

1 **Twenty years of change in benthic communities across the Belizean Barrier Reef**

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31 **Abstract**

32 Disease, ocean warming, and pollution have caused catastrophic declines in the cover of living
33 coral on reefs across the Caribbean. Subsequently, reef-building corals have been replaced by
34 invertebrates and macroalgae, leading to changes in ecological functioning. We describe changes
35 in benthic community composition and cover at 15 sites across the Belizean Barrier Reef (BBR)
36 following numerous major disturbances—bleaching, storms, and disease outbreaks—over the
37 20-year period 1997–2016. We tested the role of potential drivers of change on coral reefs,
38 including local human impacts and ocean temperature. From 1997 to 2016, mean coral cover
39 significantly declined from 26.3% to 10.7%, while macroalgal cover significantly increased from
40 12.9% to 39.7%. We documented a significant decline over time of the reef-building corals
41 *Orbicella* spp. and described a major shift in benthic composition between early sampling years
42 (1997–2005) and later years (2009–2016). The covers of hard-coral taxa, including *Acropora*
43 spp., *M. cavernosa*, *Orbicella* spp., and *Porites* spp., were negatively related to marine heatwave
44 frequency. Only gorgonian cover was related, negatively, to our metric of the magnitude of local
45 impacts (the Human Influence Index). Changes in benthic composition and cover were not
46 associated with local protection or fishing. This result is concordant with studies throughout the
47 Caribbean that have documented living coral decline and shifts in reef-community composition
48 following disturbances, regardless of local fisheries restrictions. Our results suggest that benthic
49 communities along the BBR have experienced disturbances that are beyond the capacity of the
50 current management structure to mitigate. We recommend that managers devote greater
51 resources and capacity to enforce and expand existing marine protected areas and that
52 government, industry, and the public act to reduce global carbon emissions.

53

54 INTRODUCTION

55 Coral reefs worldwide have experienced remarkable changes over the past 50 years, particularly
56 the widespread declines of reef-building corals and large, predatory fishes (1–7). These changes
57 have caused a reduction in or effective loss of essential ecological functions, including the
58 provisioning of habitat for fisheries production and the maintenance of reef structure for
59 shoreline protection (8,9). Given the substantial economic and cultural value of healthy reefs
60 (10), this degradation is affecting coastal human communities that depend on reefs for food,
61 income, and protection from storms.

62

63 Numerous factors are responsible for the well-documented degradation of Caribbean reefs.
64 Acroporid corals, which dominated Caribbean reefs for millions of years, experienced 90–95%
65 mortality due to white-band disease in the 1980s (11). This disease, likely exacerbated by ocean
66 warming (12), coupled with increased frequency and intensity of hurricanes (13–15), reduced the
67 habitat complexity, or rugosity, of Caribbean reefs (16). Several other disease syndromes have
68 greatly reduced the cover of other coral taxa, including black-band disease, which primarily
69 affects brain corals (17), yellow-band disease, which primarily affects *Orbicella* spp. (18), and,
70 more recently, stony coral tissue loss disease, which affects numerous species, including
71 *Dendrogyra cylindrus*, *Pseudodiploria strigosa*, *Meandrina meandrites*, *Eusmilia fastigiata*,
72 *Siderastrea siderea* and *Diploria labyrinthiformis* (19). Coral bleaching and other manifestations
73 of ocean warming, including increased disease severity, are primary causes of coral loss in the
74 Caribbean (20–27). On local scales, increased sedimentation from coastal development affects
75 coral reefs by increasing turbidity and smothering corals (28,29). Secondary drivers include
76 factors that have increased the cover of fleshy macroalgae (seaweeds), including the death of

77 scleractinian corals and the consequent opening of space and other resources (30), nutrient
78 loading, and the loss of herbivores, particularly the sea urchin *Diadema antillarum* due to a
79 regional disease outbreak (31), and herbivorous fishes due to fishing (32–37).

80

81 Despite the clear and well-documented changes to Caribbean reefs, there is ongoing
82 disagreement about the causes of and best remedies for reef decline (20,38–41). The crux of the
83 debate is about the relative importance of local causes—pollution, eutrophication, fishing, and
84 consequent seaweed blooms—compared with regional-to-global causes such as ocean warming
85 and acidification. Scientists, agencies, and organizations that view localized drivers as
86 predominant generally argue for local mitigation, the primary recommendation being fisheries
87 restrictions, such as within Marine Protected Areas (MPAs) (34,42–44). In contrast, the view that
88 anthropogenic climate change has been a significant or predominant cause of reef decline leads
89 to the conclusion that without rapid cuts in carbon emissions, local protections and other
90 localized management actions, such as restoration, will ultimately fail (20,39,45).

91

92 The purpose of this study was to measure changes to benthic communities of the Belizean
93 Barrier Reef (BBR) from 1997 to 2016 and to determine whether they were related to protection
94 status, fishing, local human impacts, and ocean-temperatures anomalies (i.e., ocean heatwaves).
95 We performed surveys of the coral reef benthos at 15 sites between 1997 and 2016 (46–48). We
96 found that benthic-community composition changed substantially during this period, and that the
97 observed loss of corals was negatively related to ocean heatwaves and largely unaffected by local
98 impacts, fishing or protection status.

99

100 MATERIALS AND METHODS

101 Study area

102 Scientists have tracked reef community composition across Belize for over 50 years, mostly in
103 short-term, longitudinal studies (e.g., 11,46,48–50). Belize has an extensive, 30-plus-year-old
104 MPA network (46) and a history of frequent large-scale disturbances (Table 1). We surveyed
105 fore-reef benthic communities at 15–18 m depth at 15 sites along the BBR during the summer
106 months in 1997, 1999, 2005, 2009, and 2016 (Figure 1; Table S1). Due to logistical and resource
107 constraints, only three of the 15 sites were surveyed every year: Bacalar Chico, Middle Caye,
108 and Tacklebox (Table S1). Study sites were selected to maximize spatial heterogeneity and
109 include a range of protections or management zones (5,47). These management protections
110 included five sites within fully protected (FP) zones (otherwise known as “marine reserves”),
111 where only non-extractive activities are permitted, three sites within general-use (GU) zones,
112 where fishing is permitted with some gear restrictions (e.g., prohibitions on longlines, gillnets,
113 and the use of spearguns and slings with SCUBA) and modest fishing limits (e.g., catch-size
114 limits for queen conch and lobster), and seven sites in unprotected (NP) zones, where fishing is
115 not restricted (46). Note that national seasonal closures for some species (e.g., Nassau grouper)
116 and bans (e.g., on catching parrotfishes) applied to all three zones.

