip et al., 2015).

382 Based on our results, it would appear that *Domecia acanthophora* would be more profoundly

383 affected if Limones underwent an increase in degradation. Indeed, *D. acanthophora* was far

384 more abundant on Limones, where its preferred microhabitat (*A. palmata*) abounded, but we also

385   found it on *Millepora* spp. colonies on both reefs, although proportionally more on Bonanza,

386   suggesting that these small crabs can associate with other sessile invertebrates in the absence of

387   acroporids. For example, Reed et al. (1982) recorded *D. acanthophora* in *Oculina* reefs.

388   Interestingly, Head et al. (2015) found large numbers of obligate coral-dwelling crabs on dead

389   coral colonies of *Acropora* and *Pocillopora* across five different atolls. These crabs appeared to

390   be explicitly recruiting to or moving to dead coral hosts at certain stages in their life cycle, with

391   no relationship with the abundance of live coral (Head et al., 2015).

392   In summary, we recorded a higher diversity and abundance of conspicuous

393   macrocrustaceans on a more degraded reef, dominated by macroalgae and relic coral skeletons,

394   than on a reef with extensive stands of live *A. palmata*. These results add to an increasing

395   number of studies concluding that relic skeletons and the structural complexity they create on

396   some reefs are important factors determining the diversity and structure of the invertebrate

397   communities (Idjadi & Edmunds, 2006), and that reef invertebrates, in particular crustaceans,

398   appear to be more resilient to reef degradation than reef-associated fishes (Head et al., 2015;

399   Newman et al., 2015; Nelson, Kuempel & Altieri, 2016). However, the effect of coral reef

400   degradation on small reef-associated invertebrates may depend to a large extent on small-scale

401   features that are not necessarily provided or modulated by corals (Dumas et al., 2013). Given the

402   ongoing tendency to increase of coral reef degradation, future studies should investigate the

403   relative importance of different types of microhabitats at different scales and the occurrence of

404   mutualistic relationships for maintaining diversity and abundance of reef-associated

405   macrocrustaceans.

406

407   **CONCLUSIONS**

408   Structural complexity is an important factor driving the diversity and abundance of reef-

409   associated macrocrustaceans, but so is the variety of local microhabitats and of mutualistic

410   relationships that these animals can establish with other taxa. We found a greater diversity and

411   abundance of macrocrustaceans in a more degraded coral reef (Bonanza) than in a reef

412   characterized by extensive stands of live *Acropora palmata* (Limones), but the latter exhibited a

413   higher level of dominance, reflecting the presence in high numbers of a few species that establish

414   mutualistic relationships with *A. palmata* and hydrozoans. On Limones, relic skeletons and coral

415   rubble were typically overgrown with macroalgae, thus offering refuge and food to herbivorous

416 species of macrocrustaceans. However, coral reef degradation continues to increase, making it

417 necessary to investigate the relative importance of different types of microhabitats at different

418 scales and at different levels of degradation for maintaining diversity and abundance of reef-

419 associated macrocrustaceans.

420

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431

432 **REFERENCES**

433 Abele LG. 1976. Comparative species composition and relative abundance of decapod

434   crustaceans in marine habitats of Panama. *Marine Biology* 38:263–278. DOI

435   10.1007/BF00388939

436 Álvarez-Filip L, Dulvy NC, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean

437   coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal*

438   *Society B* 276: 3019–3025. DOI 10.1098/rspb.2009.0339

439 Álvarez-Filip L, Paddack MJ, Collen B, Robertson DR, Côté IM. 2015. Simplification of

440   Caribbean reef-fish assemblages over decades of coral reef degradation. *PLoS One*

441   10(4):e0126004. DOI 10.1371/journal.pone.0126004

442 Aronson RB, Precht WF. 2001. White-band disease and the changing face of Caribbean coral

443   reefs. *Hydrobiologia* 460:25–38. DOI 10.1007/978-94-017-3284-0_2

444 Becker JA, Grutter AS. 2004. Cleaner shrimp do clean. *Coral Reefs* 23:515–520. DOI

445   10.1007/s00338-004-0429-3

446 Briones-Fourzán P, Lozano-Álvarez E. 2002. Shallow-water benthic decapod crustaceans of

447   Chankanaab Park, Cozumel Island, Mexico. In: Escobar-Briones E & Álvarez F (eds.)

448   *Modern Approaches to the Study of Crustacea*. Kluwer/Plenum, Nueva York, pp. 197–204.

449   DOI 10.1007/978-1-4615-0761-1_31

450   Briones-Fourzán P, Pérez-Ortiz M, Negrete-Soto F, Barradas-Ortiz C, Lozano-Álvarez E. 2012.

451   Ecological traits of Caribbean sea anemones and symbiotic crustaceans. *Marine Ecology*

452   *Progress Series* 470:55–68. DOI 10.3354/meps10030

453   Brown D, Edmunds PJ. 2013. The hermit crab *Calcinus tibicen* lives commensal on *Millepora*

454   spp. in St. John, United States Virgin Islands. *Coral Reefs* 32:127–135. DOI 10.1007/s00338-

455   012-0948-2

456   Bruno JF, Bertness MD. 2001. Habitat modification and facilitation in benthic marine

457   communities. In Bertness MD, Gaines SD, Hay ME (eds.) *Marine community ecology*.

458   Sunderland, MA: Sinauer, pp. 201–218.

459   Bruno JF, Precht WF, Vroom PS, Aronson RB. 2014. Coral reef baselines: How much

460   macroalgae is natural? *Marine Pollution Bulletin* 80:24–29. DOI

461   10.1016/j.marpolbul.2014.01.010

462   Butler MJ IV, Mojica AM. 2012. Herbivory by the Caribbean king crab on coral patch reefs.

463   *Marine Biology* 159:2697–2706. DOI 10.1007/s00227-012-2027-1

464   Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure.

