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1 **Assessing population changes of historically overexploited black corals**
2 **(Order: Antipatharia) in Cozumel, Mexico**

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16 **Abstract**

17 Black corals (Antipatharians) play a crucial structural and ecological role on
18 many mesophotic coral ecosystems (MCEs; reefs 30-150 m depth). In Mexico,
19 black corals are harvested for the jewellery industry, which has historically led
20 to populations depletion. Harvesting began in the early 1960s, and was
21 concentrated around Cozumel Island until 1995. Here we compare populations
22 between 1998 and 2016 for the two black coral species targeted by the jewellery
23 industry. We found that densities of *Plumapathes pennacea* in 2016 are
24 substantially lower than in 1998. However, the 2016 *P. pennacea* population has
25 shifted to be dominated by larger colonies, suggesting disproportionate juvenile
26 mortality or recruitment failure. No change in population density or colony size
27 of *Antipathes caribbeana* was detected between 1998 and 2016. We advocate for
28 the adequate protection of black corals in Mexico, and for the government to
29 ensure sustainability of the harvesting before issuing future permits.

30 Introduction

31 Mesophotic coral ecosystems (MCEs; reefs 30-150 m depth) have gained
32 more attention in the recent years. Still, they remain under-studied because of
33 technical, logistical and financial challenges associated with accessing them
34 (Hinderstein et al. 2010; Loya et al. 2016). While MCEs contain light-dependent
35 scleractinian corals, in many cases these are not the dominant benthic taxa, with
36 substantial structural complexity provided by other ecosystem engineers such as
37 calcareous macroalgae, octocorals, sponges, and black corals (Antipatharians)
38 (Kahng et al. 2010, 2014). Despite receiving some protection from threats affecting
39 shallow reefs because of their depth (Bridge et al. 2012), MCEs are known to face
40 threats in their own right (Andradi-Brown et al. 2016). These threats include
41 overexploitation of economically important organisms such as fishes (Wood et al.
42 2006; Reed et al. 2007) and precious corals (including black corals) (Wells 1981;
43 Wagner et al. 2012; Bruckner 2016).

44 Black corals are long-lived, slow growing ahermatypic corals that depend on
45 zooplankton as their major food source (Tsounis et al. 2010; Wagner 2012). About
46 150 black coral species (Phylum Cnidaria, Class: Anthozoa, Order: Antipatharia) have
47 been described (Tsounis et al. 2010). Black corals occur in all oceans from shallow to
48 abyssal depths, but are thought to be more common in tropical and subtropical
49 regions at >50 m depths (Tsounis et al. 2010). On some MCEs, black corals are crucial
50 habitat-forming species because of their complex structure and their ability to form
51 dense beds which fish and other invertebrate species associate with (Boland 2005;
52 Wagner 2012; Brucker 2016). In Hawaii, for example, Pomacanthidae and
53 Pomacentridae fishes can be resident within individual black coral colonies, and
54 many other fishes use black coral branches for shelter (Boland and Parrish 2005).
55 Black corals have slow growth rates, with annual linear growth estimates of up to 6.4
56 cm per year in Hawaii (Grigg 1976), and 5.1 cm per year in Jamaica (Oakley 1988).
57 Overexploitation of black corals for use in the jewellery industry has led to
58 harvesting regulations in many locations (Grigg 2001; Boland 2005; Bruckner 2016).
59 All black corals were included in the Convention on International Trade of in
60 Endangered in Endangered Species of Wild Flora and Fauna (CITES) Appendix II in
61 1981 (CITES 2017).

62 In the Mexican Caribbean, harvesting of black corals began in the early 1960s
63 (Kenyon 1984), and has depleted black coral populations over wide geographical
64 areas (Padilla and Lara 2003; Padilla Souza 2004). In 1994 three black coral species
65 were added to the Mexican national threatened species list (Padilla and Lara 2003):
66 *Antipathes bichitoena*, *A. grandis* and *A. ules*. While species authorities were not
67 included in the listing and taxonomy has changed, it is believed *Antipathes*
68 *bichitoena* refers to *A. dichotoma* (Pallas, 1766), *A. grandis* as in Verrill (1928), and *A.*
69 *ules* refers to *Myriopathes ulex* (Ellis & Solander, 1786) (Padilla Souza 2004). Prior to
70 the listing, no in-water studies of black corals had been conducted in Mexico. These
71 three species were added in the list by international recommendation, because of
72 concern that harvesting could lead to black coral depletion, which had been
73 recorded in other areas (Wells 1981; Wagner 2012; Bruckner 2016). However, the
74 inclusion of these species was a mistake, as they have not been recorded from the
75 Mexican Caribbean or Mexican Pacific coasts, and based on their known
76 distributions are unlikely to be found in Mexican waters (WoRMS 2004; 2008a;
77 2008b). Following surveys in 1998-1999, eight black coral species were recorded in
78 the Mexican Caribbean, with the two main harvested species identified as:
79 *Antipathes caribbeana* (Opresko 1996) and *Plumapathes pennacea* (Pallas 1766)
80 (Padilla 2001; Padilla and Lara 2003). Despite realisation of the mistake on the
81 Mexican protected species list, the original 1994 listing has not been updated,
82 resulting in no national level protection for any recorded Mexican black coral
83 species.

84 Cozumel, a small island off the north-eastern Yucatan peninsula, Mexico, is
85 the major production and sales centre for the Mexican black coral jewellery and
86 handcraft industry (Kenyon 1987; Padilla 2001). Historically, reefs around Cozumel
87 were famed for extensive, densely populated MCE black coral beds, though these
88 have long-since disappeared (La Torre Alegria 1979; Kenyon 1984; Humann and
89 Deloach 2001). Harvest rates from Cozumel in the mid-1970s were between 70-121
90 kg gross black coral product per year (La Torre Alegria 1979). By the late 1980s and
91 early 1990s rates had risen to between 1000-1500 kg per year, which likely caused
92 the loss of black coral beds in the area (Padilla and Lara 2003). Official permits for
93 commercial harvesting of black corals were first issued for Cozumel in the early

94 1980s. Mexican authorities suspended permission for black coral extraction in
95 Cozumel in 1995 citing collector safety, as commercial sized colonies had reportedly
96 been depleted to >75 m depth (La Torre Alegria 1979; Padilla Souza 2004). This
97 resulted in collectors adopting increasingly deeper high-risk bounce diving, whereas
98 in the past collectors could harvest colonies from as shallow as 20 m (Padilla Souza
99 2004).