117

118 Benthic surveys

119 Benthic surveys were conducted *in situ* using SCUBA. At each site, dive teams laid out four to
120 ten, 25-30 m x 2 m belt transects down the centers of reef spurs, perpendicular to the shoreline.
121 The transects generally began on or near the shoulders of the spurs at 15–18 m depth, shoreward
122 of the drop-off that characterizes most of the reefs, and ran upward toward the reef crest.

123 Transects were parallel to each other and were usually separated by > 10 m. Divers worked in
124 buddy pairs, in which one diver laid out the transect tape and the other used a digital camera in
125 an underwater housing to obtain videos and still-frame images of the benthos. At each site, we
126 photographed or videotaped the belt transects at a standard distance of 25 cm above the benthos
127 using a horizontal bar projected from the front of the camera housing. In all sampling years
128 except 2016, we obtained underwater videos along the belt transects and extracted still frames
129 from those videos (as outlined below). In 2016, we photographed the transects using a GoPro
130 HERO4 by swimming at a rate of 5–7 minutes along the 30-m-long transect and taking a
131 photograph every five seconds.

132

133 **Image extraction and analysis**

134 Because of changes in imaging technology and analytical software over the course of this study
135 we used several techniques to extract and analyze the benthic images from the underwater
136 transects. For sampling year 1997, we recorded Hi-8 video of each transect, using two 30-watt
137 ultrabright lights for illumination; in 1999 and 2005, we used Sony 3chip mini DVR without
138 illumination. From these video cassettes we randomly selected 50 frames per transect, processed
139 the images by de-interlacing, sharpening, and enhancing them, and saved them onto a CD-ROM.
140 In 2009, we switched to digital video. We extracted the images from the video at a rate of 1-fps
141 using Adobe Premiere Pro CC 2014. We ran the images through the Automator program in OS-
142 X software to select every third, fifth or seventh image, depending on the length (in time) of the
143 transect. We analyzed 15 images/transect/site for 2009 and 2016 because we found that we could
144 obtain a similar level of inference about community composition with 15 images per transect as
145 with the 50 images per transect suggested by Aronson et al. (51). To select the images, we

146 automated the process using a code in R version 3.6.3 [1] to randomly choose, copy, and paste
147 15 images into a new folder from our source-folder of all images.
148
149 We analyzed the benthic cover of images from 1997–2005 using Coral Point Count software
150 (52), and from 2009 and 2016 using CoralNet (53). We manually input species-level benthic
151 identifications for each of 10 random points overlaid onto each image (51). When species-level
152 identifications were not possible, benthic components were identified to genus or family. All
153 benthic components identified were pooled into five benthic categories: (1) crustose–turf–bare
154 space (abbreviated CTB), which represents substrate that is bare, dead, covered in turf algae,
155 and/or crustose coralline algae (48,54), (2) hard corals (which includes all scleractinian corals
156 and milleporine fire corals), (3) macroalgae, including algae in the genus *Halimeda*, (4)
157 gorgonians, and (5) sponges. The corals *Orbicella annularis*, *O. favelota*, and *O. franksii* were
158 pooled as *Orbicella* spp. because the species complex was not divided into three distinct species
159 during the 1997 and 1999 data collection and because they were difficult to distinguish in some
160 video frames. In all instances, image-level point-count data were converted to percent-cover
161 estimates, and we calculated overall mean percent covers of each category for each site and year.
162

163 **Putative drivers of benthic community dynamics**

164 We estimated local human impacts using the Global Human Influence Index (HII, version 2)
165 from NASA’s Socioeconomic Data and Applications Center (SEDAC) database (55). The HII is
166 a global dataset of 1-km grid cells aggregated from 1995–2004 designed to estimate location-
167 specific human influence and thus potential impacts to natural populations and ecosystems via
168 local direct and indirect human activities (e.g., harvesting and pollution). It is based on nine

169 global data layers including human population density, land use, and access (which is estimated
170 from coastlines, roads, railroads and navigable rivers). These aspects of human communities are
171 known to be predictive of local human impacts in many natural systems including coral reefs
172 (6,7,28,56–59). We extracted HII values for the BBR (Fig. S1) and calculated the sum of the HII
173 scores of grid cells within a 50-km, 75-km, and 100-km buffer from the center-coordinates of
174 each study site (Table S1). We used HII scores within the 50-km buffer for the final analysis
175 because this metric performed well in exploratory models and it has been used successfully in
176 prior work (5, 56). We then tested whether this index of local human impacts was related to
177 observed changes on the monitored benthic reef communities.

178

179 Our measure of ocean-heatwave events was the site-specific frequency of Thermal Stress
180 Anomalies (TSA Freq), obtained from the Coral Reef Temperature Anomaly Database
181 (CoRTAD, Version 6) (60,61) (Fig. S2, Table S2). We used this metric to test for effects of
182 thermal stress on the measured benthic groups. TSA Freq is defined as the number of deviations
183 of 1 °C or greater from maximum weekly climatological sea-surface temperature during the 52
184 weeks preceding a reef survey. Other studies have found that TSA Freq is a significant predictor
185 of coral-cover loss and coral-disease prevalence (62–64). The CoRTAD is based on 4-km-
186 resolution weekly measurements made by the Advanced Very High-Resolution Radiometer
187 (AVHRR) sensor (Pathfinder 5.0 and 5.2) beginning in 1982. Daytime and nighttime data were
188 averaged weekly using data with a quality flag of 4 or better.

