Diversity and abundance of conspicuous 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 and rubble (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 63 macrocrustacean species (61 Decapoda and two Stomatopoda). Contrary to our expectations, structural complexity did not differ significantly between the back-reef zones of these reefs but varied more broadly on Limones, 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.

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18   **ABSTRACT**

19   Coral reefs sustain abundant and diverse macrocrustaceans that perform multiple ecological

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

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

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

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

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

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

26   *palmata*, and the other ("Bonanza") dominated by macroalgae and relic coral skeletons and

27   rubble (i.e., degraded). We also assessed the structural complexity of each reef and the percent

28   cover of various benthic community components. Given the type of growth of *A. palmata*, we

29   expected to find a greater structural complexity, a higher cover of live coral, and a lower cover of

30   macroalgae on Limones, and hence a more diverse and abundant macrocrustacean community on

31   this reef compared with Bonanza. Overall, we identified 63 macrocrustacean species (61

32   Decapoda and two Stomatopoda). Contrary to our expectations, structural complexity did not

33   differ significantly between the back-reef zones of these reefs but varied more broadly on

34   Limones, and the diversity and abundance of macrocrustaceans were higher on Bonanza than on

35   Limones despite live coral cover being higher on Limones and macroalgal cover on Bonanza.

36   However, the use of various types of microhabitats by macrocrustaceans differed substantially

37   between reefs. On both reefs, the dominant species were the clinging crab *Mithraculus coryphe*

38   and the hermit crab *Calcinus tibicen*, but the former was more abundant on Bonanza and the

39   latter on Limones. *M. coryphe* occupied a diverse array of microhabitats but mostly coral rubble

40   and relic skeletons, whereas *C. tibicen* was often, but not always, found associated with colonies

41   of *Millepora* spp. A small commensal crab of *A. palmata*, *Domecia acanthophora*, was far more

42   abundant on Limones, emerging as the main discriminant species between reefs. Our results

43   suggest that local diversity and abundance of reef-associated macrocrustaceans are partially

44   modulated by habitat degradation, the diversity of microhabitat types, and the establishment of

45   different commensal associations rather than by structural complexity alone.

46

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 is 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

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

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

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

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

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

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

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

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

86 cover (Idjadi & Edmunds, 2006). In contrast, invertebrate assemblages were more diverse and

87 abundant on dead than on live coral habitats in Panama (Nelson, Kuempel & Altieri, 2016),

88 whereas habitat complexity accounted for very little of the variability in invertebrates (including

89 arthropods) on Caribbean *Orbicella* reefs (Newman et al., 2015). These contrasting results

90 suggest that many reef-associated invertebrates do not necessarily benefit from the presence of

91 live corals per se, but from the complex 3-D framework of coral reefs, which can persist for

92 years after the death of corals.

93   One of the most structurally complex, reef-building corals in the Caribbean region is the

94 branching coral *Acropora palmata*. This species, once dominant in the region, form thick stands

95 that provide an intricate network of crevices on shallow-water reefs (< 5 m). The populations of

96 this species have sustained extensive mortality since the early 1980s, substantially reducing coral

97 cover, increasing substratum for algal growth, and drastically reducing reef complexity (Aronson

98 & Precht, 2001; Alvarez-Filip et al., 2009; Jackson et al., 2014). Currently, *Acropora*-dominated

99 reefs are rare. For example, a recent assessment in 107 sites along the Mesoamerican Reef

100 (MAR) revealed that *A. palmata* was present (mostly at low cover values) in only 20% of the

101 sites, and that only one site ("Limones" reef), located in the northernmost Mexican portion of the

102 MAR, exhibited extensive stands of *A. palmata* resulting in a high (>35%) cover of this

103 branching coral (Rodríguez-Martínez et al., 2014). Therefore, assessing the composition and

104 structure of the ecological condition on these *Acropora*-dominated reefs is crucial to elucidate

105 how reef degradation is modifying the ecological relationships on coral reefs.

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

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

108 abundance of these macrocrustaceans between Limones reef and another reef ("Bonanza"),

109 similar in size to Limones but highly degraded, to elucidate the potential effects of coral reef

110 degradation on this type of invertebrates. We predicted that the diversity and abundance of

111 macrocrustaceans would be higher in Limones because the presence of extensive stands of live

112 *A. palmata* would presumably confer a greater structural complexity and provide a broad

113 diversity of microhabitats potentially used by reef-associated species (Roberts & Ormond, 1987;

114 Garpe et al., 2006).

115

116 **MATERIALS AND METHODS**

117 **Study site**

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

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

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

121 structural complexity (Lozano-Álvarez et al., 2017; Morillo-Velarde et al., 2018), separated from

122 the coast by a shallow (<5 m) reef lagoon. Along the reef tract, coral cover tends to be greater on

123 the back-reef and crest zones than on the low-relief fore-reef, which descends gradually into an

124 extensive sand platform at 20–25m (Jordán-Dahlgren, 1993). Two of these reef units are

125 Limones (centered at 20˚59.1' N, 86˚47.9' W) and Bonanza (centered at 20˚57.6' N, 86˚48.9' W)

126 (Fig. 1A). Both reefs are similar in length (~ 1.5 km), depth and distance from the coast, but

127 differ in their level of degradation, as indicated by several studies. Healthy and resilient

128 populations of *Acropora palmata* have been reported since 1985 on Limones (Rodriguez-

129 Martínez et al., 2014) (Fig. 1B), and recently Morillo-Velarde et al. (2018) found 50% live coral

130 cover, mostly *A. palmata*, along the central part of Limones. In contrast, live coral cover on

131 Bonanza has gradually declined from 33% in 1985 (Jordán-Dahlgren, 1993) to 12% in 2006-

132 2007 (Carriquiry et al., 2013) and 7% by 2015, when it exhibited extensive areas of relic

133 *Acropora* skeletons (Fig. 1C) and a predominance of erect macroalgae (>60% cover) (Morillo-

134 Velarde et al., 2018). Based on a number of broad- and local-scale resilience indicators,

135 including coral cover, Ladd & Collado-Vides (2013) categorized Limones as a high-resilience

136 site and Bonanza as a low-resilience site, whereas based on two different reef health indices,

137 Díaz-Pérez et al. (2016) categorized the health of Bonanza as "poor". Fishing activities are

138 banned on both Limones and Bonanza reefs since 1996. However, Bonanza is open to visitation,

139 whereas tourist activities are not allowed in Limones since 2014 given the high ecological value

140   of this reef (Rodríguez-Martínez et al., 2014).