465   *Australian Journal of Ecology* 18:117–143. DOI 10.1111/j.1442-9993.1993.tb00438.x

466   Clarke KR, Warwick RM. 2001. *Change in marine communities: an approach to statistical*

467   *analysis and interpretation*, 2nd edition. PRIMER-E: Plymouth.

468   Coen LD. 1988. Herbivory by Caribbean majid crabs: feeding ecology and plant susceptibility.

469   *Journal of Experimental Marine Biology and Ecology* 122:257–276. DOI 10.1016/0022-

470   0981(88)90127-X

471   Coker DJ, Wilson SK, Pratchett MS. 2014. Importance of live coral habitat for reef fishes.

472   *Reviews in Fish Biology and Fisheries* 24:89–126. DOI 10.1007/s11160-013-9319-5

473   Coles SL. 1980. Species diversity of decapods associated with living and dead reef coral

474   *Pocillopora meandrina*. *Marine Ecology Progress Series* 2:281–291. DOI

475   10.3354/meps002281

476   Dumas P, Jiménez H, Peignon C, Wantiez L, Adjeroud M. 2013. Small-scale habitat structure

477   modulates the effects of no-take marine reserves for coral reef macroinvertebrates. *PLoS One*

478   8(3): e58998. DOI 10.1371/journal.pone.0058998

479   Enochs IC. 2012. Motile cryptofauna associated with live and dead coral substrates: implications

480   for coral mortality and framework erosion. *Marine Biology* 159:709–722. DOI

481   10.1007/s00227-011-1848-7

482   Fabricius KE, De'ath G, Noonan S, Uthicke S. 2014. Ecological effects of ocean acidification

483   and habitat complexity on reef-associated macroinvertebrate communities. *Proceedings of the*

484   *Royal Society B* 281:20132497. DOI 10.1098/rspb.2013.2479

485   Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines

486   in Caribbean corals. Science 301:958–960. DOI 10.1126/science.1086050

487   Garpe KC, Yahya SAS, Lindahl U, Öhman MC. 2006. Long-term effects of the 1998 coral

488   bleaching event on reef fish assemblages. *Marine Ecology Progress Series* 315:237–247. DOI

489   10.3354/meps315237

490   Giraldes BW, Coelho Filho PA, Coelho PA. 2012. Composition and spatial distribution of

491   subtidal decapoda on the "Reef Coast", northeastern Brazil, evaluated through a low-impact

492   visual census technique. *Nauplius* 20:187–201. DOI 10.1590/S0104-64972012000200010

493   Giraldes BW, Coelho Filho PA, Smyth DM, Coelho PA. 2017. The nocturnal zonation of

494   decapods in the subtidal zone within the reef seascape—abiotic factors defining habitats.

495   *ICES Journal of Marine Science* 74:2180–2190. DOI 10.1093/icesjms/fsx055

496   Glynn PW, Enochs IC. 2011. Invertebrates and their roles in coral reef ecosystems. In: Dubinsky

497   Z, Stambler N, eds. *Coral reefs: an ecosystem in transition*. Dordrecht: Springer, 273–325.

498   DOI 10.1007/978-94-007-0114-4_18

499   Gotelli NJ, Colwell RK. 2001. Quantifying biodiversity: procedures and pitfalls in the

500   measurement and comparison of species richness. *Ecology Letters* 4:379–391.

501   Graham NAJ, Nash KL. 2013. The importance of structural complexity in coral reef ecosystems.

502   *Coral Reefs* 32: 315–326. DOI 10.1046/j.1461-0248.2001.00230.x

503   Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, MacNeil MA, McClanahan TR,

504   Öhman MC, Polunin NVC, Wilson SK. 2011. Extinction vulnerability of coral reef fishes.

505   *Ecology Letters* 14:341–348. DOI 10.1111/j.1461-0248.2011.01592.x

506   Gratwicke B, Speight MR. 2005. Effects of habitat complexity on Caribbean marine fish

507   assemblages. *Marine Ecology Progress Series* 292:301–310. DOI 10.3354/meps292301

508   Hazlett BA. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and*

509   *Systematics* 12:1–22. DOI 10.1146/annurev.es.12.110181.000245

510   Head CEI, Bonsall MB, Koldewey H, Pratchett MS, Speight M, Rogers AD. 2015. High

511   prevalence of obligate coral-dwelling decapods on dead corals in the Chagos archipelago,

512   central Indian Ocean. *Coral Reefs* 34:905–915. DOI 10.1007/s00338-015-1307-x

513   Hill J, Wilkinson C. 2004. *Methods for ecological monitoring of coral reefs*. Townsville:

514   Australian Institute of Marine Science.

515   Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van

516   de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M. 2017. Coral

517   reefs in the Anthropocene. *Nature* 546:82–90. DOI 10.1038/nature22901

518   Idjadi JA, Edmunds PJ. 2006. Scleractinian corals as facilitators for other invertebrates on a

519   Caribbean reef. *Marine Ecology Progress Series* 319:117–127. DOI 10.3354/meps319117

520   Jackson JBC, Donovan M, Cramer K, Lam V. 2014. *Status and Trends of Caribbean Coral*

521   *Reefs: 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN. DOI

522   10.13140/2.1.4868.6726

523   Jordán-Dahlgren E. 1993. *Atlas de los arrecifes coralinos del Caribe mexicano*. Chetumal:

524   Centro de Investigaciones de Quintana Roo.

525   Kerry JT, Bellwood DR. 2015. Do tabular corals constitute keystone structures for fishes on

526   coral reefs? *Coral Reefs* 34: 41–50. DOI 10.1007/s00338-014-1232-4

527   Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, Caley MJ. 2010. Coral reef

528   biodiversity. In: McIntyre AD, ed. *Life in the world's oceans*. Chichester: Wiley-Blackwell,

529   65–77.