189

190 **Data analyses**

191 To analyze changes in benthic composition and test for the effects of potential drivers of change,
192 we built generalized linear mixed models (GLMM) in a Bayesian setting using the *blme* package
193 (65). The response variables were the logit-transformed percent covers of key benthic categories.
194 The final models had Year, Fishing level (“fishing”, which were the sites within FP zones, and
195 “no fishing” which included GU and NP sites), HII at the 50-km buffer, and TSA Freq as fixed
196 effects; and Site as a random effect. A *blme* prior with a *wishart* distribution was imposed over
197 the covariance of the random effect and modeled coefficients. All predictor variables were
198 additive, and the REML estimation was used to fit the data as it provides unbiased estimates for
199 the variance components. Prior to fitting models, we rescaled and centered all numerical fixed
200 effects to optimize comparisons among variables. The final model structure for each benthic
201 category was as follows:

$$\begin{aligned} 202 \quad & \text{Logit (benthic cover)}_i = \\ 203 \quad & \alpha + \beta_{1j} * \text{Year}_{ij} + \beta_{2j} * \text{Fishing Level}_{ij} + \beta_{3j} * \text{HII}_{ij} + \beta_{4j} * \text{TSA Freq}_{ij} + \\ 204 \quad & \alpha_i + e_{ij} \end{aligned}$$

205
206 where α = intercept, α_i = random intercept (Site), e_{ij} = error term, and $\beta_{1j} - \beta_{4j}$ are the coefficient
207 estimates for covariates. The logit-transformed coral cover was modeled as an intercept (α), plus
208 linear effects of Year, Fishing level, HII at 50km, and TSA Freq; a random intercept (α_i) for Site,
209 which is assumed to be normally distributed with a mean of 0 and variance $\sigma\alpha^2$; and an error (e_{ij}).
210 The index i refers to sites ($i = 1, \dots, 15$), and j refers to the year of survey ($j = 1997, \dots, 2016$).
211 The term e_{ij} was the within-site variance of benthic group cover and is assumed to be normally
212 distributed with mean of 0 and a variance of σ^2 .

213

214 We evaluated collinearity among fixed factors by assessing variance-inflation factors and chose a
215 threshold of 3 to determine correlated variables. We tested for homoscedasticity (equal variances
216 across predictor variables) by plotting residuals against fitted values. Comparing fitted and
217 residual values suggested that our models were reasonable models of the means. We also
218 examined the marginal and conditional R-squared values of the models.

219

220 To examine changes in community composition of all benthic taxa within sites and across years,
221 we constructed a non-metric multidimensional scaling (NMDS) ordination using the *vegan*
222 package in R. We used the Bray–Curtis dissimilarity index to calculate distances among taxon-
223 level cover data because it handles the large numbers of zeros (which denote absences)
224 commonly found in ecological data and does not consider shared absences as being similar (66).
225 To determine the effects of covariates (Year, TSA Freq, HII_50km, and Fishing level) on
226 community composition changes of benthic taxa we ran a Permutational Multivariate Analysis of
227 Variance (PERMANOVA) using the Bray-Curtis dissimilarity index to calculate distance
228 matrices. All statistical analyses were performed in R version 3.6.3. The code and processed data
229 are available at <https://github.com/calves06/BRC>.

230

231 **RESULTS**

232 Among the five benthic groups of interest—hard corals, macroalgae, CTB, gorgonians, and
233 sponges—we identified a significant decline in hard coral and CTB cover, significant increases
234 in macroalgal and gorgonian cover, and no change in sponge cover (Figs. 2 & S3, Table 2).
235 Fishing status (fished *versus* unfished) was not predictive of observed spatiotemporal variation in
236 hard-coral, macroalgal, CTB, or sponge cover (Figs. 2 & 3, Table 2) and was marginally and

237 negatively related to gorgonian cover. The Human Influence Index (HII) was also unrelated to
238 hard-coral, macroalgal CTB, or sponge cover (Fig. 3, Table 2). HII was significantly and
239 negatively related to gorgonian cover. TSA Freq, our metric of ocean-heatwave frequency, was
240 significantly negatively related to the cover of hard corals and gorgonians, and unrelated to the
241 cover of macroalgae, CTB, and sponges (Fig. 3).

242

243 Throughout the two decades of this study, the substantial decline in hard-coral cover across the
244 Belizean Barrier Reef from 26.3 % (\pm 7.3 SD) to 10.6 % (\pm 3.5 SD) (Fig. 2) was driven by a
245 handful of reef-building coral species (Fig. 5). Notably, there was a significant decline of
246 *Orbicella* spp., with mean cover falling from 12.7 % (\pm 7.4 SD) in 1997 to 2.2 % (\pm 0.9 SD) in
247 2016 (Fig. 5, Table S4; model estimate = - 0.719, p < 0.001). This decline was predominantly
248 observed from 1997 to 1999, which included a major bleaching event and Hurricane Mitch (Fig.
249 5, Table 1), and from 2005 to 2009, which included a second bleaching event, Hurricane Dean,
250 and an earthquake (Fig. 5, Table 1). The cover of hard-coral taxa such as *Acropora* spp.,
251 *Colpophyllia natans*, and the combined cover of “other coral” taxa (e.g., *Mycetophyllia* spp.,
252 *Madracis* spp., *Favia* spp. see Table S5 for a complete list) also declined significantly from 1997
253 to 2016 (Fig. 5, Table S4). The cover of the coral taxa *Agaricia agaricities*,
254 *Diploria/Pseudodiploria* spp., *Montastrea cavernosa*, *Siderastrea* spp., *Porites astreoides*, and
255 *Porites* spp. (*P. porites*, *P. furcata*, and *P. divericata*) remained relatively low and did not
256 change significantly during the study period (Fig. 5, Table S4). The cover of *Agaricia tenuifolia*
257 slightly but significantly increased (Fig. 5, Table S4). Fishing level and HII were not significant
258 predictors of spatial and temporal changes of any coral taxa (Table S4), except for *P. astreoides*,
259 for which sites with higher cover were associated with areas of higher HII (Table S4). The cover

260 of *Acropora* spp., *M. cavernosa*, *Orbicella* spp. *Porites* spp., and “other coral” taxa were
261 negatively correlated with TSA frequency (Table S4).

262

263 Based on the ordination analysis, there were major compositional shifts in the dominant benthic
264 assemblages during 1997–2005 (left) and 2009–2016 (right) at every site (Fig. 6, Table 3),
265 supporting the results of our models. The PERMANOVA showed that, among all covariates,
266 time explained about 50% of the variability in benthic community changes ($F = 45.8$, $p < 0.001$)
267 and was the only significant predictor of change in overall community composition (Fig. 6, Table
268 3). Fishing level, HII, and TSA frequency combined only accounted for 6% of community
269 differences and were not good predictors of overall change of all taxa studied (Table 3). In 1997–
270 2005, the benthic communities of the BBR were dominated by CTB and long-lived, massive
271 reef-building corals such as *Orbicella* spp. and *C. natans*. During 2009–2016, composition had
272 shifted to domination by small and/or weedy hard-coral species, macroalgae, and gorgonians
273 (Fig. 6).

