

1 Temperature regimes impact coral assemblages along environmental gradients on lagoonal reefs
2 in Belize

3

4 Justin H. Baumann^{1*}, Joseph E. Townsend¹, Travis A. Courtney^{1,2,3}, Hannah E. Aichelman¹,

5 Sarah W. Davies^{1,2}, Fernando P. Lima⁴, Karl D. Castillo¹

6 ¹University of North Carolina at Chapel Hill, Department of Marine Sciences, 3202 Murray and
7 Venable Halls, Chapel Hill, NC 27599-3300

8 ²Northeastern University, Department of Marine and Environmental Sciences; Nahant, MA

9

10 ³Scripps Institution of Oceanography, University of California San Diego, 9500 Gilman Dr., La
11 Jolla, CA 92093-0202

12

13 ⁴CIBIO/InBIO, Centro de Investigacao em Biodiversidade e Recursos Geneticos, Universidade
14 do Porto, Campus Agrário de Vairão, Portugal

15

16 *Corresponding author: Justin H Baumann, 513-307-1516, baumannj@live.unc.edu

17

18

19 **Keywords:** climate change, coral reefs, global stressor, local stressor, Belize, lagoonal reefs,
20 coral diversity, coral community structure, Caribbean

21

22 **Short Title:** Temperature regimes impact coral assemblages of lagoonal reefs

23

24

25

26

27

28

29

30

31

32

33

34 Abstract

35 Coral reefs are increasingly threatened by global and local anthropogenic stressors such as rising
36 seawater temperature, nutrient enrichment, sedimentation, and overfishing. Although many studies
37 have investigated the impacts of local and global stressors on coral reefs, we still do not fully
38 understand how these stressors influence coral community structure, particularly across
39 environmental gradients on a reef system. Here, we investigate coral community composition
40 across three different temperature and productivity regimes along a nearshore-offshore gradient
41 on lagoonal reefs of the Belize Mesoamerican Barrier Reef System (MBRS). A novel metric was
42 developed using ultra-high-resolution satellite-derived estimates of sea surface temperatures (SST)
43 to classify reefs as exposed to low (low_{TP}), moderate (mod_{TP}), or high ($high_{TP}$) temperature
44 parameters over 10 years (2003 to 2012). Coral species richness, abundance, diversity, density,
45 and percent cover were lower at $high_{TP}$ sites relative to low_{TP} and mod_{TP} sites, but these coral
46 community traits did not differ significantly between low_{TP} and mod_{TP} sites. Analysis of coral life
47 history strategies revealed that $high_{TP}$ sites were dominated by hardy stress-tolerant and fast-
48 growing weedy coral species, while low_{TP} and mod_{TP} sites consisted of competitive, generalist,
49 weedy, and stress-tolerant coral species. Satellite-derived estimates of *Chlorophyll-a* (*chl-a*) were
50 obtained for 13-years (2003-2015) as a proxy for primary production. *Chl-a* concentrations were
51 highest at $high_{TP}$ sites, medial at mod_{TP} sites, and lowest at low_{TP} sites. Notably, thermal
52 parameters correlated better with coral community traits between site types than productivity,
53 suggesting that temperature (specifically number of days above the thermal bleaching threshold)
54 played a greater role in defining coral community structure than productivity on the MBRS.
55 Dominance of weedy and stress-tolerant genera at $high_{TP}$ sites suggests that corals utilizing these
56 two life history strategies may be better suited to cope with warmer oceans and thus may warrant
57 protective status under climate change.

58

59

60

61

62 **Introduction**

63 Coral reefs are threatened locally and globally by anthropogenic stressors such as warming
64 induced by increasing greenhouse gas emissions, excessive nutrients from runoff and sewage
65 effluent, overfishing, and habitat destruction [1,2,3]. Of particular concern are increasing
66 greenhouse gas emissions that continue to cause warming of the global oceans [1,4]. This warming
67 trend is especially troubling in the Caribbean Sea, where rates of warming are higher than in many
68 other tropical basins [5], and where coral cover has declined by up to 80% in recent decades [6].
69 Elevated sea surface temperature (SST) is the major cause of the breakdown of the essential coral-
70 algal symbiosis, which if widespread results in mass coral bleaching [7,8]. In Belize, the 1998 El
71 Niño bleaching event was the most significant bleaching induced mass coral mortality event on
72 lagoonal reefs over the last 3000 years [9]. These large-scale coral bleaching events are projected
73 to increase in frequency and severity as the climate continues to warm [4,10]. In fact, if ocean
74 warming persists, corals in the Caribbean Sea are predicted to bleach biannually within the next
75 20-30 years [11], with annual bleaching events occurring as soon as 2040 [12]. Caribbean-wide
76 and global-scale bleaching events are predicted to continue unless corals can increase their thermal
77 tolerance at a rate of 0.2-1.0°C per decade [4].

78 Annual and daily thermal variability have recently been identified as important factors
79 influencing coral thermal tolerance [13,14,15]. Indeed, previous exposure to thermally variable
80 environments increases a coral's tolerance to future temperature stress [14,16,17,18], and research
81 suggests that Pacific and Red Sea corals living in areas with high summer maximum SST are less
82 susceptible to bleaching [19,20]. Along the Belize Mesoamerican Barrier Reef System (MBRS)
83 and on Pacific Atolls, corals historically exposed to less thermal variability exhibited slower
84 growth rates and/or greater susceptibility to bleaching in response to SST increases [17,18]. In the

85 Florida Keys, coral growth rates and coral cover were higher in nearshore environments exposed
86 to more variable seawater temperatures than on deeper reefs experiencing more stable
87 temperatures [21]. In contrast, while many studies suggest that high temperature variability leads
88 to higher coral resilience [14,15,16], there is also evidence that corals experiencing moderate long
89 term temperature variability (either annual or daily variation) are better able to cope with stress
90 [13]. Collectively, these studies emphasize the importance of thermal variability on the response
91 of corals to environmental stress, and highlight its capacity to shape coral community composition
92 across a reef system.