141

142   **Macrocrustacean surveys**

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

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

145   2012). Therefore, we used SCUBA diving to conduct quantitative surveys of conspicuous

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

147   with a permit issued by Comisión Nacional de Acuacultura y Pesca (PPF/DGOPA-259/14). All

148   underwater samplings were conducted by two scientific observers, who were thoroughly trained

149   in macrocrustacean identification over several months prior to the samplings. Training was

150   achieved by repeatedly studying an extensive guide of local crustacean species created in our lab

151   with photos from many different sources, followed by direct identification in the field during

152   several preliminary dives. In all cases, the results were cross-checked between both divers

153   (Lessios, 1996; Backus, 2007). On each reef, we haphazardly laid thirty 25-m transects on the

154   back reef zone along the length of the reef. The two divers recorded all macrocrustaceans

155   observed within 1 m to the right and 1 m to the left of the transect line (i.e., an area of 50 m² per

156   transect), both over the substrata and under coral rubble. Individuals were identified *in situ* to the

157   lowest possible taxonomic level and many were extensively photographed underwater to further

158   help in their identification. Only a few individuals were collected in zip-lock bags and taken to

159   the laboratory for their identification. Also recorded was the type of microhabitat in which each

160   specimen was observed. These microhabitats included *Acropora palmata*, *Agaricia agaricites*,

161   other live corals, *Millepora* spp., dead coral skeletons, coral rubble, gorgonians, algae,

162   anemones, and sand. Despite their relatively large size, many macrocrustaceans hide deeply in

163   holes and crevices in coral reefs during the day but forage over the reef substrata at night;

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

165   surveys on each reef by recording all species observed during three separate nocturnal 1-h dives.

166

167   **Structural complexity and benthic community**

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

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

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

171   Habitat Assessment Score (HAS; Gratwicke & Speight, 2005), which is a qualitative metric, and

172   the rugosity index, which is a quantitative metric (Risk, 1972; Álvarez-Filip et al., 2009). HAS

173   provides an overall structural complexity value by visually evaluating six variables of the local

174   topography (rugosity, variety of growth forms, height, refuge size categories, percentage of live

175   cover, and percentage of hard substratum). Each variable is assigned a score between 1 and 5

176   (from smallest or lowest to largest or highest), and the sum of the individual scores is the HAS.

177   Therefore, a score of 6 would represent the least complex habitats and a score of 30 would

178   represent the most complex habitats. HAS values were obtained in three 4 m² quadrats positioned

179   at the beginning, middle, and end of nine of 25-m transects per reef, and the three values were

180   averaged to obtain the transect-level HAS.

181   Rugosity is the ratio of the length of a chain molded to the reef surface to the linear

182   distance between its start and end points. A perfectly flat surface would have a rugosity index of

183   one, with larger numbers indicating more complex surfaces (Risk, 1972). To measure rugosity, a

184   chain (0.5 cm link-length) was molded to the reef surface along 24 10-m long transects on

185   Limones and 21 on Bonanza. These 10-m transects were also used to estimate percent cover of

186   components of the benthic community via the point intercept method (Hill & Wilkinson, 2004).

187   The transects were marked every 10 cm, thus yielding 100 points per transect (Lang et al., 2010),

188   A diver recorded which of the following benthic components was found under each mark: live

189   hard corals, calcareous macroalgae, fleshy macroalgae, coralline algae, algal turf, cyanobacterial

190   mat, other invertebrates (e.g. zoanthids, *Millepora*, *Cliona*), and other components (e.g. sand,

191   seagrass).

192

193   **Data analysis**

194   **Structural complexity and benthic community**

195   HAS values and rugosity indices were compared between reefs with Mann-Whitney U

196   tests. A significance level of 95% was used in all cases. The percent data on the benthic

197   community structure were logit-transformed (Warton & Hui, 2011) and subjected to a principal

198   component analysis (PCA). Then, the transformed data for each benthic component was

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

200

201   **Characterization of the macrocrustacean community**

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

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

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

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

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

207   2014). Given the aims of the present study, we estimated both types of indices for the

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

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

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

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

212    $H'/\log S$). Each index was compared between reefs with a Mann-Whitney U test. Species

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

214   2001).

215   The community composition of macrocrustaceans was analyzed using multivariate

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

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

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

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

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

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

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

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

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

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

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

227   50 m^{-2}, between reefs with individual Student's t tests.

228

229   **RESULTS**

230   **Structural complexity and benthic community components**

231   The median rugosity over the back-reef zones of Limones (1.33 [1.13-2.21], median

232   [interquartile range]) and Bonanza (1.24 [1.07-1.38]) did not differ significantly (Mann-Whitney

233   U test, U = 182, z = 1.764, n_1 = 25, n_2 = 21, p = 0.078) (Fig 2A). A similar result was obtained

234   for the median HAS (Fig. 2B) (Limones: 18 [16-20], Bonanza: 19 [17-19]; Mann-Whitney U

235   test, U = 38.5, z = 0.133, n_1 = n_2 = 9, p = 0.895). However, the range in values of both metrics, in

236   particular rugosity (Fig. 2A), was substantially broader for Limones (1.05–3.56) than for

237   Bonanza (1.02–2.2), with rugosity values ≥2 obtained on 32% transects on Limones versus 9.5%

238   transects on Bonanza. The percent cover of various components of the benthic community

239   differed between reefs (Fig. 3). In particular, live coral cover was much higher on Limones,

240   whereas the cover of fleshy macroalgae, calcareous macroalgae, and cyanobacterial mats was

241   significantly higher on Bonanza (Fig. 3). In the PCA, the first two components explained 63% of

242   the total variance (Fig. 4). The first component explained 40.2% of the variance and was

243   positively correlated with fleshy macroalgae (loading: 0.640) and negatively correlated with live

244   hard coral (-0.685). The second component explained 22.8% of the variance and was strongly

245   positively correlated with turf algae (0.728) and negatively correlated with live hard coral (-

246   0.449) (Fig. 4). Most transects on Limones differed from those on Bonanza along the first

247   component.

248

249   **The macrocrustacean assemblage**

250   In all, we registered 63 species of macrocrustaceans (Table 1), including six that were

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

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

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

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

255   could only be identified to the superfamily or family level. The most diverse superfamily was

256   Majoidea, with 22 species. The number of species was higher on Bonanza than on Limones (43

257   vs 33 species), as was the abundance (2800 vs 2067 individuals) (Table 1).

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

259   (accumulation curves, Fig. 5), but more steeply on Bonanza than on Limones. Rarefaction curves

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

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

262   between reefs (Table 2), with Bonanza exhibiting higher levels of species richness (S, Mann-

263   Whitney U test, U = 265.5, z = -2.741, $n_1 = n_2 = 30$, p = 0.004), diversity (H', U = 208, z = -3.57,

264    $n_1 = n_2 = 30$, p = 0.0002), and evenness (J', U = 261, z = -2.787, $n_1 = n_2 = 30$, p = 0.003),

265   whereas dominance was higher at Limones (D, U = 176, z = -4.044, $n_1 = n_2 = 30$, p < 0.0001).