274

275 **DISCUSSION**

276 Belize’s network of protected areas, designed and implemented in part to prevent the degradation
277 of benthic reef assemblages on the BBR, has not achieved this goal. Our results complement
278 previous findings for Belize reporting the failure of individual MPAs or the network overall to
279 protect and restore populations of overharvested reef fishes (5,46,67,68), but see (68). We
280 documented a statistically and ecologically significant decline in hard-coral cover, an increase in
281 macroalgae and gorgonians, and a substantial decline of CTB, regardless of protection status

282 (Fig. 2). Similar coral declines in isolated, well-protected, and seemingly “pristine” locations
283 have been documented at many other sites globally (69,70).

284

285 We found that the benthic assemblages changed over time and were ecologically distinct
286 between the earlier and later sampling intervals (1997–2005 and 2009–2016) (Fig. 6). For
287 instance, the hard corals *Acropora* spp. and *Orbicella* spp. were more often present and more
288 dominant (both had higher relative and absolute cover) in the early sampling years, as opposed to
289 fleshy macroalgae and gorgonians, which dominated during later sampling years. In contrast, the
290 cover of ‘weedy’ coral taxa such as *Porites* spp. and *Agaricia* spp. remained relatively consistent
291 throughout the course of the study (Fig 5). The striking decline in *Orbicella* spp. (Fig. 5) was
292 likely due to mortality from coral bleaching in 1998 (54,71) and 2005 (21,72–74), Hurricane
293 Mitch in 1998, Hurricane Dean in 2007, and yellow-band disease in the early 2000s (Table 1).

294

295 Our results are concordant with previous studies in Belize that documented shifts in hard-coral
296 and macroalgal cover (75). For example, the patch reefs of Glovers Reef atoll had ~0% hard
297 coral and 20% fleshy-macroalgal cover in 1970–1971 but phase-shifted to 20% hard coral and
298 80% macroalgal cover by 1996–1997 (75). This change was due to massive declines in the reef-
299 building corals *Acropora cervicornis*, *A. palmata*, and *Orbicella* spp., and large increases in the
300 cover and biomass of fleshy and corticated seaweeds including *Lobophora*, *Dictyota*, *Turbinaria*,
301 and *Sargassum*. Prior to the beginning of our study, acroporid abundance had already declined
302 across much of the BBR due to both hurricanes and white-band disease (11,68,76). Most
303 remaining *A. cervicornis* and *A. palmata* was killed by high ocean temperatures during the 1998
304 mass-bleaching event (54,71). A longitudinal study of *A. palmata* along the Mexican portion of

305 the Mesoamerican Barrier Reef also reported declines in acroporids, with *A. palmata* decreasing
306 from 7.7% in 1985 to 2.9% in 2012 (76).

307

308 We attribute changes in the benthic assemblages of coral reefs along the BBR primarily to the
309 large-scale disturbances to the system over the last several decades, including seven hurricanes
310 and two mass-bleaching events caused by anthropogenic climate change (Table 1). We measured
311 the potential effects of several putative drivers, including local human impacts estimated using
312 the Human Influence Index (HII) and the frequency of ocean heatwaves (TSA Freq). Our results
313 indicate that the local impacts had no measurable effect on hard-coral cover. HII was, however,
314 significantly and negatively related to changes in gorgonians and positively associated with the
315 cover of *Porites astreoides*. There is abundant evidence that local impacts, including pollution,
316 fishing, and coastal land-use practices, can severely impact coral populations (28). Yet even
317 when these stressors are clearly present, they are often overwhelmed by the effects of large-scale
318 disturbances including ocean heatwaves and storms (20,39,57,75).

319

320 Shifts in the dominant benthic assemblages have been documented across the Caribbean, linked
321 to regional disturbances such as herbivore declines, coral diseases, and mass-bleaching events
322 (2,3,69,77,78). Across seven subregions in the Caribbean, Schutte et al. (2) found significant
323 declines in hard-coral cover and increases in macroalgal cover from 1970–2005. Corals failed to
324 recover in the Florida Keys (79) and the U.S. Virgin Islands (80) due to subsequent, repeated
325 disturbances. The coral reefs of Bonaire exhibited similar trends over 15 years of bleaching,
326 storms, and diseases, with a 22% decline in coral cover and an 18% increase in macroalgal cover
327 by 2017 (81). These trends were also apparent in our study.

328

329 The primary management response to reef degradation has been implementation of MPAs
330 (34,41,44,82). MPAs and MPA networks are areas where extractive activities are regulated via
331 fishing closures or gear restrictions among others. Within well-designed and enforced MPAs,
332 fish abundance and diversity often increase and in some cases spill over into adjacent, non-
333 protected areas (68,83–86). Some MPAs also reduce other extractive activities that could directly
334 or indirectly impact coral populations. However, a large majority of studies have found that
335 MPAs are not slowing or preventing the decline of reef-building corals (50,63,67,79,87–89). A
336 recent meta-analysis of 18 studies, encompassing 66 MPAs, reported that MPAs did not affect
337 coral loss or recovery in response to large-scale disturbances including disease, bleaching, and
338 storms (39). Our results for the BBR agree with this broad consensus.

339

340 Unlike local human impacts, anthropogenic climate change was clearly a significant driver of the
341 dramatic shifts in community composition that occurred on the BBR over the two-decade study.
342 Overall coral cover, and the cover of four coral taxa—*Acropora* spp., *Orbicella* spp., *Montastrea*
343 *cavernosa*, and *Porites* spp.—were negatively related to heatwave frequency (Figs. 3 and 4).
344 This result is in agreement with other studies that have documented coral mortality and
345 consequent declines in coral cover following the temperature-induced mass-bleaching events on
346 the BBR in 1998 and 2005 (48,54). Many other studies have documented the role of ocean
347 heatwaves in coral decline around the world (21,22,63,69,88–93).

348

349 Our data show a substantial shift in the state of coral reefs along the Belizean Barrier Reef over a
350 two-decade period rife with large-scale disturbances. The results illustrate the shortcoming of

351 protected areas in mitigating these impacts. We documented declines in the key reef-building
352 coral genera *Acropora* and *Orbicella*, subsequent increases in macroalgal and gorgonian cover,
353 and an overall change in the benthic assemblages over the two-decade study. Ocean-heatwave
354 frequency was the only significant predictor of coral population declines over time. Our results
355 provide insight into the overriding influence of regional, and global drivers at a time of rapid
356 climate change, which will help managers improve their decision-making.

357

358

359

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368

369 **Competing interests:** The authors have declared that no competing interests exist.