93 Multi-species coral assemblages have recently been proposed to comprise four major life
94 history guilds: competitive (large, fast growing, broadcast spawning, e.g., Caribbean *Acropora*
95 *spp.*), weedy (small, opportunistic colonizers of recently disturbed habitat, e.g., Caribbean *Porites*
96 *spp.*), stress-tolerant (massive, slow growing, broadcast spawning, e.g., *Siderastrea siderea*), and
97 generalist (share traits characteristic of all three other groups, e.g., *Orbicella spp.*) [22]. Grouping
98 species by life history strategy allows for prediction of responses to disturbance (e.g., temperature
99 stress) as life history strategies are trait based [23]. Additionally, each guild is expected to be
100 differentially impacted by stressors and life histories predict coral community response to multiple
101 stressors [24]. Therefore, life history strategies offer a more elegant and predictive alternative to
102 traditional genus or species level analysis.

103 Competitive corals are by definition not very stress tolerant [22]. As such, region-wide
104 decline of these species would be expected as the impact of anthropogenic stressors increase
105 (including coral disease). This decline has already occurred in the Caribbean [6]. Generalist corals
106 became dominant on Caribbean reefs in the late 1970s following mass die off of competitive corals.
107 Generalists are more stress tolerant than competitive species but bleaching and other stressors have

108 led to high mortality of *Orbicella spp.* in the Caribbean [25] and continued decline is expected as
109 temperature stress increases [6,26,27], leading to a decline in reef complexity [28]

110 Weedy and stress tolerant corals have been shown to be more resilient than competitive
111 and generalist species [22,24], and are hypothesized to dominate warmer and more impacted reefs
112 (e.g., reefs closer to the shore). A shift from dominance of competitive and generalist species to
113 weedy and stress tolerant species occurred on Okinawan reefs following the 1998 El Niño
114 bleaching event [29,30] and an overall decline in coral cover and abundance currently occurring
115 in the Caribbean has been coupled with an increase in abundance of weedy species [27,31].
116 Interestingly, fossil assemblages from excavated pits on reefs in Panama reveal that mortality and
117 changes in reef communities caused by anthropogenic impact (such as land clearing and
118 overfishing) predate mass bleaching events, indicating that other sub-lethal stressors can impact
119 coral community structure [32,33,34]. Collectively, evidence suggests that differential responses
120 between coral species to increasing anthropogenic stressors may lead to community scale shifts in
121 reef composition from dominance of competitive and generalist species to dominance of stress
122 tolerant and weedy species.

123 The purpose of the current study was to investigate the impact of thermal regimes on
124 present day coral community composition (coral abundance, species richness, diversity, percent
125 cover, density, and life history strategies) of lagoonal reefs (i.e., region extending from the barrier
126 reef's crest to the mainland) across the Belize MBRS. A novel GIS-based metric was developed
127 to characterize lagoonal reefs across this reef system into three thermally distinct regimes. Within
128 these three regimes, thirteen reef sites were identified and benthic surveys were conducted to
129 quantify coral community composition. These thermal regimes exist along a nearshore-offshore
130 productivity gradient, which may also influence coral community structure. Quantifying coral

131 community differences among these thermally distinct reefs will help us better predict how coral
132 community structure may be impacted by climate change. Identifying which areas and species are
133 best able to cope with environmental stress (and which are least able) may allow for more targeted
134 management strategies, as it is important to protect both high-risk and low-risk reef sites to
135 improve our chances of conservation success [35].

136 **Materials and Methods**

137 **Site identification**

138 *SST Estimate Assembly*

139 Daily 1-km horizontal resolution SST estimates were acquired from the Jet Propulsion
140 Laboratory's Multi-Scale High Resolution SST (JPL MUR SST) records via the Physical
141 Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA JPL, Pasadena, CA
142 (<http://podaac.jpl.nasa.gov>). Conventional 1-km resolution satellite-derived SST measurements
143 (infrared, IR) are contaminated by clouds, creating data-void areas. Microwave (MW) data sets
144 can penetrate clouds to gain better temporal coverage, but with a much coarser spatial resolution
145 (25 km) [36]. MUR combines these two datasets to present a more comprehensive and complete
146 SST product. It employs multi-resolution variational analysis (MRBA) as an interpolation method
147 to combine high resolution datasets with more conventional datasets, generating a product that
148 contains no cloud contamination [36]. MUR reports estimates of foundation SST, or SST at the
149 base of the diurnal thermocline (~5-10m depth). Comparison of in-situ temperature (recorded by
150 HOBO® v2 data loggers), MUR, and other SST products revealed that MUR outperforms other
151 products in estimating in-situ temperature, although it also underestimates the temperature corals
152 experience at depth (S1 Fig). However, due to its temporal coverage and temporal resolution, high

153 spatial resolution, lack of cloud contamination, and smaller method error compared to similar
154 products such as Group for High Resolution SST (GHRSST), MUR was determined to be the ideal
155 SST product for use in the current study.