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

267   p < 0.001) but with some overlap (Fig. 6), suggesting a similar abundance of some species on

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

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

270   62.2% of the similarities observed in Limones and Bonanza, respectively (Table 3). Within

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

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

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

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

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

276   90% of the observed similarity, whereas on Bonanza, this same percentage was accounted for by

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

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

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

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

281   species differed significantly between reefs (Fig. 7). This was the case for *D. acanthophora*,

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

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

284   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

285   for *M. sculptus* and *N. oerstedii* (Fig. 7). In contrast, the density of *C. tibicen* did not differ

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

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

288   *Paguristes cadenati*) and one was recorded on Bonanza only (*Paguristes tortugae*) (Fig. 7).

289

290   **Microhabitats used by macrocrustaceans**

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

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

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

294   *agaricites*, and *Millepora* spp. (Fig. 8). Some of these microhabitats constitute components of the

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

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

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

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

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

300   rubble, relic coral skeletons, sand) were not quantified because they are not components of the

301   benthic community.

302

303   **DISCUSSION**

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

305   macrocrustacean community than Limones, although there were differences between reefs in the

306   percent cover of distinct benthic community components and the types of microhabitats used by

307   macrocrustaceans. Live coral cover (mostly *Acropora palmata*) was much greater on Limones

308   than on Bonanza, whereas the opposite occurred for fleshy and calcareous macroalgae, and

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

310   sustained substantial degradation over the past few decades (Carriquiry et al., 2013; Ladd &

311   Collado-Vides, 2013; Díaz-Pérez et al., 2016; Morillo-Velarde et al., 2018), whereas Limones is

312   an exceptional site in that it has maintained healthy populations of *Acropora palmata*

313   (Rodríguez-Martínez et al., 2014). Previously, Morillo-Velarde et al. (2018) found a significant

314   difference in rugosity between Limones and Bonanza, but these authors measured this variable in

315   only eight transects over the central part of each reef, where development of *A. palmata* on

316   Limones appears to be greater. In contrast, we did not find a significant difference in the median

317   rugosity between the back-reef zones of these reefs, which could be partially explained by the

318   presence of extensive areas of dead coral skeletons on Bonanza as opposed to the extensive

319   stands of live *A. palmata* on Limones. Thus, although our study was conducted in only two reefs,

320   our results are consistent with studies suggesting that live coral cover is not necessarily a key

321   factor determining the level of structural complexity as long as the reef structure persists

322   (Lindahl, Ohmann & Schelten, 2001; Nelson, Kuempel & Altieri, 2016), i.e., that the relic

323   skeletons (i.e. those left behind after the coral tissue dies) and the structural diversity they create

324   can be important factors determining the diversity and structure of invertebrate communities

325   (Idjadi & Edmunds, 2006). However, the wider range in rugosity over Limones, especially of

326   values >2, reflects the patchy presence of more complex substrates interspersed with less rugose

327   substrates. In contrast, the narrower range of values over Bonanza, with few values >2, suggests

328   a lower heterogeneity in substrate rugosity.

329   Reef invertebrates are highly diverse but hard to sample; in particular, many crustaceans

330   hide deeply in reef crevices or under sediments during the day and only emerge at night to forage

331   (Glynn & Enochs, 2011). Therefore, even for conspicuous taxa, visual census methods have

332   several limitations that may result in underestimation of individuals present and sampling error,

333   such as observer variability, characteristics of the target taxa (e.g. crypticity, escape responses),

334   and difficulties imposed by environmental factors (e.g. turbidity, waves, current) (Lessios, 1996;

335   Backus, 2007). Indeed, a few individuals could only be identified to the superfamily level

336   because they either swam away rapidly (i.e. carideans) or retreated deeply into crevices, or

337   because time or environmental restrictions limited further identification. In addition, because our

338   studied reefs are within a marine protected area, we refrained from collecting but a few

339   individuals for further identification in the laboratory. Despite these limitations, species richness

340   was high on both Limones and Bonanza, as previously reported for other Caribbean reef systems

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

342   2002). However, a more exhaustive sampling would undoubtedly increase the number of

343   macrocrustacean species recorded in these reefs (e.g. Alpheidae and Thalassinidae) as indicated

344   by the rarefaction curves (see Fig. 5).

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

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

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

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

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

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

351   abundance of relic coral skeletons, coral rubble, and erect fleshy and calcareous macroalgae

352   (Morillo-Velarde et al., 2018; the present study), than on Limones, which is characterized by

353   extensive stands of *A. palmata* and short algal turf (Rodríguez-Martínez et al., 2014; the present

354   study). The latter would also explain why *Domecia acanthophora*, a small commensal crab of

355   *Acropora* spp. (Patton, 1967), was the main contributor to the dissimilarity between reefs. This

356   species is considered an obligate coral-dwelling crab (Patton, 1967), i.e., a species having strong

357   reliance on live corals for food, habitat, and/or recruitment (Stella et al., 2011). On the other

358   hand, fleshy and calcareous macroalgae, which were more abundant on Bonanza, offer high

359   quality microhabitats to grazing species (Roff et al., 2013) such as majoid crabs of the genera

360   *Mithraculus*, *Mithrax*, *Omalacantha*, and *Maguimithrax*, which use their modified, spooned-

361   shaped chelae to feed on these algae (Coen, 1988; Stachowicz & Hay, 1996; Butler & Mojica,

362   2012). Consequently, majoids were among the most abundant macrocrustaceans on Bonanza,

363   particularly *M. coryphe*, which on this reef was often found in coral rubble overgrown by

364   macroalgae. In Caribbean seagrass habitats, *M. sculptus* outranked *M. coryphe* in abundance

365   (Carmona-Suárez, 2000), but similar to our results, *M. coryphe* was the most abundant crab on

366   coralline substrates around an eastern Caribbean island (García, Hernández & Bolaños, 1998).

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

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

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

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

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

372   (2013) discovered that *C. tibicen* can live commensally on hydrozoans of the genus *Millepora*

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

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

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

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

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

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

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

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

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

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

395   2015; Giraldes et al., 2017), as is the diversity of mutualistic relationships that these animals can

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

397   2013). For example, *A. palmata* provides habitat for many species, but is very vulnerable to

398   diseases (Aronson & Precht, 2001; Stella et al., 2011). In Australia, coral colonies displaying a

399   significant reduction in live tissue cover due to partial mortality exhibited an increase in the

400   abundance and richness of small invertebrate species, suggesting that as coral cover is reduced,

401   new microhabitats arise within the colony, allowing other species to occupy new niches (Stella,

402   Jones & Pratchett, 2010). Thus, dead *A. palmata* may become important for macrocrustaceans

403   for which the relic coral skeletons and coral rubble are preferred microhabitats. Several studies

404   have already highlighted the importance of dead corals and coral rubble as key microhabitats for

405   reef-dwelling decapod crustaceans (e.g. Coles, 1980; Enochs, 2012; Kramer, Bellwood &

406   Bellwood, 2014; Head et al., 2015) and other small invertebrates (Nelson, Kuempel & Altieri,

407   2016). In addition to providing refuge, relic skeletons and coral rubble are typically overgrown

408   by macroalgae, increasing their microhabitat value for herbivorous species (Roff et al., 2013).