100 Despite declining Cozumel black coral populations, no assessments were
101 conducted until 1998 when extensive baseline surveys were carried out. These
102 surveys recorded black coral densities and colony height, width and stem diameter
103 at 15 sites on the west coast of Cozumel (Padilla 2001; Padilla and Lara 2003; Padilla
104 Souza 2004). With no available historic data, Padilla and Lara (2003) compared the
105 Cozumel black coral densities and sizes to remote offshore Mexican reefs. They
106 found low black coral densities around Cozumel, suggesting that harvesting has
107 caused a ‘serious deterioration’ of Cozumel black coral populations. While the
108 Mexican government continues to issue permits for black coral harvesting on the
109 Mexican Caribbean coast, since the 1995 no new permits have been issued for
110 Cozumel. However, because of the rapid overexploitation black coral beds on
111 mainland, harvesters have expressed interest on obtaining permits to harvest in
112 Cozumel again (E. Gress, pers. comm.).

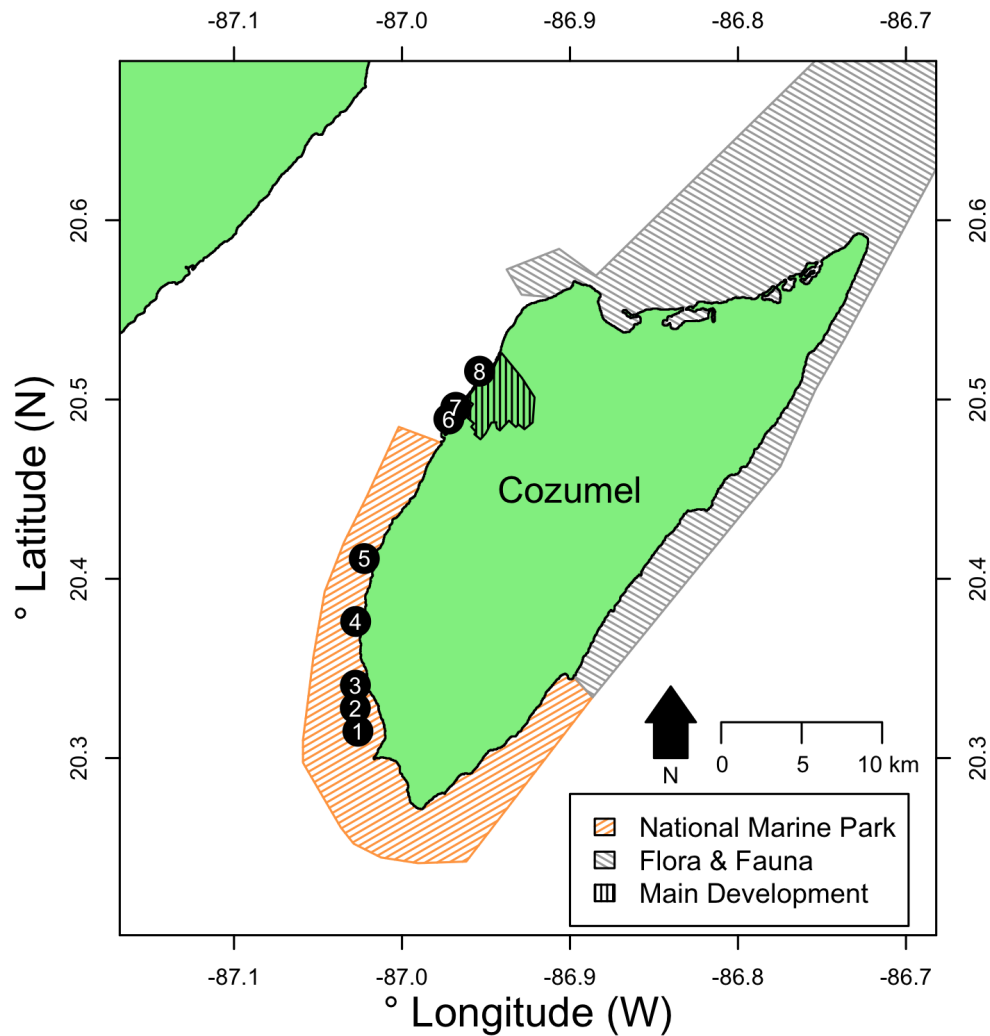
113 Here we report a new black coral population assessment conducted around
114 Cozumel during 2016. We compare changes in the population densities and size
115 distribution of the two historically harvested species of black coral, *A. caribbeana*
116 and *P. pennacea*, on MCEs between 1998 and 2016 to evaluate current population
117 trajectories and inform on-going harvesting management.

118 **Methods**

119 **Black Coral Surveys**

120 Surveys were conducted at eight sites on the west coast of Cozumel, Mexico
121 during August-September 2016. Five sites were within the Cozumel National Marine
122 Park, and three were in an area with no protection adjacent to the main town. MPA
123 sites were Santa Rosa, Colombia, Punta Tunich, Palancar Jardines and Herradura,

124 and non-MPA sites were Transito Transbordador, Purgatorio and Villa Blanca (Figure
125 1).