370

371 **Data Availability:** All relevant code and data are available at here:

372 https://github.com/calves06/Belizean_Barrier_Reef_Change

373

374

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392

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394 MM, RBA, NB, CF, and JFB designed the study

395 MM, RBA, NB, CC, CF, and JFB obtained the study funding

396 MM, NB, KC, CC, CF, CA, LM, AV, and JFB performed the surveys

397 MM, NB, CF, CC, and JFB performed the pre-survey expedition planning

398 CA, MM, NB, CF, CC, and AV organized the study data

399 MM, NB, CF, CA, ZL, LM, and JFB analyzed the benthic videos and images

400 CA, JU, AV, and JFB analyzed the data

401 CA, RA, AV, and JFB wrote the manuscript with contributions from the other authors

402

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644

645 **TABLES AND FIGURES**

646

647 **Table 1.** Timeline of major disturbances to the Belizean Barrier Reef.

Year	Disturbance	References
1980s	Acroporid-specific white-band disease	(54)
1983	<i>Diadema</i> -specific disease	(31)
1998	Temperature-induced coral bleaching	(54,71)
1998	Hurricane Mitch	(94)
2001	Tropical Cyclone Iris	(95)
2005	Temperature-induced coral bleaching	(21,72–74)
2007	Hurricane Dean	(96)
2009	Earthquake	(97)

648

649

650 **Table 2. Estimated regression parameters for benthic groups coverage.** Estimated regression
 651 parameters, standard errors, F-statistics, p-values, significance levels, and *marginal/conditional*
 652 R^2 from the final Bayesian generalized linear mixed models for each benthic group. Significance
 653 levels (Sig.) are: *** < 0.001; ** < 0.01, * < 0.05.

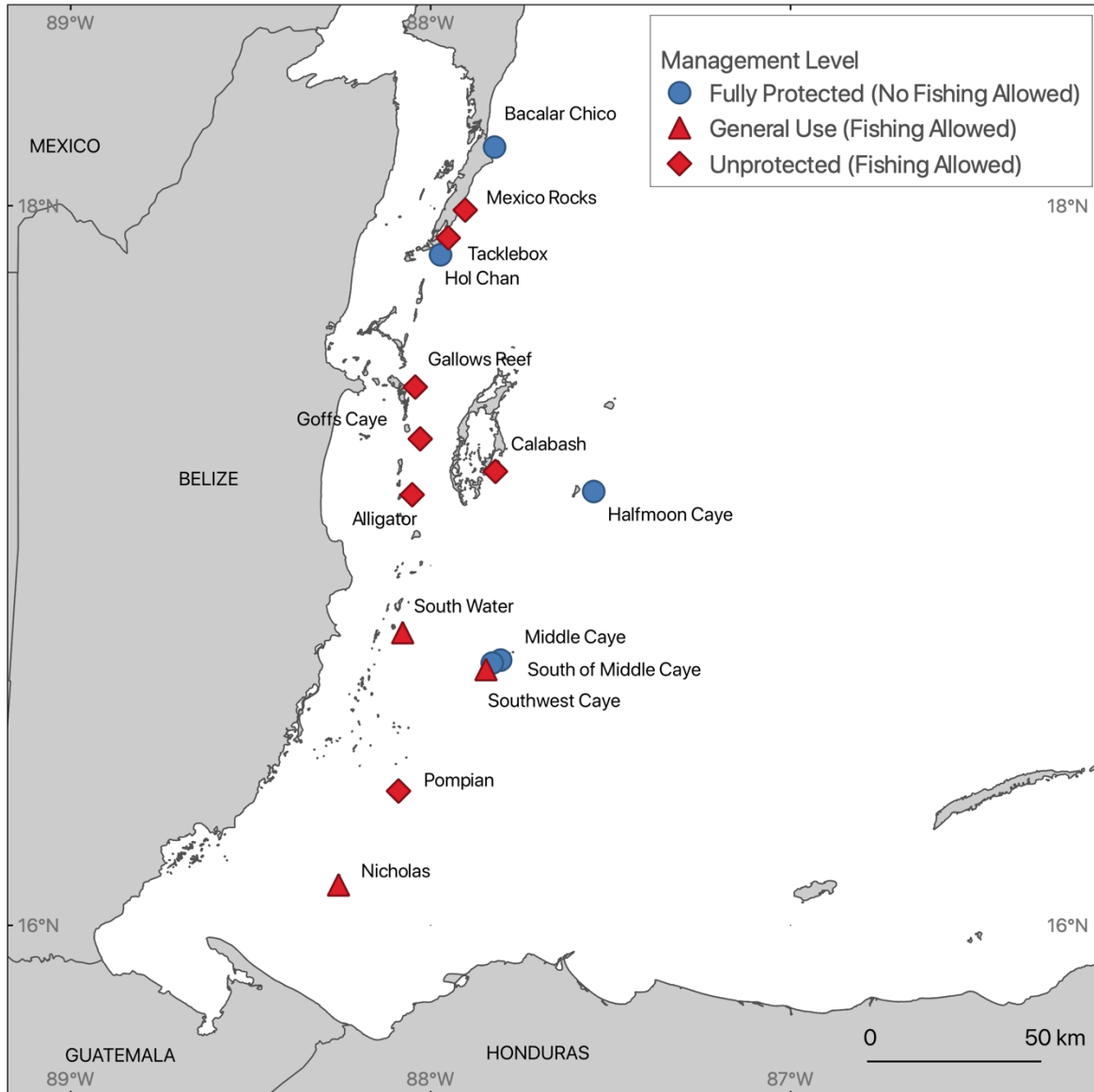
Benthic group/Terms	Estimates	Std. error	Statistic	p-value	Sig.
Hard Coral					
(Intercept)	-1.877	0.126	-14.849	< 0.001	***
Year	-0.492	0.103	-4.773	< 0.001	***
Fishing vs. No Fishing	0.127	0.225	0.567	0.570	
HII at 50 km	0.324	0.217	1.492	0.136	
TSA Freq	-0.383	0.117	-3.278	0.001	**
<i>Marginal R²/Conditional R²</i>	<i>0.347/ 0.665</i>				
Macroalgae					
(Intercept)	-0.929	0.148	-6.274	< 0.001	***
Year	0.925	0.108	8.576	< 0.001	***
Fishing vs. No Fishing	0.138	0.265	0.522	0.602	
HII at 50 km	0.307	0.256	1.202	0.229	
TSA Freq	0.225	0.123	1.829	0.067	
<i>Marginal R²/Conditional R²</i>	<i>0.480/0.775</i>				
CTB					
(Intercept)	-0.998	0.149	-6.695	< 0.001	***
Year	-1.622	0.194	-8.360	< 0.001	***
Fishing vs. No Fishing	0.212	0.248	0.853	0.394	
HII at 50 km	-0.243	0.243	-0.999	0.318	
TSA Freq	0.255	0.205	1.245	0.213	
<i>Marginal R²/Conditional R²</i>	<i>0.613/0.652</i>				
Gorgonian					
(Intercept)	-2.152	0.097	-22.092	< 0.001	***
Year	0.407	0.111	3.658	< 0.001	***
Fishing vs. No Fishing	-0.373	0.166	-2.240	0.025	*
HII at 50 km	-0.450	0.162	-2.777	0.005	**
TSA Freq	-0.352	0.121	-2.921	0.003	**
<i>Marginal R²/Conditional R²</i>	<i>0.430/0.550</i>				
Sponge					
(Intercept)	-3.443	0.159	-21.724	< 0.001	***
Year	-0.209	0.172	-1.215	0.224	
Fishing vs. No Fishing	0.070	0.273	0.258	0.797	
HII at 50 km	-0.125	0.265	-0.469	0.639	
TSA Freq	-0.299	0.188	-1.591	0.112	
<i>Marginal R²/Conditional R²</i>	<i>0.099/0.329</i>				