409   An increase in the abundance and availability of mobile invertebrates with reef

410   degradation may have positive effects on food web productivity by delaying the loss of other reef

411   components such as fish (Rogers, Blanchard & Mumby, 2018), thus potentially giving more time

412   to reef communities to adapt to the new, more unfavorable, conditions. This hypothesis could

413   explain why Morillo-Velarde et al. (2018) found a very similar food chain length between

414   Limones and Bonanza reefs despite their contrasting levels of structural and benthic integrity.

415   However, this does not mean that reef-associated crustaceans will benefit from coral reef

416   degradation over the long term, because degraded coral reefs continue to erode over time (Perry

417 et al., 2012), eventually reducing the availability of microhabitats with increasing loss of

418 structure and ecosystem functionality (Prezlawski et al., 2008; Head et al., 2015; Lozano-Álvarez

419 et al., 2017), resulting in low productivity over the longer term (Rogers, Blanchard & Mumby,

420 2018). Given the ongoing tendency to increase of coral reef degradation, future studies should

421 investigate the relative importance of different types of microhabitats at different scales and the

422 occurrence of mutualistic relationships for maintaining diversity and abundance of reef-

423 associated macrocrustaceans.

424

425 **CONCLUSIONS**

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

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

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

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

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

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

432 mutualistic relationships with *A. palmata* and hydrozoans. On Bonanza, relic skeletons and coral

433 rubble were typically overgrown by macroalgae, thus offering refuge and food to herbivorous

434 macrocrustaceans. However, coral reef degradation continues to increase, making it necessary to

435 investigate the relative importance of different types of microhabitats at different scales and at

436 different levels of degradation for maintaining diversity and abundance of reef-associated

437 macrocrustaceans.

438

439 **ACKNOWLEDGEMENTS**

440 The authors wish to acknowledge the invaluable technical assistance provided by C Barradas-

441 Ortiz and F Negrete-Soto throughout the study. Additional assistance in field and/or laboratory

442 work was provided by PS Morillo-Velarde, A Espinosa-Magaña, R Martínez-Calderón, R

443 Candia-Zulbarán, R Muñoz de Cote-Hernández, L Cid-González, N Luviano-Aparicio, and CE

444 Davies. E Escalante-Mancera helped with the use of software. Comments by Darren Brown

445 improved an earlier draft of the manuscript.

446

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651

652 **FIGURE LEGENDS**

653 Figure 1. Study area.
654 (A) Location of the studied reef units, Limones (well-preserved) and Bonanza (degraded), at
655 Puerto Morelos, México, and photographs showing the current state of (B) Limones and (C)
656 Bonanza. (Photo credits B: Lorenzo Álvarez-Filip; C: Fernando Negrete-Soto).

658 Figure 2. Metrics of reef structural complexity.
659 Box plots of (A) rugosity index and (B) habitat assessment score (HAS) on Limones (green
660 boxes) and Bonanza reefs (blue boxes). The lower and higher boundaries of the box indicate the
661 25th and 75th percentiles, respectively. The horizontal line within the box marks the median.
662 Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Black dots
663 denote outliers.

665 Figure 3. Percent cover of benthic community components.
666 Percent cover of different benthic community components over Limones reef (green columns)
667 and Bonanza reef (blue columns). Error bars are 95% confidence intervals. Asterisks at the end
668 of a component name denote significant differences between reefs ($\alpha = 0.05$).

670 Figure 4. Principal Components Analysis (PCA) of percent cover of benthic components.
671 Bi-plot on logit-transformation of percent cover of benthic components over the two studied
672 reefs, Limones (green dots) and Bonanza (blue dots). Each dot represents a transect. LHC: live
673 hard coral, TA: turf algae, FMA: fleshy macroalgae, CMA: calcareous macroalgae; CCA:
674 coralline algae, CYAN: cyanobacterial mats, OINV: other sessile invertebrates, Other: other
675 components (sand, seagrass).

677 Figure 5. Species accumulation and rarefaction curves.
678 Accumulation curves (continuous lines) and rarefaction curves (dashed lines) for
679 macrocrustacean species recorded in Limones (green lines) and Bonanza (blue lines) reefs.
680 Thirty belt transects, 50 m² each, were sampled on each reef. Rarefaction curves for either reef
681 do not reach an asymptote, indicating the existence of more species.

683 Figure 6. nMDS ordination.
684 Non-metric multidimensional (nMDS) ordination of macrocrustacean community structure in
685 samples from Limones reef (green triangles and dashed lines) and Bonanza reef (blue circles and
686 continuous lines), based on species abundances. Each symbol denotes a transect.

688 Figure 7. Density of macrocrustaceans per reef.
689 Mean density (number of individuals 50 m^{-2}) of the most abundant macrocrustaceans per reef:
690 Limones (green columns) and Bonanza (blue columns). Error bars are 95% confidence intervals.

692 Figure 8. Types of microhabitats used by macrocrustaceans.
693 Comparison of the types of microhabitats used by macrocrustaceans on each reef, Limones
694 (green columns) and Bonanza (blue columns).
695

Figure 1

Study area.