156 *Site Classification*

157 Multiple thermal parameters were calculated at different temporal resolutions and examined
158 across thirteen lagoonal reef sites (S1 Table). Lagoonal reefs are located between the barrier reef's
159 crest and the mainland, and therefore do not include the seaward facing fore-reef. Instead, lagoonal
160 reefs include nearshore reefs, patch reefs, and the back reef. Four thermal parameters produced
161 distinct environments for the reef sites across the Belize MBRS: average annual maximum
162 temperature (S2A Fig), average annual temperature range (S2B Fig), average annual number of
163 days above the regional bleaching threshold of 29.7°C [9] (S2C Fig), and average annual
164 consecutive days above the regional bleaching threshold (i.e., longest potential thermal stress
165 events) (S2D Fig). A metric that combined all four thermal parameters was generated using
166 ArcGIS[®] in order to assess thermal environments across the Belize MBRS. Data from each of the
167 four parameters in the metric (Table 1) were divided into 8-10 bins (0.5 standard deviations (SD)
168 of the mean) and overlaid on a map of the Belize MBRS. Reefs were not present in areas where
169 the value of any single variable was <1 SD below or >2 SD above the mean (across the entire data
170 set from 2003-2012). For all four parameters, areas that were classified in bins ≥ 1 SD above the
171 mean were designated high temperature parameter (high_{TP}) sites (Fig 1). Moderate temperature
172 parameter (mod_{TP}) sites were classified as areas where all values were 0.5 to 1 SD above the
173 average annual temperature range and the average annual maximum temperature, and within 1 SD
174 of the average annual consecutive days and the average annual number of days above the regional
175 bleaching threshold (Fig 1). Low temperature parameter (low_{TP}) sites were classified as bins that

176 were 0.5 SD above the average to 2 SD below the average for annual temperature range and annual
 177 maximum temperature, and below the average for consecutive and annual days above the regional
 178 bleaching threshold (Fig 1). Using the metric presented in Fig 1, fifteen sites were identified,
 179 thirteen of which were visited and surveyed in November 2014 (the two northernmost high_{TP} sites
 180 were not surveyed as corals were not located within the marked geographic area) (Table 1, Fig 1).

181 **Fig 1. Thermal Regimes and Site Locations**

182 The Belize Mesoamerican Barrier Reef System (MBRS) classified by site type based on four
 183 thermal parameters. Blue, green and red regions represent low_{TP}, mod_{TP}, and high_{TP} areas across
 184 the reef system. Stars indicate surveyed sampling sites.

185 **Table 1. Thermal Parameters Used For Site Classification**

Factor	Min	Mean	Max	SD	low _{TP} Sites	mod _{TP} Sites	high _{TP} Sites
Mean Annual Max Temp	30.2°C	30.6°C	31.3°C	0.27°C	30.2-30.8°C	30.8-30.9°C	30.9-31.3°C
Mean Annual Temp Range	4.4°C	5.2°C	7.1°C	0.69°C	4.4-5.5°C	5.5-5.9°C	5.9-7.1°C
Mean Annual Days Above Bleaching Threshold	20.0 days	40.1 days	78.4 days	14.3 days	20.0-40.1 days	40.1-54.4 days	54.4-78.4 days
Mean Consecutive Days Above Bleaching Threshold	3.0 days	4.8 days	7.5 days	0.92 days	3.0-4.8 days	4.8-5.7 days	5.7-7.5 days

186 Values for the four thermal parameters included in site selection metrics. Values are all averages
 187 from 2003-2012 and include measurements for minimum, mean, maximum, and standard
 188 deviation (SD) for each thermal parameter. The range at which each factor was classified as
 189 low_{TP}, mod_{TP}, or high_{TP} site is also shown.

191 **Benthic surveys**

192 In November 2014, benthic surveys were performed at the thirteen reef sites. Depth of each
193 reef site was standardized to 3-5m. Reef types surveyed included back reefs, patch reefs, and
194 nearshore reefs. A team of three divers surveyed six belt transects (dimension 6 x 10 m) at each
195 site following Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology [37]. Briefly, a
196 diver classified the genus and species of every coral $>6\text{cm}^2$ within 1m of the transect line along a
197 10m transect. The number and size (length, width, and height) of individual colonies of each coral
198 species were recorded on underwater data sheets. The collected data were used to calculate coral
199 species diversity, abundance, richness, and coral life history (following Darling *et al.* [22]) for
200 each site.

201 Additionally, six video belt transects (1 x 20m) were also performed at each site using GoPro®
202 cameras attached to PVC stabilizing apparatuses allowing each diver to stabilize the camera while
203 surveying transects. Video transects were analyzed at the University of North Carolina at Chapel
204 Hill (UNC-Chapel Hill) in a manner similar to the AGRRA method used in the field, except two
205 additional parameters (percent coral cover and coral density) were calculated. Results of the diver
206 and video transect surveys were not significantly different ($p=0.300$). As a result diver and video
207 survey data were pooled at each site when possible. Full details and a comparison of the methods
208 employed are available in S1 Appendix.

209 **Coral life history**

210 Coral species were grouped into four life history strategies as previously described by
211 Darling *et al.* 2012 [22]. In their study, Darling *et al.* 2012 identified four life history guilds for
212 corals based on multivariate trait analysis: competitive, weedy, stress-tolerant, and generalist [22].
213 The four guilds are primarily separated by colony morphology, growth rate, and reproductive rate.
214 The classification was based on a thorough sampling of global Scleractinian coral diversity. Each

215 coral that is included in a guild in Darling *et al.* 2012 [22] was classified into the appropriate guild
216 for this study and comparisons of life history strategies between sites and site types were made.