530   Kramer MJ, Bellwood DR, Bellwood O. 2014. Benthic Crustacea on coral reefs: a quantitative

531   survey. *Marine Ecology Progress Series* 511:105–116. DOI 10.3354/meps10953

532   Ladd MC, Collado-Vides L. 2013. Practical applications of monitoring results to improve

533   managing for coral reef resilience: a case study in the Mexican Caribbean. *Biodiversity*

534   *Conservation* 22:1591–1608. DOI 10.1007/s10531-013-0493-5

535   Lindahl U, Öhman MC, Schelten CK. 2001. The 1997/1998 mass mortality of corals: effects on

536   fish communities on a Tanzanian coral reef. *Marine Pollution Bulletin* 42:127–131. DOI

537   10.1016/S0025-326X(00)00167-3

538   Lozano-Álvarez E, Luviano-Aparicio N, Negrete-Soto F, Barradas-Ortiz C, Aguíñiga-García S,

539   Morillo-Velarde PS, Álvarez-Filip L, Briones-Fourzán P. 2017. Does reef architectural

540 complexity influence resource availability for a large reef-dwelling invertebrate? *Journal of*
541 *Sea Research* 128:84–91. DOI 10.1016/j.seares.2017.08.010

542 Magurran AE, Dornelas M. 2010. Biological diversity in a changing world. *Philosophical*
543 *Transactions of the Royal Society B* 365:3593–3597. DOI 10.1098/rstb.2010.0296

544 Martínez-Iglesias JC, García-Raso JE. 1999. The crustacean decapod communities of three coral
545 reefs from the southwestern Caribbean Sea of Cuba: species composition, abundance and
546 structure of the communities. *Bulletin of Marine Science* 65:539–557.

547 McKeon CS, Moore JM. 2014. Species and size diversity in protective services offered by coral
548 guard-crabs. *PeerJ* 2:e574. DOI 10.7717/peerj.574

549 Morillo-Velarde PS, Briones-Fourzán P, Álvarez-Filip L, Aguíñiga-García S, Sánchez-González
550 A, Lozano-Álvarez E. 2018. Habitat degradation alters trophic pathways but not food chain
551 length on shallow Caribbean coral reefs. *Scientific Reports* (in press).

552 Morris EK, Caruso T, Buscot F, Fischer M, Hancock C, Maier TS, Meiners T, Müller C,
553 Obermaier E, Prati D, Socher SA, Sonnemann I, Wäschke N, Wubet T Wurst S, Rillig MC.
554 2014. Choosing and using diversity indices: insights for ecological applications from the
555 German Biodiversity Exploratories. *Ecology and Evolution* 4:3514–3524. DOI
556 10.1002/ece3.1155

557 Munday PL. 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Global*
558 *Change Biology* 10:1642–1647. DOI 10.1111/j.1365-2486.2004.00839.x

559 Nelson HR, Kuempel CD, Altieri AH. 2016. The resilience of reef invertebrate biodiversity to
560 coral mortality. *Ecosphere* 7(7), e1399. DOI 10.1002/ecs2.1399

561 Newman SP, Meesters EH, Dryden CS, Williams SM, Sanchez C, Mumby PJ, Polunin NVC.
562 2015. Reef flattening effects on total richness and species responses in the Caribbean. *Journal*
563 *of Animal Ecology* 84:1678–1689. DOI 10.1111/1365-2656.12429

564 Patton WK. 1967. Studies on *Domecia acanthophora*, a commensal crab from Puerto Rico, with
565 particular reference to modifications of the coral host and feeding habits. *Biological Bulletin*
566 132:56–67. DOI 10.2307/1539878

567 Patton WK. 1994. Distribution and ecology of animals associating with branching corals
568 (*Acropora* spp.) from the Great Barrier Reef, Australia. *Bulletin of Marine Science* 55:193–
569 211.

570 Perry CT, Edinger EN, Kench PS, Murphy GN, Smithers SG, Steneck RS, Mumby PJ. 2012.

571  Estimating rates of biologically driven coral reef framework production and erosion: a new

572  census based carbonate budget methodology and applications to the reefs of Bonaire. *Coral*

573  *Reefs* 31:853–868. DOI 10.1007/s00338-012-0901-4

574 Przeslawski R, Ahyong S, Byrne M, Worheide G, Hutchings P. 2008. Beyond corals and fish:

575  the effects of climate change on non-coral benthic invertebrates of tropical reefs. *Global*

576  *Change Biology* 14:2773–2795. DOI 10.1111/j.1365-2486.2008.01693.x

577 Randall JE. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical*

578  *Oceanography* 5:655–847.

579 Reed JK, Gore RH, Scotto LE, Wilson KA. 1982. Community composition, structure, areal and

580  trophic relationships of decapods associated with shallow- and deep-water *Oculina varicosa*

581  coral reefs. *Bulletin of Marine Science* 32:761–786.

582 Risk MJ. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*

583  193:1–6.