(A) Location of the studied reef units, Limones (well-preserved) and Bonanza (degraded), at Puerto Morelos, México, and photographs showing the current state of (B) Limones and (C) Bonanza (Photo credits B: Lorenzo Álvarez-Filip; C: Fernando Negrete-Soto).
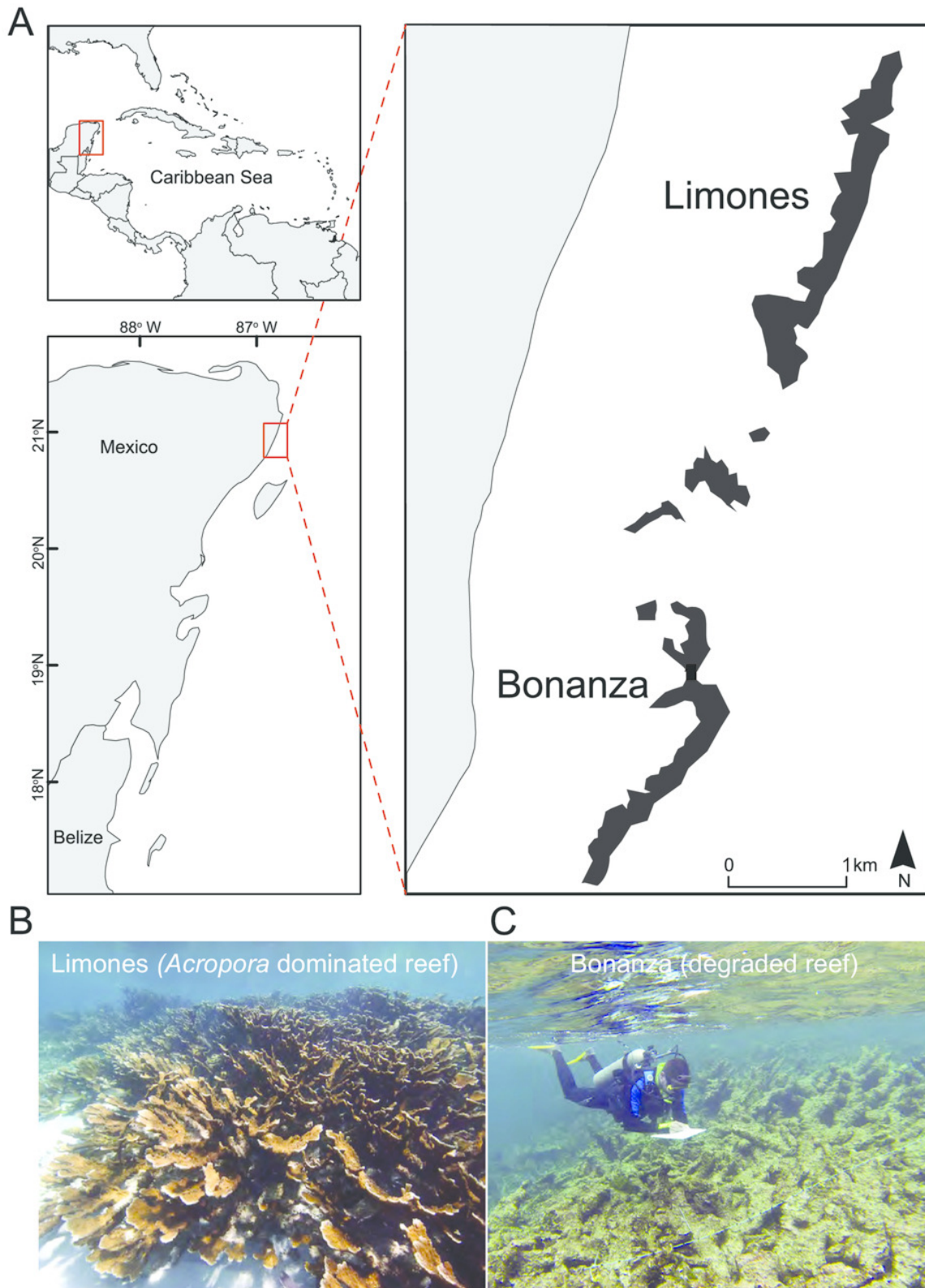
A

B Limones (*Acropora* dominated reef)

C Bonanza (degraded reef)

Figure 2

Metrics of reef structural complexity.

Box plots of (A) rugosity index and (B) habitat assessment score (HAS) on Limones (green boxes) and Bonanza reefs (blue boxes). The lower and higher boundaries of the box indicate the 25th and 75th percentiles, respectively. The horizontal line within the box marks the median. Whiskers (error bars) above and below the box indicate the 90th and 10th percentiles. Black dots denote outliers.
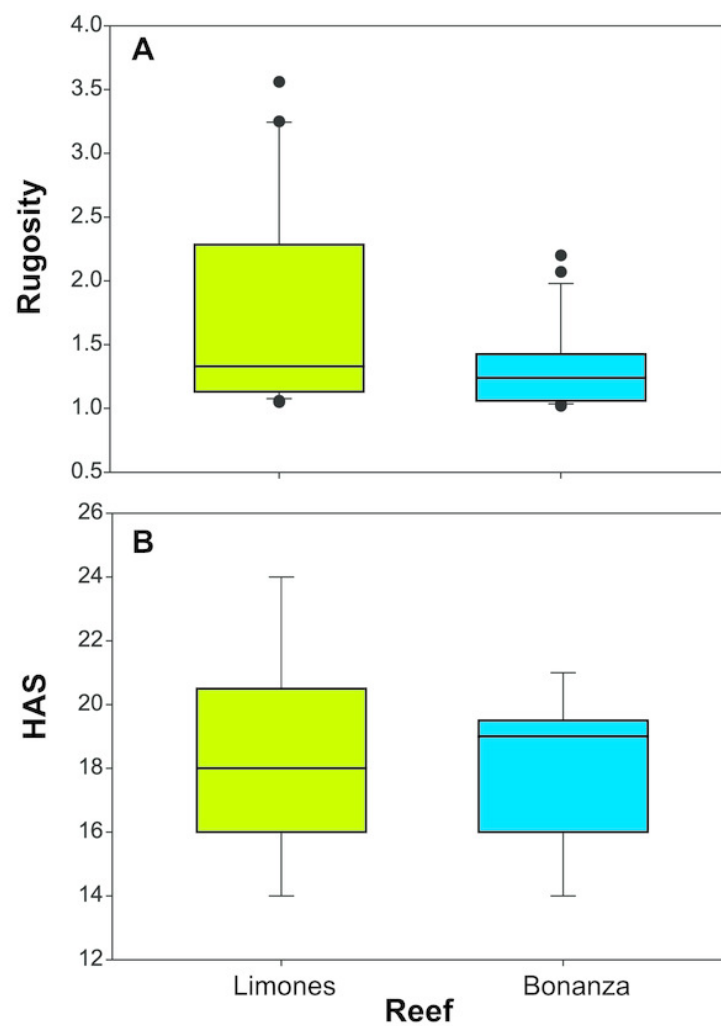
Figure 3