217 **Chlorophyll-a**

218 Eight-day composite 4-km horizontal resolution *chlorophyll-a* (*chl-a*) estimates over the interval
219 2003-2015 were obtained from NASA's Moderate Resolution Imaging Spectroradiometer (AQUA
220 MODIS) via NOAA's Environmental Research Division's Data Access Program (ERDDAP) [38].
221 Eight-day composite data were selected in order to minimize gaps in data from cloud cover. Unlike
222 the MUR SST data used for temperature calculations, there is no integrated, high-resolution
223 product for *chl-a*. Similar to temperature calculations, monthly and yearly average *chl-a* values
224 were calculated for each survey site (S2E Fig). *Chl-a* is a widely used proxy for primary
225 productivity and nutrient delivery in seawater [39,40], as it is the main photosynthetic pigment
226 present in phytoplankton which can often quickly deplete nutrient concentrations below detectable
227 limits. It has been shown that remotely sensed data, such as *chl-a* concentration, yields better
228 metrics for water quality than traditional measures such as distance from shore and distance from
229 the nearest river [41]. Here, *chl-a* data are used as a proxy for primary production across the Belize
230 MBRS.

231 **Statistical analysis**

232 Standard deviations used for temperature bins and site classification were calculated in
233 ArcGIS[®]. All other statistical analysis were carried out in R 3.2.2 [42]. Transect averaged survey
234 data for species richness, abundance, Shannon diversity, coral cover, coral density, and log-
235 transformed *chl-a* data were analyzed using analyses of variance (ANOVA). Three fixed factors
236 were included in the ANOVA (survey method, site, and site type) for species richness, abundance,
237 and Shannon diversity. Only two fixed factors (site and site type) were included in the ANOVA

238 for coral cover and coral density, since only data from video surveys were used to calculate these
239 averages. Two fixed factors (site and site type) were included in the ANOVA for *chl-a*
240 concentrations since they were calculated using satellite estimates and survey type was not a factor.

241 If factors were significant ($p < 0.050$), a post-hoc Tukey's HSD test was used to evaluate the
242 significance of each pair-wise comparison. Spatial autocorrelation was evaluated using Moran's I
243 [43]. Significant *p-values* for Moran's I ($p < 0.050$) indicate an effect of spatial autocorrelation.
244 Spatial autocorrelation was only a factor for coral cover ($p = 0.040$). To correct for the effect of
245 spatial autocorrelation, the cut-off value for significance within the ANOVA for coral cover was
246 decreased to $p < 0.010$, following Dale and Fortin [44].

247 To visualize coral community differences between site types, non-metric multidimensional
248 scaling (NMDS) ordination was implemented using Bray-Curtis similarity coefficients in the
249 vegan package in R [45]. An optimal stress test was performed to determine the optimal k value
250 ($k = 20$). Resulting NMDS scores were visualized in two-dimensional ordination space. A
251 PERMANOVA test was performed to analyze the site type differences using the *adonis* function
252 in the vegan package in R [45].

253 Linear models tested for the influence of temperature parameters and *chl-a* on the variation
254 observed along NMDS1 and NMDS2 (within and between site type community variations). Linear
255 models were run using the *lm* function in R (R Core Team, 2014). R^2 and *p-values* were calculated
256 for each parameter based on each linear model (S2 Table). For NMDS1, data were also divided by
257 site type in order to assess within site type variation (S3 Table).

258

259 **Ethics statement**

260 All research related to this project was completed under official permit from the Belize
261 Fisheries Department (#000045-14).

262

263 **Results**

264 **Coral community composition**

265 Combined results of AGRRA diver surveys and GoPro[®] video surveys for all thirteen sites
266 revealed that coral species richness varied as a function of site location ($p < 0.001$) as well as site
267 type ($p = 0.002$). Coral abundance was significantly lower at high_{TP} sites compared to low_{TP}
268 ($p = 0.005$) and mod_{TP} ($p = 0.020$) sites, but was not significantly different between low_{TP} and mod_{TP}
269 sites (Fig 2A). Coral cover, Shannon diversity, coral density, and species richness also followed
270 these same patterns ($p \leq 0.020$; Fig 2B-E). NMDS analysis of the ecological parameters showed
271 that community structure was significantly different (stress=0.018, adonis test $p = 0.006$) between
272 high_{TP} sites and low_{TP}/mod_{TP} sites along the NMDS2 axis, but was not different between low_{TP}
273 and mod_{TP} sites ($p > 0.050$) (Fig 3). The most dominant taxa at low_{TP} and mod_{TP} sites were
274 *Orbicella* spp., *Porites* spp., *Undaria* spp., *S. siderea*, and *Pseudodiploria* spp, while at high_{TP}
275 sites they were *Siderastrea* spp., *P. astreiodes*, and *Pseudodiploria* spp. Variation along the
276 NMDS1 axis represents within site type differences while variation along the NMDS2 axis
277 represent between site type differences (Fig 3).

278

279 **Fig 2. Differences in coral community structure across site type**

280 Average coral abundance (A), percent coral cover (B), coral species diversity (C), coral density
281 (D), and coral species richness (E) at each site type. Statistically significant differences ($p < 0.05$)
282 are marked with an *. Blue, green, and red bars (± 1 SE) represent low_{TP}, mod_{TP}, and high_{TP},
283 respectively.