584 Roberts CM, Ormond RFG. 1987. Habitat complexity and coral reef fish diversity and

585  abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 4:1–8. DOI

586  10.3354/meps041001

587 Rodríguez-Martínez RE, Banaszak AT, McField MD, Beltrán-Torres AU, Álvarez-Filip L. 2014.

588  Assessment of *Acropora palmata* in the Mesoamerican Reef System. *PLoS One* 9(4):e96140.

589  DOI 10.1371/journal.pone.0096140

590 Roff G, Wabnitz CCC, Harborne AR, Mumby PJ. 2013. Macroalgal associations of motile

591  epifaunal invertebrate communities on coral reefs. *Marine Ecology* 34:409–419. DOI

592  10.1111/maec.12040

593 Stachowicz JJ, Hay ME. 1996. Facultative mutualism between an herbivorous crab and a

594  coralline alga: advantages of eating noxious seaweeds. *Oecologia* 105:377–387. DOI

595  10.1007/BF00328741

596 Stella JS, Jones GP, Pratchett MS. 2010. Variation in the structure of epifaunal invertebrate

597  assemblages among coral hosts. *Coral Reefs* 29:957–973. DOI 10.1007/s00338-010-0648-8

598 Stella JS, Pratchett MS, Hutchings PA, Jones GP. 2011. Coral-associated invertebrates: diversity,

599  ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology*

600  *Annual Review* 49:43–104.

601 Stewart HL, Holbrook SJ, Schmitt RJ, Brooks AJ. 2006. Symbiotic crabs maintain coral health

602   by clearing sediments. *Coral Reefs* 25:609–615. DOI 10.1007/s00338-006-0132-7

603   Suchley A, McField MD, Álvarez-Filip L. 2016. Rapidly increasing macroalgal cover not related

604   to herbivorous fishes on Mesoamerican reefs. *PeerJ* 4:e2084. DOI 10.7717/peerj.2084

605   Tews J, Brose U, Grimm V, Tielborger K, Wichmann MC, Schwager M, Jeltsch F. 2004. Animal

606   species diversity driven by habitat heterogeneity/diversity: the importance of keystone

607   structures. *Journal of Biogeography* 31:79–92. DOI 10.1046/j.0305-0270.2003.00994.x

608   Vytopil E, Willis BL. 2001. Epifaunal community structure in *Acropora* spp. (Scleractinia) on

609   the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs*

610   20:281–288. DOI 10.1007/s003380100172

611   Warton DI, Hui FKC. 2011. The arcsine is asinine: the analysis of proportions in ecology.

612   *Ecology* 92:3–10. DOI 10.1890/10-0340.1

613

614   **FIGURE LEGENDS**

615   Figure 1. Study area
616   Location of the studied reef units, Limones (well-preserved) and Bonanza (degraded), at Puerto
617   Morelos.
618
619   Figure 2. Percent cover of benthic community components
620   Percent cover of different benthic community components over Limones reef (green columns)
621   and Bonanza reef (blue columns). Error bars are 95% confidence intervals. Asterisks at the end
622   of a component name denote significant differences between reefs ($\alpha = 0.05$).
623
624   Figure 3. Principal Components Analysis (PCA) of percent cover of benthic components.
625   Bi-plot on logit-transformation of percent cover of benthic components over the two studied
626   reefs, Limones (green dots) and Bonanza (blue dots). Each dot represents a transect. LHC: live
627   hard coral, TA: turf algae, FMA: fleshy macroalgae, CMA: calcareous macroalgae; CCA:
628   coralline algae, CYAN: cyanobacterial mats, OINV: other sessile invertebrates, Other: other
629   components (sand, seagrass).
630
631   Figure 4. Species accumulation and rarefaction curves.
632   Accumulation and rarefaction curves for macrocrustacean species recorded in Bonanza and
633   Limones reefs. Thirty belt transects, 50 m² each, were sampled on each reef. Rarefaction curves
634   for either reef do not reach an asymptote, indicating the existence of more species.
635
636   Figure 5. nMDS ordination
637   Non-metric multidimensional (nMDS) ordination of macrocrustacean community structure in
638   samples from Limones reef (green triangles and dashed lines) and Bonanza reef (blue circles and
639   continuous lines), based on species abundances. Each symbol denotes a transect.
640
641   Figure 6. Density of macrocrustaceans per reef
642   Mean density (number of individuals 50 m^{-2}) of the most abundant macrocrustaceans per reef:
643   Limones (green columns) and Bonanza (blue columns). Error bars are 50% confidence intervals.
644
645   Figure 7. Types of microhabitats used by macrocrustaceans
646   Comparison of the types of microhabitats used by macrocrustaceans on each reef, Limones
647   (green columns) and Bonanza (blue columns).
648

Study area.

Location of the studied reef units, Limones (well-preserved) and Bonanza (degraded), at Puerto Morelos, México.

Figure 1

Figure 2

Percent cover of benthic community components.

Percent cover of different benthic community components over Limones reef (green columns) and Bonanza reef (blue columns). Error bars are 95% confidence intervals. Asterisks at the end of a component name denote significant differences between reefs (α = 0.05).