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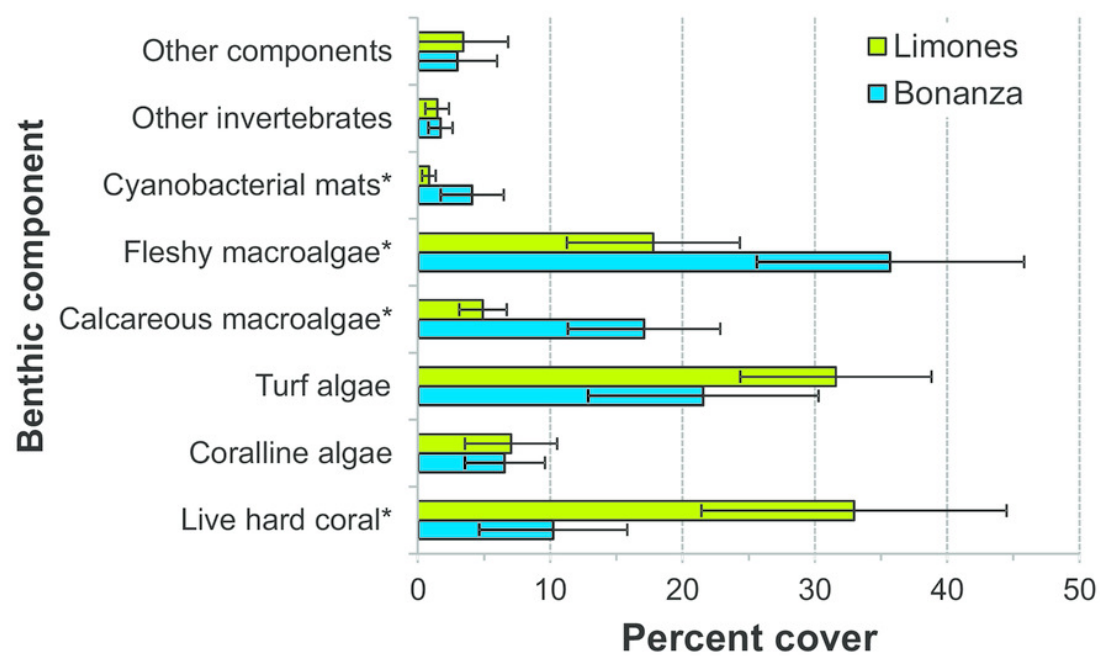
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Principal Components Analysis (PCA) of percent cover of benthic components.

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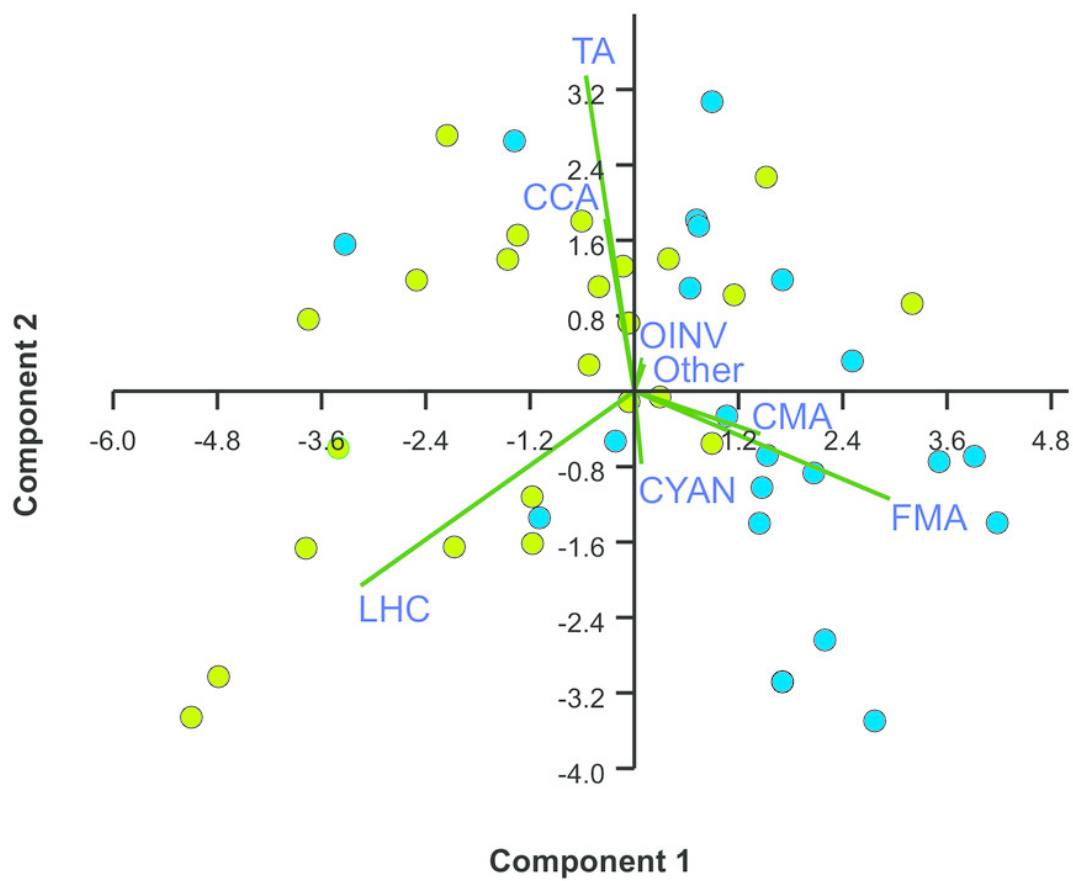
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Accumulation curves (continuous lines) and rarefaction curves (dashed lines) for macrocrustacean species recorded in Limones (green lines) and Bonanza (blue lines) reefs. Thirty belt transects, 50 m² each, were sampled on each reef. Rarefaction curves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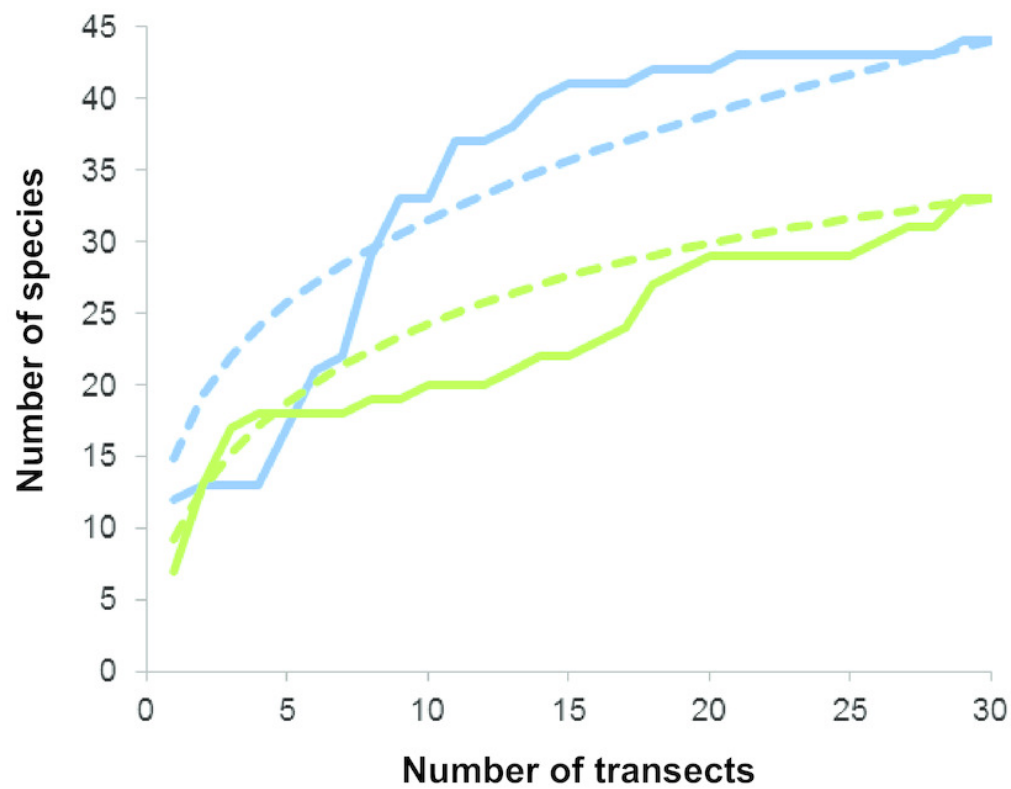
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nMDS ordination.