284 **Fig 3. NMDS of coral community variables by site type.**

285 Nonmetric multidimensional scaling (NMDS) plot of coral community differences clustered by
286 site type. Blue circles, green triangles, and red squares represent low_{TP}, mod_{TP}, and high_{TP} site
287 types, respectively.

288

289 Linear modeling of temperature and productivity parameters against NMDS1 and NMDS2
290 revealed that average annual maximum temperature, average annual temperature range, average
291 annual days above the bleaching threshold, and average annual consecutive days above the
292 bleaching threshold all had significant effects on the NMDS1 variation. All four temperature
293 parameters, as well as *chl-a*, also had significant effects on NMDS2 variation (S2 Table; S3 Fig).
294 Average annual consecutive days above the bleaching threshold explained the most variation for
295 NMDS1 and NMDS2 ($R^2=0.1026, 0.604$ respectively; $p < 0.001$ for both; S2 Table; S3 Fig).

296 Linear regressions of temperature parameters and *chl-a* within site types along NMDS1
297 revealed significant effects ($p < 0.050$) of average annual maximum temperature, average annual
298 days above the bleaching threshold, and average annual consecutive days above the bleaching
299 threshold for all site types, average annual temperature range for mod_{TP} and high_{TP} sites, and *chl-*
300 *a* for high_{TP} sites only (S3 Table; S3 Fig). Average annual days above the bleaching threshold
301 yielded the highest R^2 for low_{TP} and mod_{TP} sites, while average annual temperature range yielded
302 the highest R^2 for high_{TP} sites (S3 Table; S3 Fig).

303

304 **Coral life history**

305 Site exhibited a significant effect on the number of corals in each of the four coral life
306 history guilds [22] ($p < 0.001$). The distribution of coral life history strategies differed significantly
307 between low_{TP} and high_{TP} site types ($p = 0.049$; Fig 4), while mod_{TP} sites did not differ from low_{TP}
308 or high_{TP} sites (Fig 4). Overall, there appears to be a pattern of lower abundances of all life history

309 guilds at high_{TP} sites compared to low_{TP} sites. Competitive species were not present and generalist
310 species were only present in very small number at high_{TP} sites.

311 **Fig4. Coral life history strategy by site type**

312 Abundance (count) of corals (± 1 SE) grouped by life history (from Darling *et al.* 2012). Letters
313 'a' and 'b' show significant differences between site types ($p < 0.050$) acquired from post hoc
314 Tukey tests.

315 **Chlorophyll-a**

316 Annual average *chl-a* concentrations varied over time and differed by site type ($p < 0.001$),
317 but were consistently lowest at low_{TP} sites and highest at high_{TP} sites regardless of year (Fig 5A).
318 *Chl-a* concentrations averaged over 2003-2015 were significantly different across all three site
319 types ($p < 0.001$ in all cases). Low_{TP} sites exhibited the lowest average 13-year *chl-a*
320 concentrations. Mod_{TP} sites exhibited average 13-year *chl-a* concentrations that were significantly
321 higher than low_{TP} sites, but significantly lower than high_{TP} sites. High_{TP} sites exhibited
322 significantly higher average 13-year *chl-a* values than both low_{TP} and mod_{TP} sites ($p < 0.001$ in all
323 cases, Fig 5B). The pattern seen in *chl-a* concentrations is positively correlated with the patterns
324 seen in all temperature parameters (*chl-a* and temperature parameters are lowest at low_{TP} sites and
325 highest at high_{TP} sites) (Fig 1, S2 Fig).

326

327 **Fig 5. Average *chl-a* by site type**

328 *Chl-a* concentration by site type (\pm SE) Annual average *chl-a* for low_{TP} (blue), mod_{TP} (green),
329 high_{TP} (red) site types over the interval 2003-2013 (A). *Chl-a* concentrations averaged over the
330 13-year interval (B). Letters x, y, and z indicate results of post hoc Tukey tests showing
331 significant differences in 13-year *chl-a* concentrations across site types ($p < 0.050$).

332

333

334 **Discussion**

335 **Coral community composition**

336 Coral species richness, abundance, diversity, density, and percent cover were all lower at
337 high_{TP} sites compared to low_{TP} and mod_{TP} sites (Fig 2). Differences in coral community
338 composition between high_{TP} sites and low_{TP}/mod_{TP} sites are historically explained by more
339 stressful conditions nearshore and less stressful conditions offshore [46,47]. These nearshore
340 stressors include, but are not limited to temperature, eutrophication, sedimentation, and wave
341 energy [46,47]. Our findings suggest that lower coral species richness, diversity, abundance,
342 percent cover, and density at high_{TP} sites may be driven by high thermal variability, elevated
343 maximum temperatures, and prolonged duration of exposure to temperatures above the bleaching
344 threshold; three variables that have been shown to cause coral community decline
345 [13,29,48,49,50]. These temperature parameters were more strongly correlated with changes in
346 coral community composition between site types than with *chl-a* (S3 Fig), indicating that they
347 likely play a greater role in determining coral community composition than productivity. High
348 weekly thermal variability has also been shown to correlate with low coral cover on nearshore
349 reefs in the Florida Keys [13]. Therefore, differences in thermal variability observed across site
350 types may have influenced coral community composition in Belize.