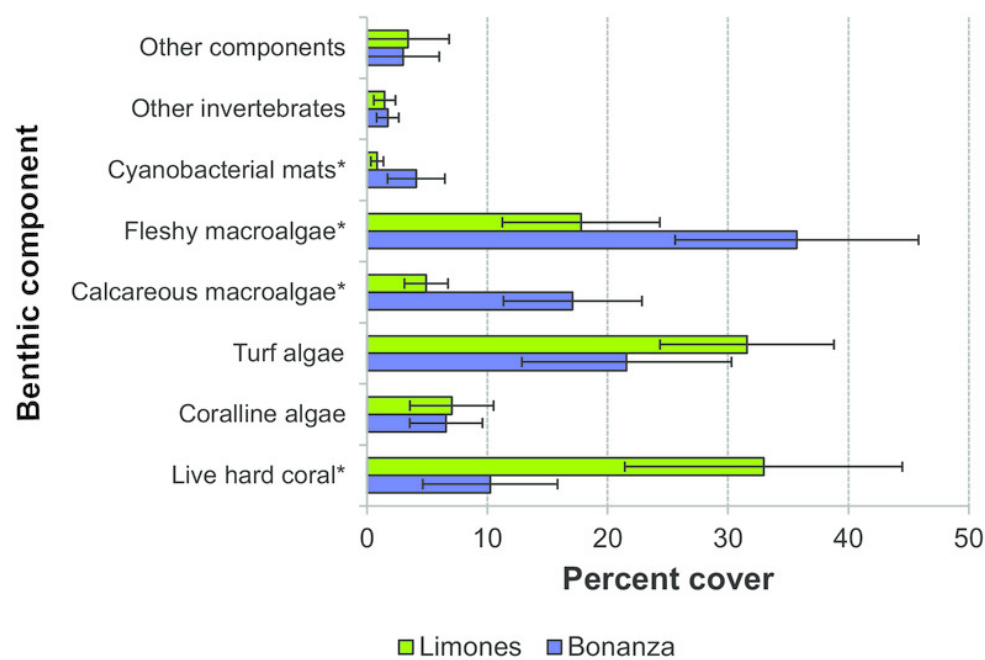



Figure 3

Principal Components Analysis (PCA) of percent cover of benthic components.

Bi-plot on logit-transformation of percent cover of benthic components over the two studied reefs, Limones (green dots) and Bonanza (blue dots). Each dot represents a transect. LHC: live hard coral, TA: turf algae, FMA: fleshy macroalgae, CMA: calcareous macroalgae; CCA: coralline algae, CYAN: cyanobacterial mats, OINV: other sessile invertebrates, Other: other components (sand, seagrass).

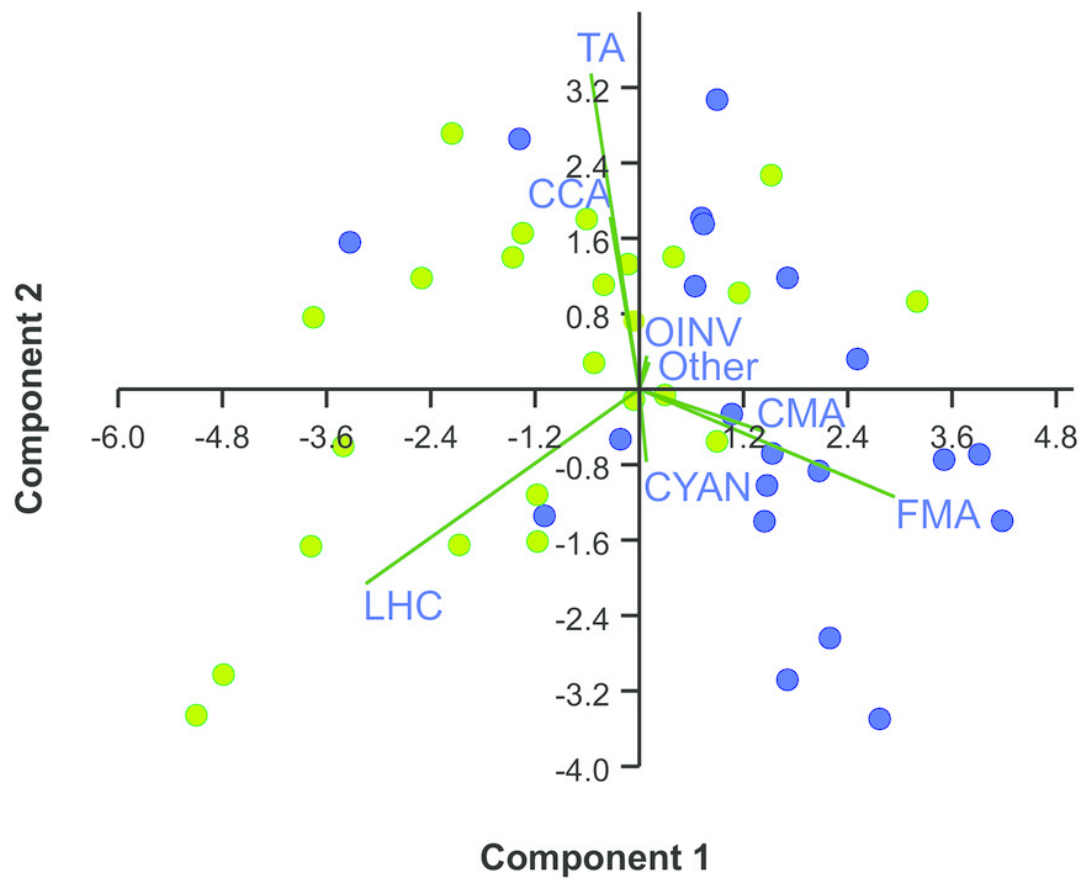



Figure 4

Species accumulation and rarefaction curves.

Accumulation and rarefaction curves for macrocrustacean species recorded in Bonanza and Limones reefs. Thirty belt transects, 50 m² each, were sampled on each reef. Rarefaction curves for either reef do not reach an asymptote, indicating the existence of more species.