126
127 Figure 1. Location of survey sites relative to Cozumel and the National Marine Park
128 and Flora & Fauna protected areas on Cozumel. Sites (and their GPS locations in
129 WGS84 format included in parenthesis) were: 1 – Colombia (20.31497 N, 87.02625
130 W), 2 – Herradura (20.3299 N, 87.0278 W), 3 – Palancar Jardines (20.33565 N,
131 87.02773 W), 4 – Santa Rosa (20.37618 N, 87.02757 W), 5 – Punta Tunich (20.41128
132 N, 87.02245 W), 6 – Villa Blanca (20.48913 N, 86.9721 W), 7 – Transito
133 Transbordador (20.49565 N, 86.96798 W) and 8 – Purgatorio (20.51578 N, 86.95383
134 W).
135

136 Black coral surveys were conducted using a diver-operated stereo-video
137 system (stereo-DOV), consisting of two cameras separated by 0.8 m and with
138 approximately 3 ° convergence angle filming forward along the reef. A stereo-DOV
139 system records two synchronised images of the reef, allowing accurate length
140 measurements of reef benthic organisms (Turner et al. 2015; Bennett et al. 2016).
141 The stereo-DOV used two GoPro Hero 4 Black cameras and a spool system with
142 biodegradable (100% cotton) line for measuring out each transect (see Gress et al. in
143 review for details). Transects were 30 m in length and each separated by 10 m
144 intervals. On each site, four transects were conducted at 55 m depth, giving 32
145 transects in total across all eight sites. Transects were filmed during daylight hours
146 using natural ambient light. When filming transects, the stereo-DOV operator swam
147 with the cameras recording forward along the reef at the 55 m depth contour while
148 carefully looking for colonies. Upon encountering a black coral, the operator slowed
149 and angled the cameras to ensure the coral was captured clearly on both cameras.
150 Permits for surveys were issued by the Comisión Nacional de Áreas Naturales
151 Protegidas (CONANP) Cozumel, Permit Number: FOO.9.DPNAC/305-16.

152 We also obtained the raw Cozumel data from Padilla Souza (2004), which
153 contains densities and colony sizes for *A. caribbeana* and *P. pennacea* from 15 sites
154 from the west coast of Cozumel from 1998. These 1998 surveys were conducted by
155 open-circuit divers at each site and spanned from 18–80 m depth. The area surveyed
156 was estimated, and the height, width and depth of each black coral colony
157 encountered was recorded (Padilla Souza 2004).

158 Analysis

159 Stereo-DOV footage was analysed using EventMeasure (v4.42, SeaGIS,
160 Melbourne, Australia). All *A. caribbeana* and *P. pennacea* colonies within a 4 m
161 transect width (constrained using EventMeasure) were identified, giving a total
162 density for each species per 120 m² transect. The maximum height and maximum
163 width of each colony was measured using EventMeasument built in length
164 measurement tools.

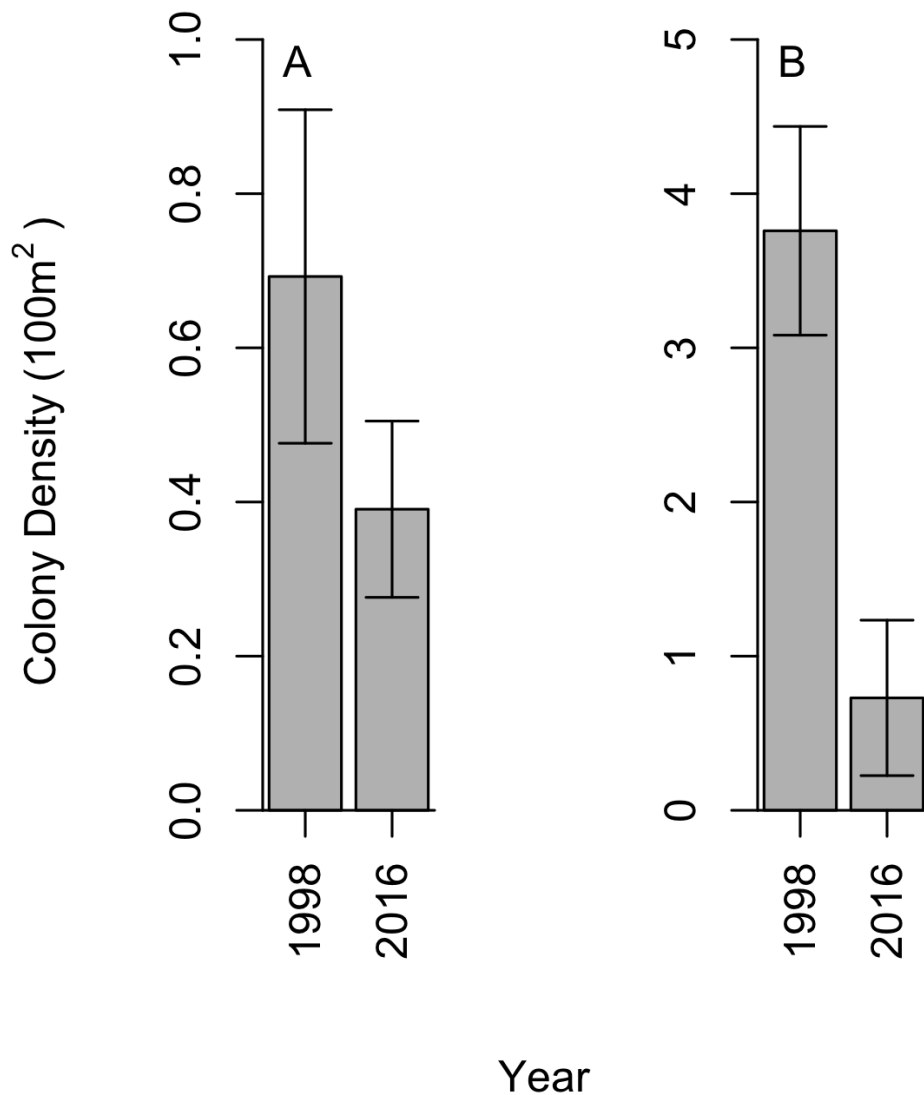
165 As the black coral density data did not meet assumptions for parametric
166 statistics, differences in *A. caribbeana* and *P. pennacea* density between 1998 and

167 2016 was assessed using Mann-Whitney U tests. Changes in colony size (maximum
168 height and maximum width) were tested using kernel density estimates (KDEs) and
169 permutation tests, following Langlois et al. (2010). This method allows differences
170 between two length distributions to be tested, while also providing an indication of
171 which regions of the distributions are different if significant differences are detected.
172 KDEs are fitted separately to the two groups with the Sheather-Jones selection
173 procedure (Sheather and Jones 1991) using the 'KernSmooth' package (Wand 2013),
174 and plotted. A permutation test then randomly allocated the data into two groups,
175 and the mean and standard error of these randomly allocated distributions can be
176 plotted. The permutation test was run for 9999 permutations, and used the function
177 'sm.density.compare' in the package 'sm' (Bowman and Azzalini 2014), in R (R Core
178 Team 2013). As 2016 data was limited to transects at 55 m depth, while the 1998
179 data incorporated colonies surveyed from 18-80 m depth, we tested for changes in
180 colony size with depth within the 1998 data using linear models. Linear model
181 residual plots were inspected to ensure model assumptions were not violated.
182 Permutation tests comparing changes in colony size between years were run
183 comparing 2016 surveys with all 1998 data, and just colonies recorded between 50-
184 60 m depth in 1998.