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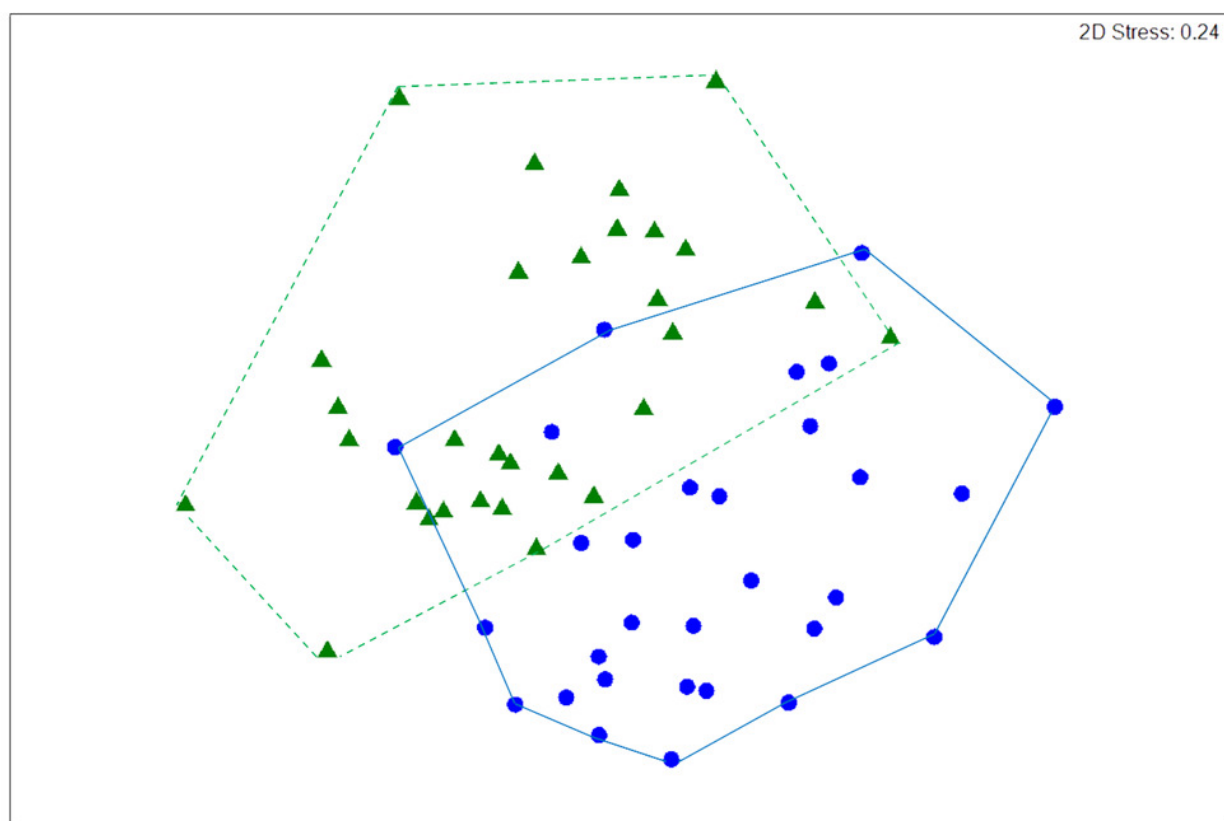

2D Stress: 0.24

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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 95% confidence intervals.
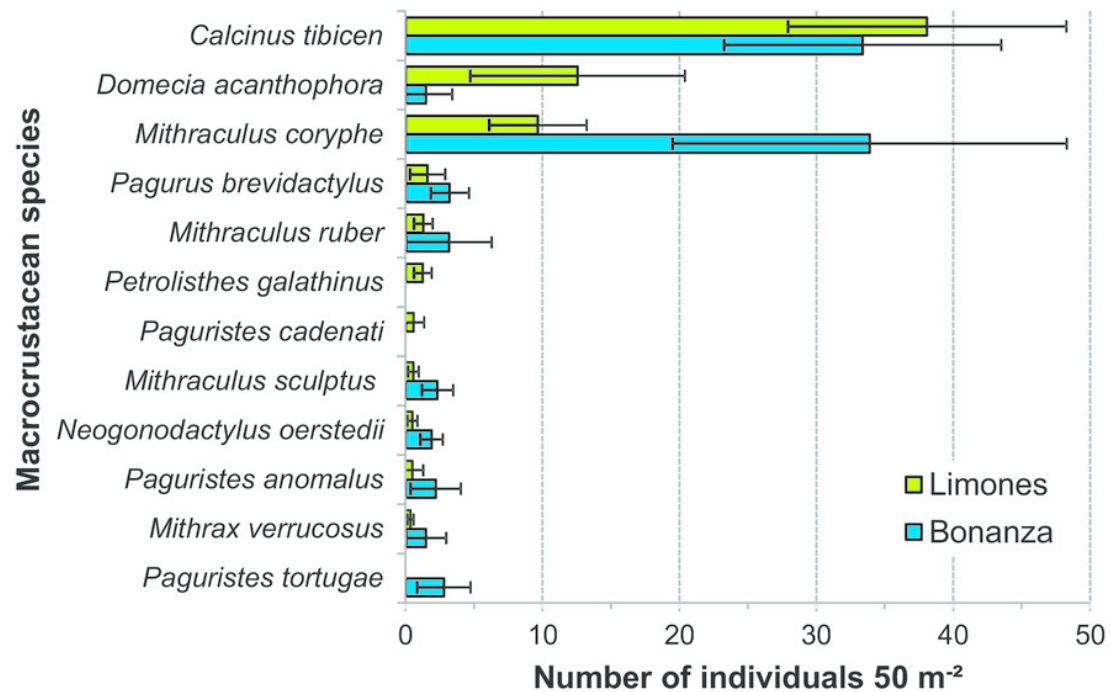
Figure 8