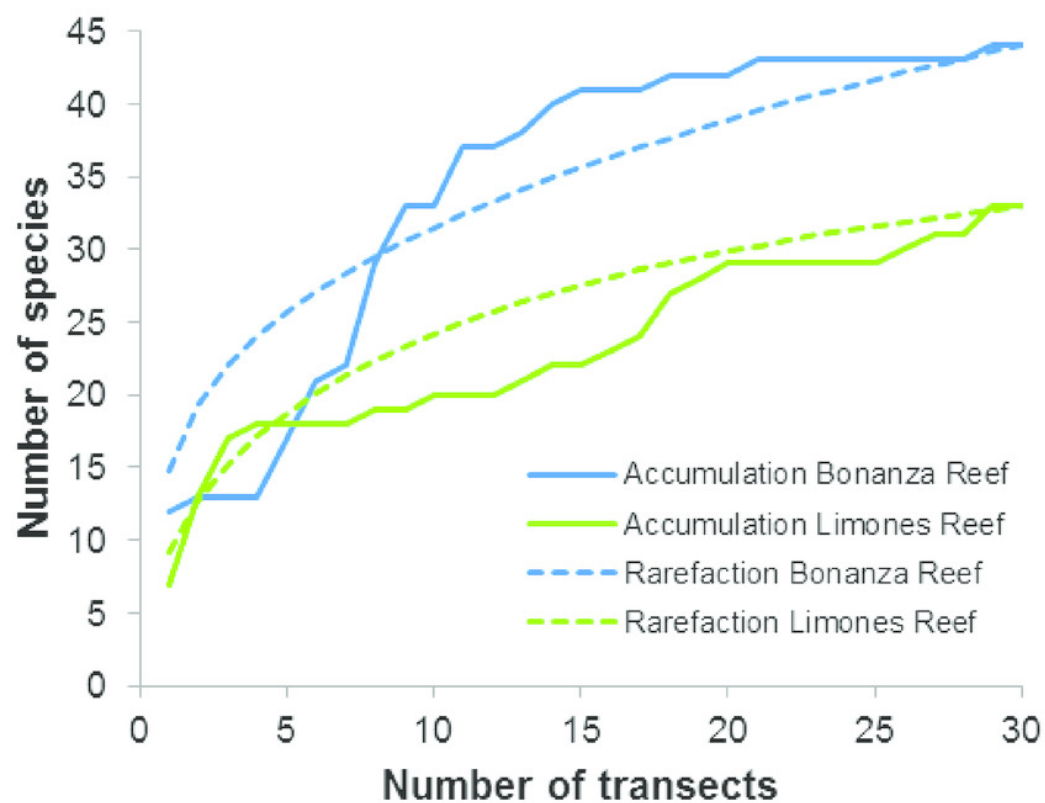



Figure 5

nMDS ordination.

Non-metric multidimensional (nMDS) ordination of macrocrustacean community structure in samples from Limones reef (green triangles and dashed lines) and Bonanza reef (blue circles and continuous lines), based on species abundances. Each symbol denotes a transect.

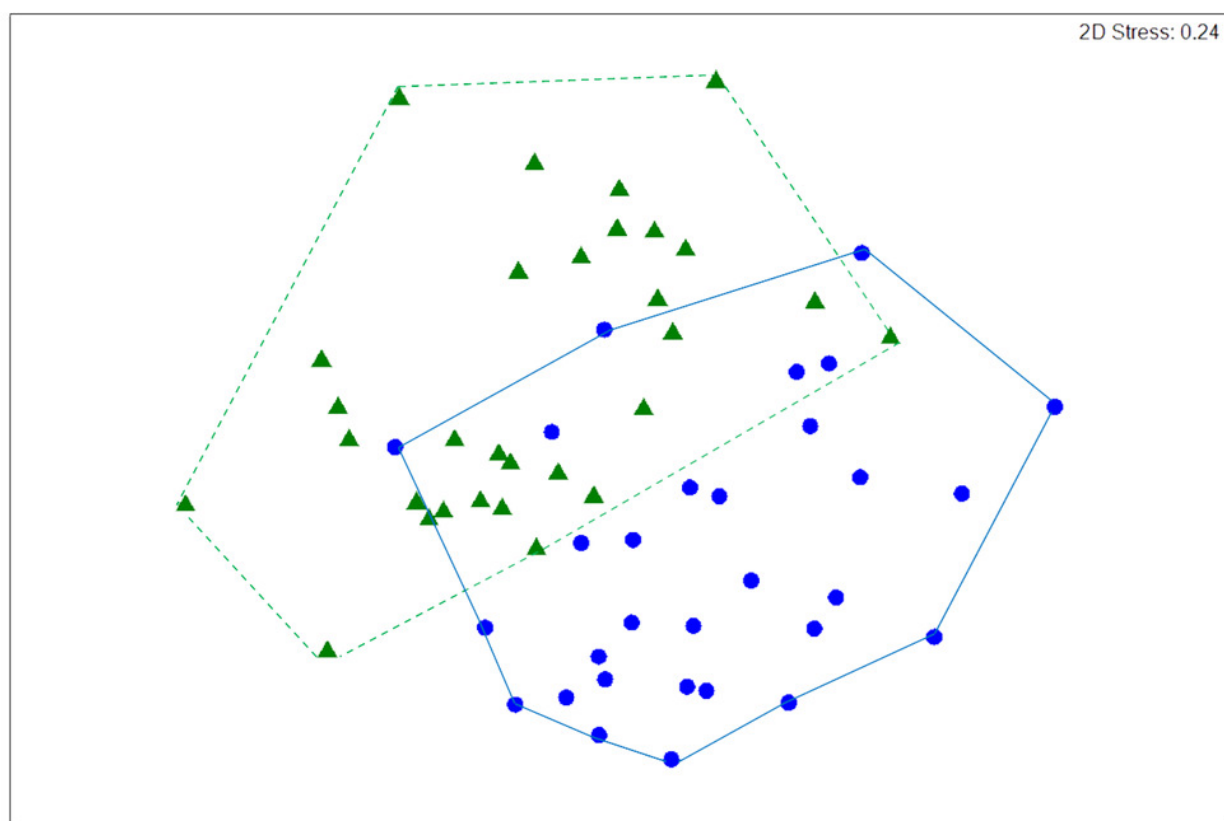



Figure 6

Density of macrocrustaceans per reef.