185 Results

186 Changes in black coral density

187 In 2016, a total of 28 *P. pennacea* and 15 *A. caribbeana* colonies across all 32
188 transects were recorded. *P. pennacea* was more abundant than *A. caribbeana* in
189 2016, with mean densities of 0.73 ± 0.50 and 0.39 ± 0.11 per 100 m² respectively
190 (mean \pm SE; Figure 2). Mean black coral colony density was lower for both *A.*
191 *caribbeana* and *P. pennacea* in 2016 than 1998 (Figure 2). However, while this
192 represented a significant decline for *P. pennacea* (Mann-Whitney U=107, $p=0.003$), it
193 was not significant for *A. caribbeana* (Mann-Whitney U=69, $p=0.582$).



194
 195 Figure 2. Change in black coral density between 1998 and 2016 for (A) *A. caribbeana*,
 196 and (B) *P. pennacea*. Error bars show 1 standard error above and below the mean.

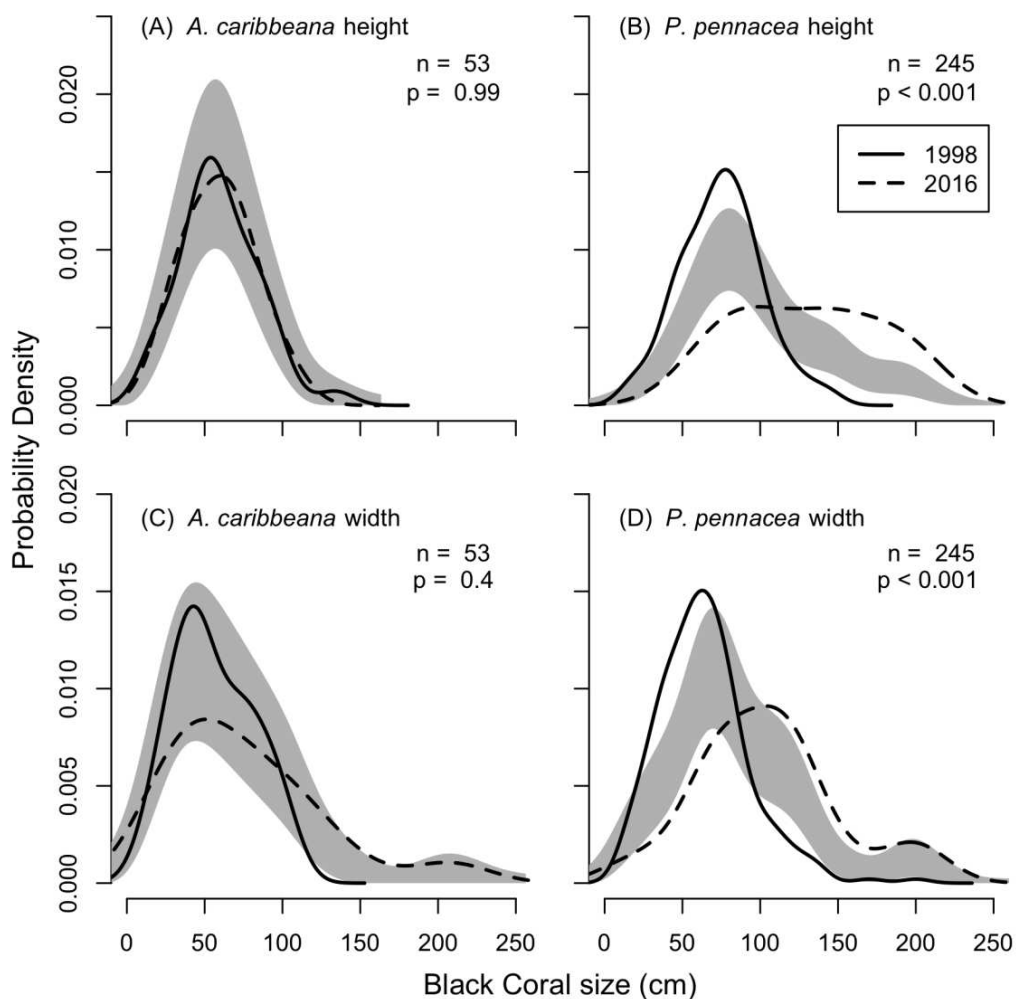
197

198 We also compared 2016 black coral density between our five sites inside the
 199 Cozumel MPA and the three sites outside. *A. caribbeana* density was greater inside
 200 the MPA than outside (Mann-Whitney $U=14.5$, $p=0.044$), with 0.58 ± 0.10 colonies
 201 per 100 m² inside the MPA compared to 0.07 ± 0.07 colonies per 100 m² outside the

202 MPA. There was no difference in *P. pennacea* density between sites inside the MPA
 203 and those outside (Mann-Whitney $U=9$, $p=0.73$).

204 Changes in black coral colony size

205 KDEs indicated that there was no change in *A. caribbeana* size between the
 206 two surveys, while *P. pennacea* colonies were larger in 2016 than 1998 (Figure 3). *A.*
 207 *caribbeana* colony height was surprisingly consistent between years, with median
 208 colony heights of 59 cm in both 1998 and 2016 (Figure 3A). *A. caribbeana* median
 209 colony width had a larger magnitude of difference, 50 cm in 1998 versus 66 cm in
 210 2016, although this was not significant (Figure 3C). In contrast, *P. pennacea* colonies
 211 were both taller (median: 75 cm in 1998, 134 cm in 2016; Figure 3B) and wider
 212 (median: 61 cm in 1998, 105 cm in 2016; Figure 3D) in 2016.