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).
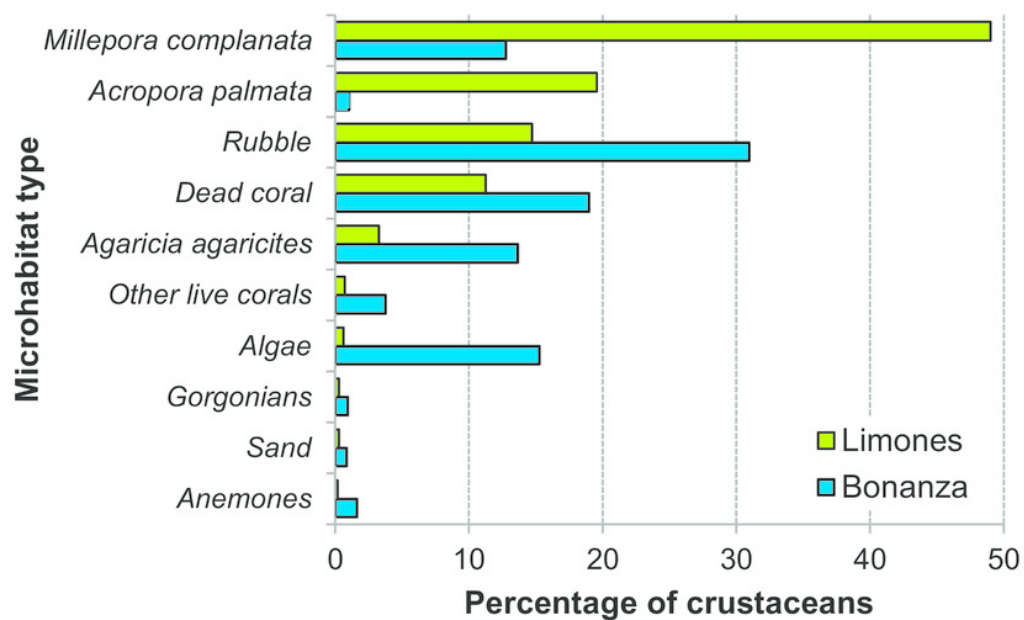
Table 1(on next page)

Macrocrustacean species by reef.

Number of macrocrustacean species and individuals registered by visual census (n = 30 transects). Bonanza reef: 43 species; 2800 individuals; Limones reef: 33 species; 2067 individuals. An X denotes that a species was only qualitatively recorded during nocturnal dives.

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	Species	Bonanza	Limones
1	*Mithraculus coryphe* (Herbst, 1801)	1017	290
2	*Calcinus tibicen* (Herbst, 1791)	1002	1143
3	*Pagurus brevidactylus* (Stimpson, 1859)	97	48
4	*Teleophrys ruber* (Stimpson, 1871)	95	40
5	*Paguristes tortugae* Schmitt, 1833	84	0
6	*Mithraculus sculptus* (Lamarck, 1818)	70	17
7	*Paguristes anomalus* Bouvier, 1918	66	15
8	*Neogonodactylus oerstedii* (Hansen, 1895)	57	15
9	*Domecia acanthophora* (Desbonne in Desbonne & Schramm, 1867)	45	377
10	*Mithrax aculeatus* (Herbst, 1790)	45	11
11	*Omalacantha bicornuta* (Latreille, 1825)	43	1
12	*Alpheus armatus* Rathbun, 1901	19	4
13	*Paguristes puncticeps* Benedict, 1901	19	4
14	Callianassid A	19	1
15	*Thor amboinensis* (de Man, 1888)	19	0
16	*Panulirus argus* (Latreille, 1804)	18	4
17	*Macrocoeloma subparellelum* (Stimpson, 1860)	14	0
18	*Axiopsis serratifrons* (A. Milne-Edwards, 1873)	12	4
19	*Percnon gibbesi* (H. Milne-Edwards, 1853)	8	7
20	*Nonala holderi* (Stimpson, 1871)	7	0
21	*Petrolisthes galathinus* (Bosc, 1802)	5	38
22	*Macrocoeloma diplacanthum* (Stimpson, 1860)	5	0
23	Xanthid E	4	0
24	*Mithraculus cinctimanus* Stimspon, 1860	3	3
25	*Stenopus hispidus* (Olivier, 1811)	3	0
26	*Actaea acantha* (H. Milne-Edwards, 1834)	2	0
27	*Ancylomenes pedersoni* (Chace, 1958)	2	0
28	*Ratha longimanus* (H. Milne-Edwards, 1834)	2	0
29	*Macrocoeloma trispinosum* (Latreille, 1825)	2	0
30	*Mithraculus forceps* A. Milne-Edwards, 1875	2	0
31	*Panulirus guttatus* (Latreille, 1804)	1	3
32	*Lysmata wurdemanni* (Gibbes, 1850)	1	1
33	Anomuran A	1	0
34	*Brachycarpus biunguiculatus* (Lucas, 1846)	1	0
35	Majoid B	1	0
36	Majoid C	1	0
37	Majoid D	1	0
38	*Neogonodactylus torus* (Manning, 1869)	1	0

39	*Pitho lherminieri* (Desbonne in Desbonne & Schramm, 1867)	1	0
40	*Pitho mirabilis* (Herbst, 1794)	1	0
41	*Podochela macrodera* Stimpson, 1860	1	0
42	*Stenorhynchus seticornis* (Herbst, 1788)	1	0
43	Xanthid C	1	0
44	Xanthid D	1	0
45	*Paguristes cadenati* Forest, 1954	0	18
46	*Phimochirus holthuisi* (Provenzano, 1961)	0	5
47	Caridean A	0	3
48	*Pachycheles pilosus* (H. Milne Edwards, 1837)	0	3
49	*Cinetorhynchus manningi* (Okuno, 1996)	0	2
50	Majoid A	0	2
51	*Nemausa acuticornis* (Stimpson, 1871)	0	2
52	*Damithrax hispidus* (Herbst, 1790)	0	1
53	*Maguimithrax spinosissimus* (Lamarck, 1818)	0	1
54	*Achelous sebae* (H. Milne Edwards, 1834)	0	1
55	*Synalpheus* sp.	0	1
56	Xanthid A	0	1
57	Xanthid B	0	1
58	*Cinetorhynchus rigens* (Gordon, 1936)	X	X
59	*Metapenaeopsis goodei* (Smith, 1885)	X	X
60	*Palinurellus gundlachi* von Martens, 1878		X
61	*Parribacus antarcticus* (Lund, 1793)	X	
62	*Scyllarides aequinoctialis* (Lund, 1793)	X	X
63	*Carpilius corallinus* (Herbst, 1783)	X	

2
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Table 2(on next page)

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.

1

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

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Table 3(on next page)

Similarity measures within and between reefs.

Analysis of similarity percentage (SIMPER) for macrocrustacean assemblages within Limones and Bonanza, and of dissimilarity percentage between reefs.

1

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.

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