654

655 **Table 3.** Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) using
656 the Bray-Curtis dissimilarity index to determine the effects of covariates in changes of benthic
657 community composition cover. df: degrees of freedom, SS: sum of squares. Significance level
658 (Sig.): *** < 0.001

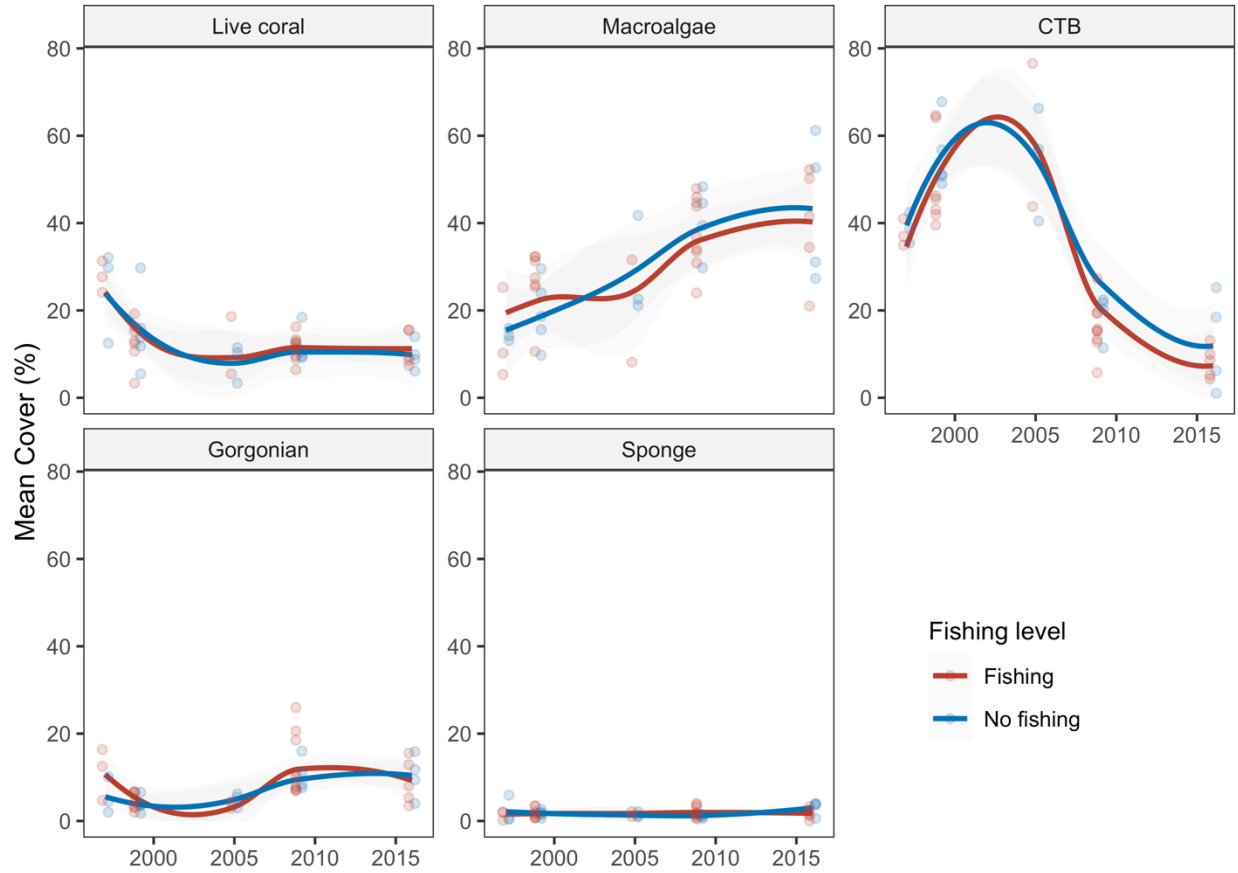
Term	df	SS	R²	F	Pr(>F)	Sig.
Year	1	2.347	0.501	45.761	<0.001	***
HII 50km	1	0.137	0.029	2.679	0.062	
TSA Freq	1	0.072	0.015	1.401	0.218	
Fishing level	1	0.075	0.016	1.465	0.200	
Residual	40	2.051	0.438			
Total	44	4.683	1.000			

659



660

661 **Figure 1. Study sites along the Belizean Barrier Reef.** Sites are categorized by management
662 and fishing level. Fishing is allowed in general use and unprotected sites (red), whereas fishing is
663 prohibited in fully protected sites (blue).