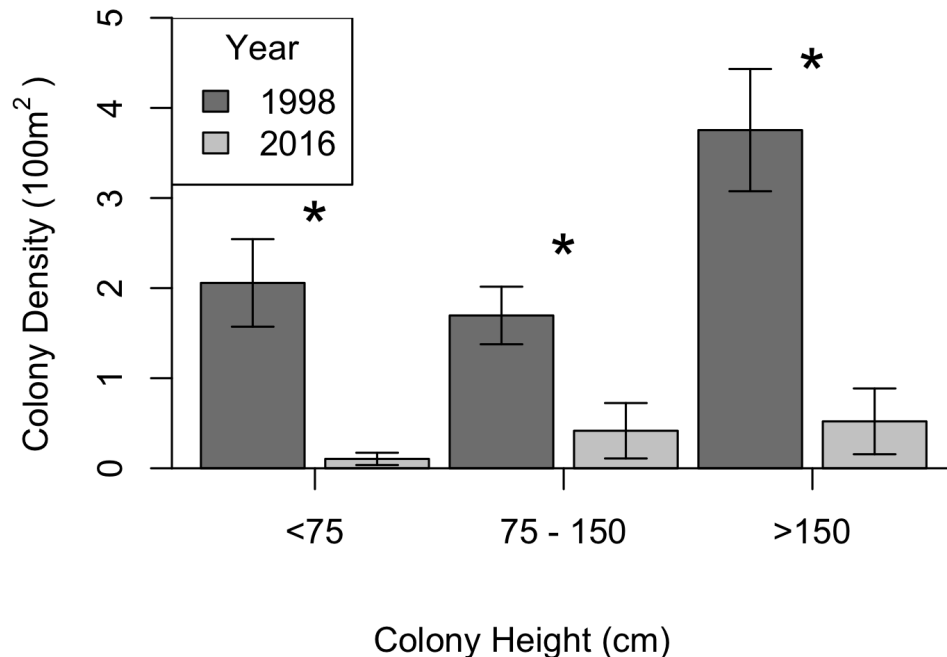
213

214 Figure 3. Change in black coral colony size between 1998 and 2016, for (A) *A.*

215 *caribbeana* colony height, (B) *P. pennacea* colony height, (C) *A. caribbeana* colony
216 width, and (D) *P. pennacea* colony width. Kernel density estimates were used,
217 followed by a permutation test to identify differences between years. The grey
218 shaded area indicates one standard error either side of the null model of no
219 difference in colony size distribution based on year. Locations where the lines
220 representing 1998 and 2016 are outside the grey zone indicate significant
221 differences in the proportion of colonies of that size. n =number of colonies.
222

223 As surveys in 2016 were conducted at 55 m, whereas surveys conducted in
224 1998 spanned 18-80 m depth we tested for effects of depth on colony size in the
225 1998 data. No depth changes in colony height ($F_{1,36}=1.7$, $p=0.199$) or width
226 ($F_{1,36}=3.1$, $p=0.089$) were detected for *A. caribbeana*. However, *P. pennacea* colonies
227 were both taller ($F_{1,215}=14.8$, $p<0.001$) and wider ($F_{1,215}=8.4$, $p=0.004$) at shallower
228 depths (Figure S1). Though there was high variability in colony size across this depth
229 gradient, with low R^2 values of 0.06 and 0.03 for height and width respectively
230 (Figure S1). To ensure differences identified in colony size between 1998 and 2016
231 were not caused by comparisons of colonies from different depths, we reran the size
232 comparison analysis using only colonies recorded from 50-60 m depth in 1998
233 (Figure S2). This restricted 50-60 m depth range analysis produced results highly
234 consistent to those using the full 1998 dataset (Figure S2; Figure 3).

235 To check if the change in *P. pennacea* colony size was caused by losing small
236 individuals from the population, or density declines affected all sizes; we separated
237 density data by height class. Colonies of all three-height classes (<75 cm, 75-150 cm,
238 >150 cm) declined in density between 1998 and 2016 (Figure 4).



239

240 Figure 4. Change in black coral density between 1998 and 2016 for *P. pennacea*
 241 grouped by colony height. Stars indicate significant differences at $p < 0.05$ using
 242 Mann-Whitney U tests. Error bars show 1 standard error above and below the mean.

243 Discussion

244 Results show that *P. pennacea* population densities have declined between
 245 1998 and 2016 on MCEs around Cozumel. Colonies of *P. pennacea* identified in 2016
 246 were larger than those recorded in 1998, but colonies of all sizes have declined in
 247 density. No significant changes in density or size were recorded for *A. caribbeana*
 248 through time; although *A. caribbeana* densities were much lower than *P. pennacea*.
 249 Unexpectedly, given the easier accessibility of shallower colonies, *P. pennacea*
 250 colonies were reported to decreased in size with increased depth in 1998.

251 Differences in black coral density

252 As black coral commercial harvesting has not been allowed anywhere in
 253 Cozumel since 1995, we did not anticipate any effects of the Cozumel MPA on
 254 density. Therefore, we expected the 2016 surveys to identify stable or increasing
 255 black coral populations. Results show no effect of the MPA on *P. pennacea* density,
 256 and declines across all height classes were observed between 1998 and 2016. Only

257 the total area of reef surveyed at each site was recorded in 1998, with no record of
258 the area surveyed at each depth. The 1998 surveys were conducted by open-circuit
259 technical divers, with divers quickly descending to 80 m and then slowly ascending
260 up the reef wall to 18 m recording all colonies they encountered and trying to keep
261 survey effort roughly equal across the depth gradient (Padilla Souza 2000, 2004). As
262 the 1998 surveys recorded the depth of each individual colony identified, we plotted
263 the number of colonies recorded at each depth for both species, finding the greatest
264 frequency of *P. pennacea* colonies between 50-60 m (Figure S3). Surveys from 2016
265 were conducted at 55 m depth which could raise the concern that differences in
266 density between years could be driven by natural variation in black coral colony
267 density with depth. Although this cannot be ruled out definitively, as the highest
268 frequency of *P. pennacea* was found in the 50-60 m depth band in 1998, we believe
269 it is highly unlikely. In addition, Padilla and Lara (2003) states that the greatest black
270 coral abundance for all species was observed at approximately 60 m. Therefore, as
271 there was roughly equal sampling effort across the depth gradient, and the greatest
272 *P. pennacea* frequency was at 50-60 m, it is likely that the overall site densities from
273 1998 are underestimates of *P. pennacea* density at 50-60 m. If 1998 density data was
274 available broken down by depth, we would expect more severe declines in *P.*
275 *pennacea* density than the ones detected.