Mean density (number of individuals 50 m^{-2}) of the most abundant macrocrustaceans per reef: Limones (green columns) and Bonanza (blue columns). Error bars are 50% confidence intervals.

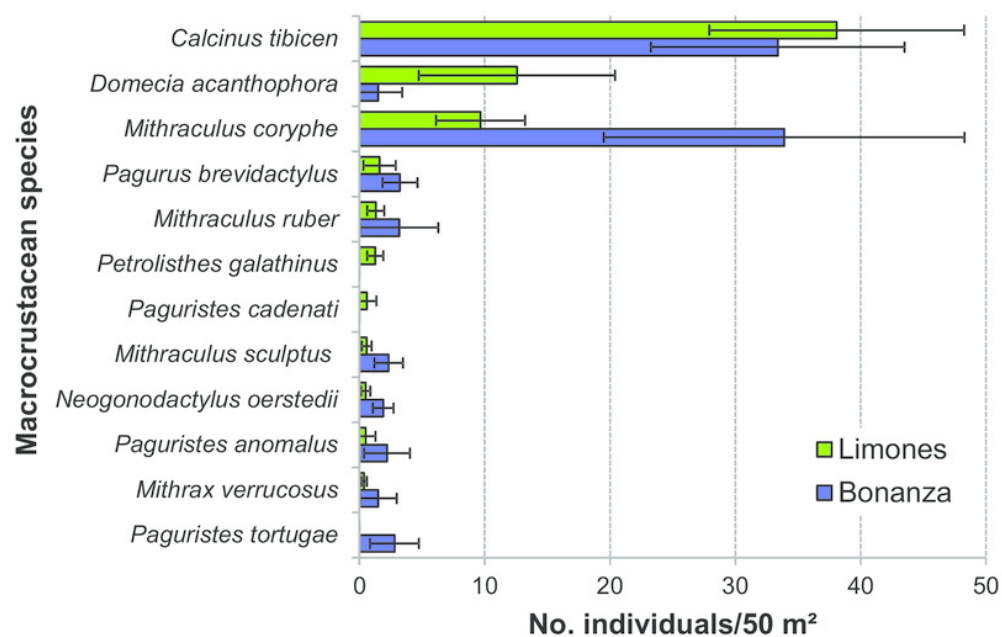
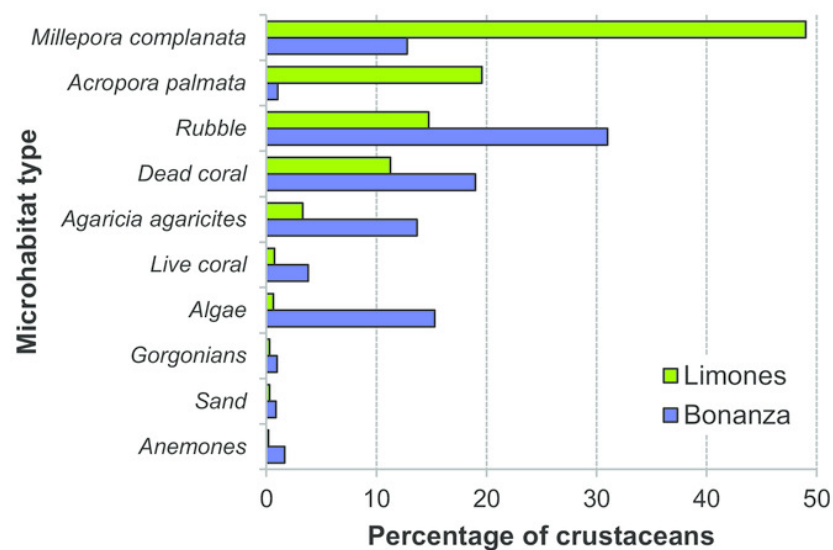



Figure 7

Types of microhabitats used by macrocrustaceans.

Comparison of the types of microhabitats used by macrocrustaceans on each reef, Limones (green columns) and Bonanza (blue columns).

Macrocrustacean species by reef.

Number of macrocrustacean species and individuals registered by visual census (n = 30 transects). Bonanza reef: 44 species; 2800 individuals; Limones reef: 33 species; 2067 individuals. An X denotes that a species was only qualitatively recorded during nocturnal dives.