351 Our findings are contrary to the results of Soto *et al.* (2011) [13], which showed that reef
352 sites with moderate temperature variability (equivalent to mod_{TP} sites in the current study) in
353 Florida had higher coral cover than sites exposed to low (offshore deep reefs) or high
354 temperature variability. Soto *et al.* (2011) [13] suggests that corals exposed to moderate weekly
355 thermal variation are able to acclimatize to a wide range of environmental conditions, making them
356 more resilient than corals that experience less variation. At the same time, corals exposed to
357 extremely high thermal variation generally do not survive [13]. Our results may contrast with that
358 of Soto *et al.* (2011) because fore reef locations were not included in the present study (i.e.,

359 low_{TP} sites are located in the back reef). Our high_{TP} sites follow the same pattern seen in Soto *et*
360 *al.* (2011) [13] as they have lower coral cover than mod_{TP} sites (Fig 2).

361 Our results also contrast those of Lirman and Fong (2007) [21], which showed that
362 nearshore reefs (equivalent to our high_{TP} sites) exhibited higher coral cover and growth rates than
363 offshore reefs (equivalent to our low_{TP} sites) in the Florida Keys. Interestingly, these nearshore
364 Florida reefs also experienced lower water quality than the offshore reefs [21]. The authors
365 hypothesized that higher coral cover and growth rates on nearshore reefs were due to the ability
366 of some corals to switch trophic mode under adverse conditions [21], a pattern that has been
367 observed in previous studies, but was not quantified in the current study [51,52]. Differences in
368 coral community composition between the Florida Reef tract and the Belize MBRS may explain
369 our contrasting results in coral cover as nearshore patch reefs in Florida appear to have relatively
370 high numbers of *Orbicella spp.* [21], whereas high_{TP} sites in Belize were almost void of this
371 species.

372 **Life history strategies**

373 In the current study, high_{TP} sites contained no competitive species, few generalists, and
374 were dominated by stress-tolerant and weedy genera, while both low_{TP} sites and mod_{TP} sites
375 contained all 4 life history types (Fig 4). Low_{TP} sites contained all four life history strategies in
376 roughly equal proportions. Mod_{TP} sites were similar but with fewer competitive species than low_{TP}
377 sites, and high_{TP} sites had comparatively fewer of all four life histories, but were dominated by
378 weedy and stress tolerant genera. Shifts toward weedy and stress tolerant genera under climate
379 change conditions were predicted by Darling *et al.* (2012) [22], and have been recorded in many
380 areas of the world [29,53], including the Caribbean [25,31,54]. Even in the face of region-wide
381 decline in coral cover and decrease in abundance of competitively dominant species [6], some

382 weedy species, such as *Porites astreoides*, are actually increasing in prevalence within the
383 Caribbean [31]. This weedy coral species is likely able to succeed in high stress environments due
384 to its ability to brood and mature quickly, which allows it to rapidly colonize a recently disturbed
385 area [22,31].

386 In contrast, a stress-tolerant species such as *S. siderea* is likely able to survive in high_{TP}
387 environments due to its massive size and long life span, which allows it to sustain a population in
388 the absence of successful recruitment. This can increase the long-term survival potential of this
389 species in harsh conditions [55]. These two contrasting strategies seem most effective in high_{TP}
390 environments (Fig 4), and are likely to be most effective in future conditions as the oceans continue
391 to warm. This prediction is corroborated by Loya *et al.* (2001) [29], who showed that mounding
392 (e.g., *S. siderea*) and encrusting (e.g., *P. astreoides*) species survived a mass bleaching event in
393 1997-1998 better than corals of other morphologies (e.g., branching). Ten years after the bleaching
394 event these same types of coral continued to dominate. However, some branching species
395 recovered and increased in abundance [56]. In the current study, branching species were almost
396 non-existent in high_{TP} sites, which indicates that these sites have experienced a recent thermal
397 stress event or are exposed to chronic stress (e.g., temperature, eutrophication) that prevents such
398 species from succeeding in these environments. It is also possible that high_{TP} sites are more
399 frequently disturbed than both low_{TP} and mod_{TP} sites. Disturbances such as bleaching events,
400 eutrophication, sedimentation, and overfishing are known to cause declines in coral cover, species
401 richness, and diversity [29,30]. These more disturbed or impacted reefs can then become
402 dominated by stress-tolerant corals and corals that quickly colonize areas after a perturbation (i.e.,
403 weedy corals) [13,29,30,57], as observed in the current study (Fig 4). Historical and/or geological
404 investigation of reef assemblages (i.e., through pit excavating or coring of reef framework

405 [9,32,34]) would be a useful next step, as it would allow insight into how reef communities within
406 the three thermal regimes have changed after disturbances and over long periods of time.

407 **Influence of primary productivity on coral community composition**

408 Cross-reef *chl-a* concentrations follow the same patterns as temperature (elevated
409 nearshore and decreasing with increasing distance from the Belize coast) (Fig 1, S2 Fig). This
410 means that reefs with higher *chl-a* concentrations have lower coral species richness, abundance,
411 diversity, density, and percent cover. This supports a previous finding that shows a strong
412 negative relationship between *chl-a* and coral cover, species richness, and abundance at
413 nearshore reefs on the Great Barrier Reef (GBR) [58]. However, our results reveal that *chl-a*
414 concentrations are not strongly correlated ($R^2=0.040$) with changes in coral community structure
415 (e.g., percent cover, abundance, diversity, species richness, and density) across site types (S5H
416 Fig), suggesting that *chl-a* concentrations may not best explain differences in community
417 composition between site types in Belize. This may be due to spatial scale (e.g., we focused on
418 nearshore, patch reef, and back reef sites as opposed to exclusively nearshore sites) [58], or the
419 coarse scale of the *chl-a* dataset (4 km x 4 km grid; each survey site is <1 km). Focusing on
420 variation within nearshore (high_{TP}) sites, we do see a correlation between *chl-a* and changes in
421 coral community structure (S4H Fig), which supports results from previous work [58,59].