276 Interpreting the possible influence of changing colony densities with depth
277 on *A. caribbeana* is harder. In contrast to *P. pennacea*, the greatest 1998 colony
278 frequency was recorded at 60-70 m (Figure S3). However, the 50-60 m depth range
279 contained the second greatest frequency, and few colonies were encountered >70 m
280 or <40 m (Figure S3). In a similar way to *P. pennacea*, this also suggests that 1998 *A.*
281 *caribbeana* density in the 50-60 m range may have been higher than the overall site
282 estimates. If this were the case it may be possible that *A. caribbeana* densities have
283 declined as well through time. However, this interpretation requires caution, as we
284 only found 15 *A. caribbeana* colonies in 2016. Low densities of *A. caribbeana* around
285 Cozumel were previously identified in the 1998 population assessment (Padilla Souza
286 2004). This low density reduces statistical power, and makes comparisons less
287 reliable, especially because of the lack of colony density broken down by depth in
288 1998. Low *A. caribbeana* density appears to be widespread across the Mexican

289 Caribbean (Padilla and Lara 2003). Similarly, a preliminary study in Honduras
290 recorded *P. pennacea* but found no colonies of *A. caribbeana* (Guzman 1998). We
291 detected no significant difference in *A. caribbeana* density between years. It is
292 unclear whether results would be different if 1998 density data were available for
293 only the 50-60 m depth range.

294 Understanding the potential causes of *P. pennacea* loss in Cozumel requires
295 further work. Despite no harvesting permits issued for Cozumel since 1995, the black
296 coral jewellery market has not moved, and Cozumel is still the major production and
297 sales centre as of 2017. Moreover, illegal harvesting of black corals continues to be a
298 problem around Cozumel. Recent images and videos posted on social media show
299 divers collecting black corals from locations identifiable as Cozumel (E. Gress, pers.
300 comm.). Whilst there is no data available on how frequently this occurs, we believe
301 that continued illegal harvesting might contribute to the declines in *P. pennacea*
302 density we report.

303 **Differences in size**

304 Our size distribution analysis suggests that colonies of *P. pennacea* were both
305 taller and wider on average in 2016 than in 1998, but no changes were detected for
306 *A. caribbeana* (Figure 3). At first glance this may suggest some *P. pennacea* colonies
307 are recovering from the historical harvesting pressure and maturing. However, *P.*
308 *pennacea* density declined across all height classes (Figure 4). This shift to larger
309 colonies suggests juvenile colonies have been disproportionately affected by the
310 harvesting activities. Padilla Souza (2000) reported high abundance of juvenile black
311 corals and colonies regenerating from standing bases of previously harvested
312 colonies in Cozumel. Disentangling possible causes for a disproportionate loss of
313 smaller colonies in the population between 1998 and 2016 is complex, but implies
314 reduced black coral recruitment or juvenile survival. There have been few long-term
315 studies of black coral populations conducted, and the processes affecting black coral
316 recruitment and juvenile survival are poorly understood (Wagner et al. 2012). In
317 Hawaii, black coral recruitment has declined (Grigg 2004), most likely caused by
318 overharvesting mature colonies (Grigg 2004; Tsounis et al. 2010), though
319 competition with an invasive species might also be involved (Grigg 2004; Kahng and

320 Grigg 2005). This implies that while harvesting typically targets the largest colonies
321 (Padilla and Lara 2003), the decline in large colony density in Cozumel could be
322 reducing juvenile recruitment rates.

323 Other factors on Cozumel MCEs could play a part in *P. pennacea* size
324 distribution shifts and density declines. Black corals need hard substrate for
325 recruitment and to firmly attach onto for growth (Wagner et al. 2012), and in the
326 Caribbean are generally associated with steep outer reef slopes (Sanchez et al.
327 1998). In Cozumel, surveys down to 33 m depth in the 1980s recorded mean
328 macroalgal cover at 25 % (Jordán Dahlgren 1988), but surveys at 55 m in 2016
329 recorded mean macroalgal coverage at 44 % (Gress et al. in review). If macroalgal
330 cover has increased, it could reduce substrate availability for *P. pennacea*
331 recruitment. *P. pennacea* settlement has been studied in Jamaica, where areas
332 adjacent to unstable sediment beds had lower settlement rates (Oakley 1988). On
333 Cozumel, shallow reef scleractinian cover has dropped from 44 % to as low as 4 % at
334 some sites, caused by coastal development (Reyes-Bonilla et al. 2014). It is unknown
335 if reduced availability of substrate for recruitment could also be affecting the *P.*
336 *pennacea* population. If this is the case, it is unclear why no effects on *A. caribbeana*
337 density and size distribution were observed between 1998 and 2016. However, with
338 only 15 colonies of *A. caribbeana* identified during 2016, the lack of size distribution
339 difference with time could be due to low statistical power. *A. caribbeana* densities
340 were also higher inside the MPA in 2016 than at sites outside the MPA (adjacent to
341 the main coastal development where there has been the greatest shallow reef loss).
342 Further research is required to understand factors causing the reduced densities of
343 *P. pennacea* colonies.