	Species	Bonanza	Limones
1	*Mithraculus coryphe*	1017	290
2	*Calcinus tibicen*	1002	1143
3	*Pagurus brevidactylus*	97	48
4	*Teleophrys ruber*	95	40
5	*Paguristes tortugae*	84	0
6	*Mithraculus sculptus*	70	17
7	*Paguristes anomalus*	66	15
8	*Neogonodactylus oerstedii*	57	15
9	*Domecia acanthophora*	45	377
10	*Mithrax aculeatus*	45	11
11	*Omalacantha bicornuta*	43	1
12	*Alpheus armatus*	19	4
13	*Paguristes puncticeps*	19	4
14	Callianassid A	19	1
15	*Thor amboinensis*	19	0
16	*Panulirus argus*	18	4
17	*Macrocoeloma subparellelum*	14	0
18	*Axiopsis serratifrons*	12	4
19	*Percnon gibbesi*	8	7
20	*Nonala holderi*	7	0
21	*Petrolisthes galathinus*	5	38
22	*Macrocoeloma diplacanthum*	5	0
23	Xanthid E	4	0
24	*Mithraculus cinctimanus*	3	3
25	*Stenopus hispidus*	3	0
26	*Actaea acantha*	2	0
27	*Ancylomenes pedersoni*	2	0
28	*Ratha longimanus*	2	0
29	*Macrocoeloma trispinosum*	2	0
30	*Mithraculus forceps*	2	0
31	*Panulirus guttatus*	1	3
32	*Lysmata wurdemanni*	1	1
33	Anomuran A	1	0
34	*Brachycarpus biunguiculatus*	1	0
35	Majoid B	1	0
36	Majoid C	1	0
37	Majoid D	1	0
38	*Neogonodactylus torus*	1	0
39	*Pitho lherminieri*	1	0

40	*Pitho mirabilis*	1	0
41	*Podochela macrodera*	1	0
42	*Stenorhynchus seticornis*	1	0
43	Xanthid C	1	0
44	Xanthid D	1	0
45	*Paguristes cadenati*	0	18
46	*Phimochirus holthuisi*	0	5
47	Caridean A	0	3
48	*Pachycheles pilosus*	0	3
49	*Cinetorhynchus manningi*	0	2
50	Majoid A	0	2
51	*Nemausa acuticornis*	0	2
52	*Damithrax hispidus*	0	1
53	*Maguimithrax spinosissimus*	0	1
54	*Achelous sebae*	0	1
55	*Synalpheus* sp.	0	1
56	Xanthid A	0	1
57	Xanthid B	0	1
58	*Cynetorhynchus rigens*	X	X
59	*Cynetorhynchus fasciatus*	X	
60	*Metapenaeopsis goodei*	X	X
61	*Palinurellus gundlachi*		X
62	*Parribacus antarcticus*	X	
63	*Scyllarides aequinoctialis*	X	X
64	*Carpilius corallinus*	X	

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Ecological indices for macrocrustaceans by reef.

Mean value (± 95% confidence interval) of species richness (S), Shannon-Wiener diversity (H'), dominance (D), and evenness (J') of macrocrustaceans on Bonanza and Limones reefs.

Ecological Index	Bonanza reef	Limones reef
S	8.66 ± 1.18	6.53 ± 0.71
H'	2.07 ± 0.19	1.54 ± 0.15
D	0.33 ± 0.04	0.47 ± 0.05
J'	0.69 ± 0.04	0.58 ± 0.04

Similarity measures within and between reefs.

SIMPER analysis of similarity for macrocrustacean assemblages within Limones and Bonanza, and of dissimilarity between reefs.

Limones. Average similarity: 48.10

Species	AA	AS	Sim/SD	Contrib%	Cum %
Calcinus tibicen	2.33	21.73	4.10	45.18	45.18
Mithraculus coryphe	1.52	12.62	2.07	26.23	71.41
Domecia acanthophora	1.04	4.16	0.57	8.65	80.06
Petrolisthes galathinus	0.58	2.18	0.50	4.54	84.60
Teleophrys ruber	0.52	1.71	0.41	3.55	88.16
Pagurus brevidactylus	0.51	1.66	0.41	3.46	91.61

Bonanza: Average similarity: 46.90

Species	AA	AS	Sim/SD	Contrib%	Cum %
Mithraculus coryphe	2.22	15.54	3.64	33.14	33.14
Calcinus tibicen	2.15	13.64	2.51	29.09	62.22
Neogonodactylus oerstedii	0.85	4.12	0.89	8.79	71.02
Pagurus brevidactylus	0.90	3.40	0.77	7.25	78.27
Mithraculus sculptus	0.76	2.85	0.64	6.08	84.35
Omalacantha bicornuta	0.52	1.29	0.45	2.75	87.10
Paguristes tortugae	0.57	1.07	0.37	2.29	89.39
Teleophrys ruber	0.52	0.80	0.33	1.70	91.09

Limones and Bonanza: Average dissimilarity: 58.49

Species	Limones AA	Bonanza AA	AD	Dis/SD	Contrib%	Cum %
Domecia acanthophora	1.04	0.29	4.76	0.96	8.14	8.14
Mithraculus coryphe	1.52	2.22	3.88	1.23	6.63	14.77
Pagurus brevidactylus	0.51	0.90	3.73	1.17	6.38	21.15
Calcinus tibicen	2.33	2.15	3.55	0.99	6.07	27.22
Neogonodactylus oerstedii	0.33	0.85	3.43	1.21	5.86	33.08
Mithraculus sculptus	0.34	0.76	3.39	1.07	5.80	38.88
Teleophrys ruber	0.52	0.52	3.10	0.97	5.30	44.18
Petrolisthes galathinus	0.58	0.11	2.61	0.90	4.46	48.64
Paguristes tortugae	0.00	0.57	2.28	0.72	3.90	52.54

2 AA: average abundance; AS: average similarity; Sim/SD: similarity/standard deviation; Contrib
3 %: contribution in %; Cum %: cumulative contribution in %; AD: average dissimilarity; Dis/SD:
4 dissimilarity/standard deviation). Species are listed in decreasing order of AS within each reef
5 and AD between reefs. Cum.% does not reach 100% in order to facilitate interpretation.