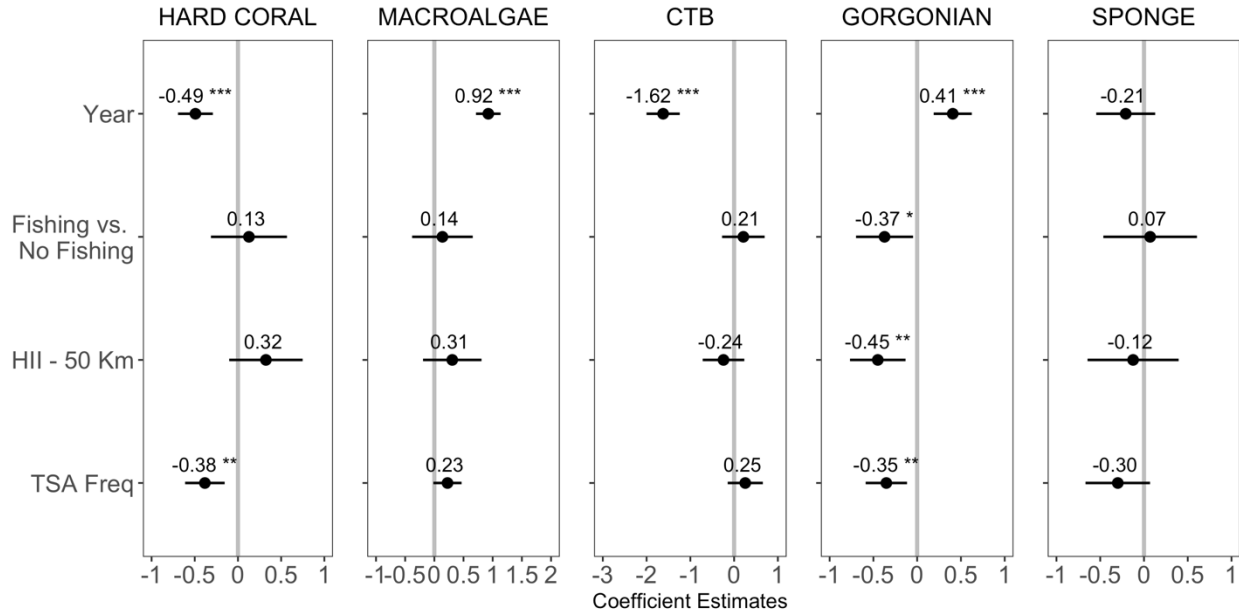


664

665 **Figure 2. Percent cover of five benthic categories over time grouped by fishing level. Points**

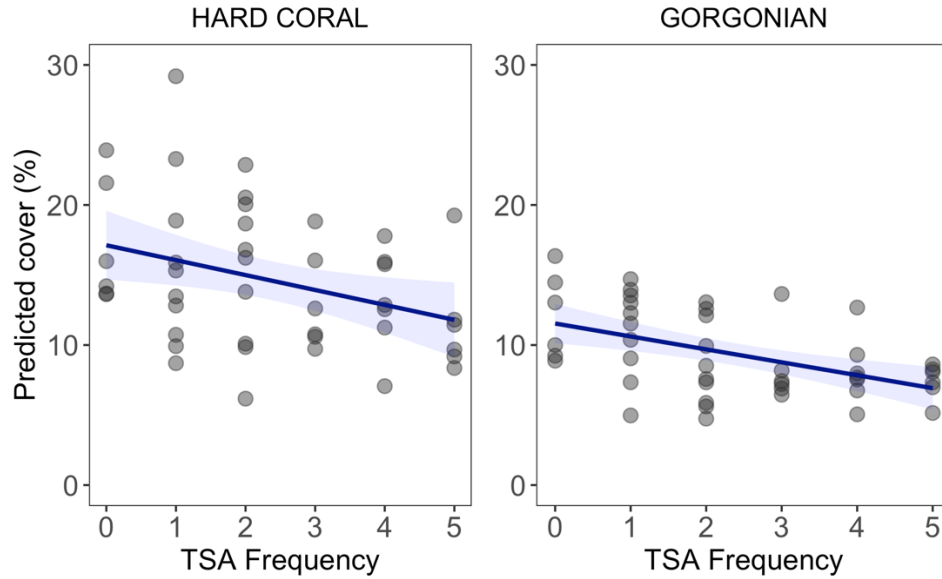
666 are site means, lines are loess smoothed curves with a span of 1, shading indicates the 95%

667 confidence intervals of the loess fits.