344 **Management status**

345 The Mexican government continues to issue commercial black coral
346 harvesting permits stating the harvesting locations allowed. Since 1995, when
347 harvesting permits ceased being issued for Cozumel, harvest locations on the
348 mainland coast have changed regularly due to rapid black coral depletion (Padilla
349 and Lara 2003). A harvesting permit is currently issued until October 2018 for
350 locations in the southern Mexican Caribbean. However, prior to our study, no black

351 coral monitoring has been conducted in Mexico since 1998-1999 (Padilla Souza 2000,
352 2004; Padilla and Lara 2003). As all black corals are CITES Appendix II listed, the
353 Mexican government is committed to ensure that black coral harvesting for export
354 'will not be detrimental to the survival of that species', and 'export of specimens of
355 any such species should be limited in order to maintain that species throughout its
356 range at a level consistent with its role in the ecosystems' (CITES 2017). Yet, harvest
357 areas are currently designated based on diver and industry requests following
358 harvest depletion, rather than harvest sustainability (Padilla and Lara 2003). The
359 CITES Trade database (trade.cites.org) contains Mexican black coral export records
360 for the jewellery industry up to 2016, although the quantity of black coral items
361 reported can be as low as 1 per year. These low number or reports might be because
362 the major market for the jewellery in Cozumel is sales to tourists, who are unlikely to
363 obtain CITES export permits, rather than large commercial exports for sale
364 internationally. With no black coral population assessments conducted since 1998-
365 1999, and no studies on recruitment rates or any other biological and ecological
366 traits, it is unclear how the Mexican government is currently evaluating sustainability
367 to continue issuing harvest permits and CITES export permits.

368 Moving forward, we recommend three key steps to improve protection for
369 black corals in the Mexican Caribbean: Firstly, the Mexican threatened species list
370 should be updated to correctly list the eight species of black coral known from the
371 Mexican Caribbean, while acknowledging the outstanding harvesting permit. This
372 will have several results: Primarily, it will require an increased evidence base before
373 harvesting permits can be issued. It will also make illegal harvesting of black corals a
374 more serious criminal offence. In addition, adding these targeted black coral species
375 to the Mexican threatened species list will also force a review of the legal status of
376 the existing harvesting permits. As other well-managed black coral fisheries have
377 struggled to maintain long-term sustainability (Tsounis et al. 2010; Bruckner 2016),
378 there is an urgent need to evaluate the biological and economic sustainability of the
379 industry. Evidence from the few available reports show that unregulated and
380 uninformed harvesting of black corals have quickly lead to overexploitation and
381 population depletion in many areas in the Caribbean (Bruckner 2016). Secondly, the
382 Mexican government has recently announced a large MPA that includes most of the

383 Mexican Caribbean. We strongly recommend that consideration is given to protect
384 MCEs and their ecosystem engineers, such as black corals. Thirdly, we also
385 encourage urgent research to understand drivers of black coral population decline
386 both within Cozumel and the Mexican Caribbean, but also the wider western Atlantic
387 region.

388 Conclusion

389 We surveyed black coral populations around Cozumel finding severe declines
390 in density between 1998 and 2016 for the historically most abundant species, *P.*
391 *pennacea*. These declines affected corals of all size classes, though appeared to
392 disproportionately affect smaller colonies. Based on these trends, we suggest the
393 updating of the existing legal status of black corals. We highlight the urgent need to
394 assess the potential of biological and economical sustainability of black corals
395 harvesting.

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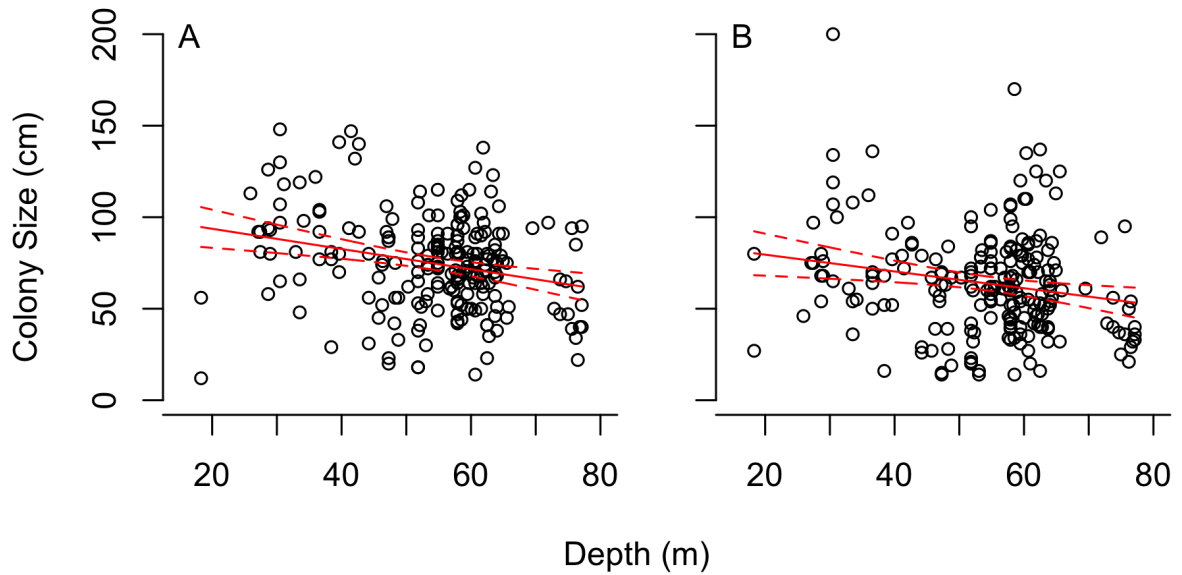
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514