422 **Other potential factors influencing coral community structure across reef types**

423 *Eutrophication*

424 Eutrophication has led to local degradation of reefs [60,61,62]. However, larger scale
425 (regional) reef degradation due to nutrients alone has not been quantitatively shown [63].

426 Wooldridge (2009) [64] demonstrates that lower water quality (e.g., higher nutrient

427 concentrations) are linked to lower bleaching thresholds on nearshore reefs in Australia. If
428 bleaching thresholds are depressed at high_{TP} sites for some species, it may help explain lower
429 diversity measured at these sites, as they experience warmer temperatures and spend more time
430 above the regional bleaching threshold than do mod_{TP} and low_{TP} sites (S2 Fig). While *chl-a* does
431 not correlate well with changes in coral community structure in this study (S3 Fig), it should be
432 noted that *chl-a* is an estimate of nutrient delivery and primary productivity, not a measurement
433 of the concentration of any one nutrient pool. Due to this limitation, manipulative field
434 experiments such as Vega-Thurber et al. (2014)[65] and Zaneveld et al. (2016)[66] are needed to
435 understand the influence of nutrients on coral community structure and bleaching thresholds at
436 local scales.

437 *Sedimentation*

438 Coastal (nearshore) reefs throughout Belize are influenced by runoff from smaller local
439 rivers, and reefs in southern Belize experience additional runoff and river plumes originating
440 from larger watersheds in Honduras and Guatemala [67,68]. It has been previously shown that
441 *Orbicella faveolata* corals on reefs with higher sedimentation rates exhibited suppressed skeletal
442 extension rates for a longer duration than corals on reefs with lower sedimentation rates
443 following the 1998 bleaching event in Belize [69]. In contrast, increased sedimentation did not
444 affect skeletal extension of *S. siderea* or *P. astreoides* corals in Puerto Rico [70]. The results of
445 these two studies suggest that there may be species-specific responses to increased sedimentation
446 rates. In Barbados, reefs with high sedimentation rates were dominated by coral species with
447 high recruitment and high natural mortality (e.g., *P. astreoides*) and reefs with lower
448 sedimentation rates were dominated by coral species with lower recruitment and low natural

449 mortality (e.g., boulder corals) [71]. As sedimentation rate was not quantified in this study, the
450 impacts of sedimentation on coral community structure are not clear.

451 *Circulation and wave energy*

452 The Belize MBRS lies west of the Honduras Gyre, a hydraulic feature that recirculates
453 water inside the Cayman basin [72]. The coastal waters of northern Belize are influenced by the
454 Cayman and Yucatan currents, which move water northwest up the coastline toward Mexico
455 [72,73,74,75]. In central and southern Belize, current velocities are lower and dominant
456 circulation patterns are less consistent throughout the year [74]. However, currents appear to
457 bring water and potentially pollution, nutrients, or sediment plumes from coastal Honduras and
458 Guatemala west to southern Belize where they recirculate before slowly moving northward
459 [67,68,74,75,76,77,78]. These circulation patterns have the potential to influence the stress
460 tolerance of corals across sites and latitude in the current study. Our results reveal no spatial
461 autocorrelation between sites for any of our measured variables with the exception of *chl-a*
462 suggesting that the influence of these currents may be minimal. Additionally, wave energy may
463 play a role in shaping coral communities. Wave energy may be elevated at low_{TP} sites as they are
464 located near channels in the fore reef and may not be as sheltered by the reef crest as other
465 mod_{TP}. Similarly, wave energy may be elevated at high_{TP} sites due to the large fetch between the
466 reef crest and nearshore reefs and the prevailing wind direction from offshore to inshore.

467 *Light*

468 Irradiance (light intensity) has been shown to decrease along an offshore-nearshore
469 gradient on the GBR as *chl a* concentrations increase [79]. *Chlorophyll-a* concentrations increase
470 with proximity to shore in Belize (Fig 1), so this pattern of decreasing light intensity towards the

471 nearshore likely holds for Belize as well. However, in southern Belize offshore reefs (and
472 nearshore reefs) are subject to seasonal sedimentation and runoff from larger rivers in Honduras
473 and Guatemala [77,78]. Irradiance is a known stressor, proven to cause coral bleaching alone or
474 in consort with elevated temperatures [80]. Although depth was held constant in the present
475 study, it is possible that differing light levels both between site types and between individual
476 sites may influence coral community composition across the site types investigated in the current
477 study.

478 *Proximity to human populations*

479 Declining health of coral reefs worldwide has been linked to land-based stressors
480 including nutrients and human use and exploitation (e.g., overfishing) [60,80,81] as well as
481 proximity to sources of these stressors (e.g., major human population centers) [82]. However, not
482 all reefs that are near to or influenced by land-based stressors are unhealthy [21,83]. Some of the
483 study sites were within close proximity to a major human population center, particularly the
484 high_{TP} sites (populations of major towns and cities in Belize can be seen in S4 Table). Analysis
485 of spatial autocorrelation revealed no significant differences between high_{TP} sites or between
486 high_{TP} sites and sites that were further offshore, suggesting that proximity to human population
487 centers did not have a major impact on coral community composition.