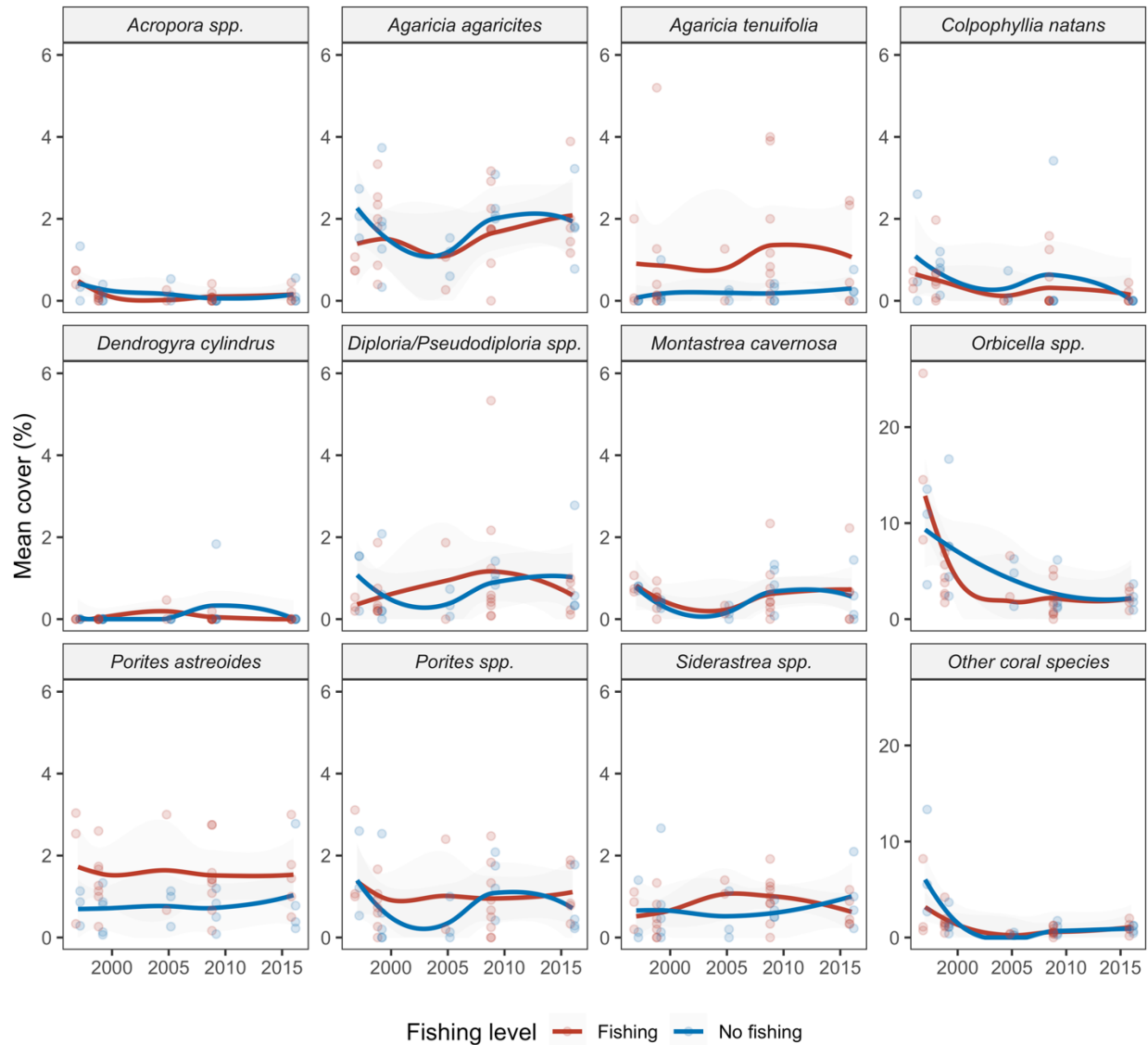
668

669 **Figure 3. Effect-sizes (\pm 95% CI) of covariates from the Bayesian generalized linear mixed-**
670 **effect model on the five benthic groups.** Values above points are effect sizes. CIs crossing the
671 vertical grey line represents a non-significant effect. Significance levels: *** = 0.001; ** = 0.01,
672 * = 0.05.



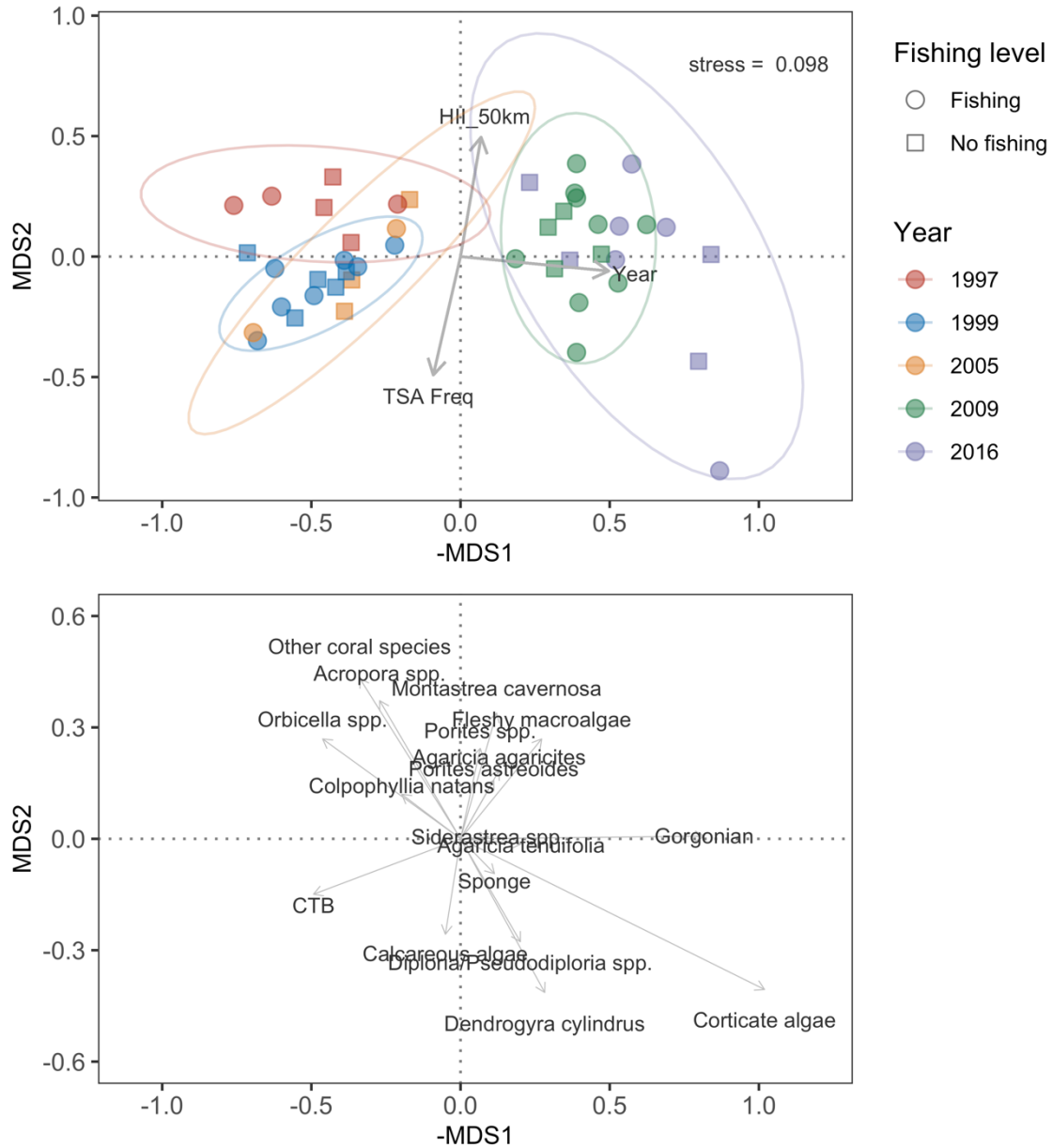
673

674 **Figure 4. Predicted effect of TSA frequency on hard-coral and gorgonian cover.** Points are
675 predicted benthic group cover (back calculated from logit transformation) from Bayesian
676 generalized liner mixed model accounting for time, fishing level, and human influence index.
677 Blue lines are the fitted curves of the models and shaded areas are the 95 % CIs.



678

679 **Figure 5. Mean percent cover of twelve taxonomic categories of hard corals, grouped by**
680 **fishing level.** Fishing occurs in red sites and is prohibited in blue sites. Points are site means for
681 each surveyed year, lines are a loess smoothed curves with a span of 1, and shading indicates the
682 95% confidence intervals of the loess fits.



683

684 **Figure 6. Non-metric multidimensional scaling (MDS) plot depicting taxon-level cover data**

685 **colored by year.** In the top panel, points represent individual sites, circles are fishing sites, and

686 squares are no-fishing sites. Arrows represent the fitted loadings scores for Year, TSA_Freq, and

687 HII_50km. In the bottom panel, the arrows and labels represent specific benthic categories

688 loadings. The Bray–Curtis dissimilarity matrix was used and the stress value was 0.098.