515 Figure S1. Differences in *P. pennacea* colony (A) height and (B) width with depth

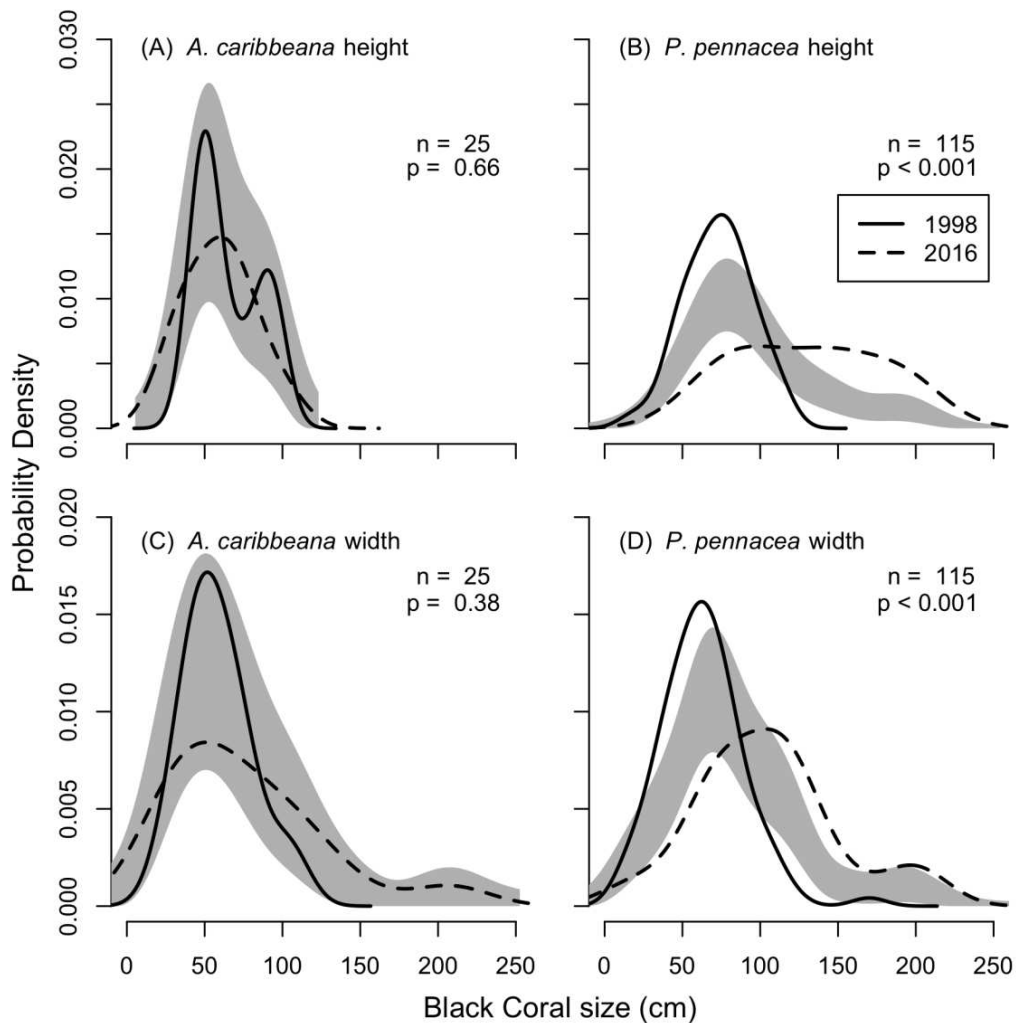
516 from the 1998 surveys. Solid red line shows linear model, while the dashed red lines

517 show 95 % prediction intervals. *P. pennacea* colonies were both taller ($F_{1,215}=14.8$,

518 $p<0.001$) and wider ($F_{1,215}=8.4$, $p=0.004$) at shallower depths, though R^2 values were

519 0.06 and 0.03 for height and width respectively.

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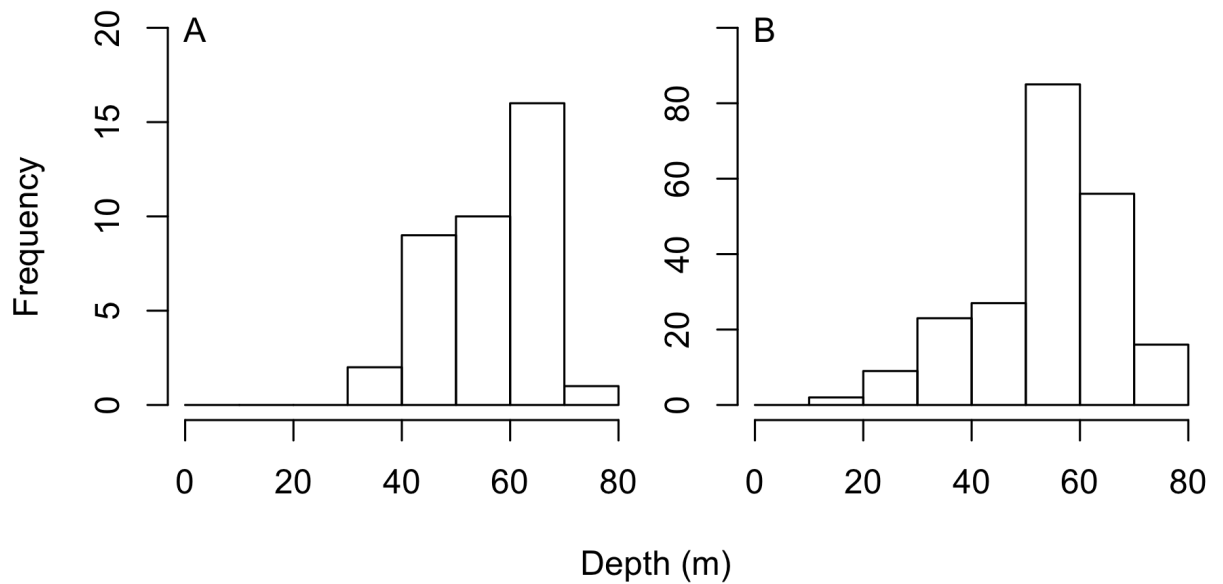


521

522 Figure S2. Change in black coral colony size between 1998 and 2016, using only
 523 colonies recorded between 50-60 m depth in 1998. (A) *A. caribbeana* colony height,
 524 (B) *P. pennacea* colony height, (C) *A. caribbeana* colony width, and (D) *P. pennacea*
 525 colony width. Kernel density estimates were used, followed by a permutation test to
 526 identify differences between years. The grey shaded area indicates one standard
 527 error either side of the null model of no difference in colony size distribution based
 528 on year. Locations where the lines representing 1998 and 2016 are outside the grey
 529 zone indicate significant differences in the proportion of colonies of that size.

530 n =number of colonies.

531



532

533 Figure S3. Frequency distribution showing the number of black coral colonies

534 recorded in 1998 in 10 m across the depth gradient for (A) *A. caribbeana*, and (B) *P.*

535 *pennacea*. Survey effort was approximately equal at different depths in 1998 (Padilla

536 Souza 2000; 2004).