488 **Conclusions**

489 High_{TP} reefs exhibit lower coral diversity, abundance, species richness, and cover than do
490 low_{TP} and mod_{TP} reefs in Belize. These high_{TP} reefs are exposed to higher annual temperatures,
491 greater temperature variability, more time above the regional bleaching threshold, elevated *chl-a*
492 concentrations, and likely increased sedimentation rates and lower flow than low_{TP} and mod_{TP}
493 reefs. Temperature parameters, most notably time spent above the bleaching threshold, correlate

494 best with differences in coral community structure. In addition, stress-tolerant and weedy coral
495 life history strategies dominate at high_{TP} reefs. Due to exposure to generally more stressful
496 environmental conditions, high_{TP} reefs may offer a snapshot into the projected future of coral
497 reefs as they become increasingly exposed to local (pollution, runoff, land-use change, and
498 overpopulation) and global (warming and acidification) stressors. Previously, such reefs have
499 been suggested as possible refugia against climate change [84]. Globally, this would mean a shift
500 towards dominance of stress-tolerant and weedy corals [53]. Such a shift would dramatically
501 impact the structure and function of reefs, essentially creating novel ecosystems [85]. High_{TP}
502 reefs should be protected in addition to more pristine reefs in order to improve conservation
503 success [35]. More pristine reefs should be protected as they contain more diversity and provide
504 more ecosystem services than do high_{TP} reefs [86]. However, high_{TP} reefs host coral holobionts
505 that may be best suited to survive in future ocean conditions. To ensure survival and future
506 success of reefs while maintain current diversity both heavily impacted and pristine ecosystems
507 must be protected. The results of the current study highlight the need to better protect and
508 understand impacted nearshore reef systems, including investigations into what conditions allow
509 more sensitive species (e.g., competitive and generalist) to survive and persist on nearshore reefs.

510 **Data Accessibility**

511 All data are archived on PANGAEA at the following DOI:
512 doi.pangaea.de/10.1594/PANGAEA.859972

513

514 **Supporting Information**

515

516 **S1 Appendix. Additional detail of AGGRA and video survey methods**

517

518 **S1 Fig. *In situ* temperature versus satellite SST products**

519 A comparison of *in situ* temperature and MUR SST. *In situ* loggers were collected from 6 sites
520 along the BBRS (site numbers are listed in the gray headers above each panel). Each panel
521 shows a month by month comparison of *in situ* logger measurements and SST products. Zero on

522 the y-axis represents the average value for the Hobo Pro V2 loggers at each site. Red errors bars
523 the standard deviation over a month for each logger. Gray squares show average values for an
524 additional *in situ* logger that was placed at the site (± 1 standard deviation). Blue, green, and
525 black symbols show monthly average values for various SST products (± 1 standard deviation).

526

527 **S2 Fig. Temperature parameter and *chl-a* maps**

528 Maps showing the 4 parameters used to calculate site type: yearly maximum temperature (A),
529 Mean annual temperature range (B), Annual mean number of days above the bleaching threshold
530 (C), Annual mean consecutive days above the bleaching threshold (D), and 13 year mean *chl-a*
531 concentration from 2002-2015 (E). Maps generated from means calculated from daily satellite
532 measurements taken from Jan 2003-Dec 2012.

533

534 **S3 Fig. Linear regression of Physical Parameters vs. NMDS1 and NMDS2 by site type**

535 Linear regression of average annual max temp (A, F), average annual temp range (B, G), average
536 annual days above the bleaching threshold (C, H), average annual consecutive days above the
537 bleaching threshold (D, I), and *Chl-a* (E, J) vs. NMDS1 and NMDS2 by site type. R^2 values are
538 included for each regression that yielded a significant slope ($p < 0.05$).

539

540

541 **S1 Table. Site locations**

542 Summary of survey sites, how they were classified, and where they were located (latitude/
543 longitude).

544

545 **S2 Table. p -values and R^2 from Linear Regression of Physical Parameters vs. NMDS1 and 546 NMDS2**

547 Summary of p and R^2 values for physical parameters vs. NMDS1 and NMDS 2. Significant p -
548 values are in bold.

549

550 **S3 Table. p -values and R^2 for Linear Regression of Physical Parameters vs. NMDS1 by Site 551 Type**

552 Summary of p and R^2 values for physical parameters vs. NMDS1 by site type. Significant p -
553 values are in bold.

554

555 **S4 Table. Population of major towns in Belize**

556 Populations of major towns in Belize from 2010-2015. Data source: Statistical Institute of
557 Belize.

558

559 **Author Contributions**

560 Planned and designed the field surveying: JHB KDC. Identified sites and designed temperature
561 metric: JHB. Downloaded and manipulated the temperature data FPL. Carried out field work and
562 surveys: JHB JET TAC HEA SWD KDC. Analyzed the data: JHB JET TAC SWD FPL. Wrote/
563 edited the paper: JHB JET TAC HEA SWD FPL KDC.

564

565 **Acknowledgements**

566 We thank D. Hoer, L. Speare, and A. Knowlton for laboratory assistance, P. McDaniel for
567 providing GIS expertise, and C. Berger and S. Hackerott for assistance with coding. We also
568 thank NASA JPL for access to MUR SST data used in this paper, NOAA ERDAAP for access to
569 *chl-a* and temperature data, Belize Fisheries Department for issuing permits that has allowed this
570 research to occur, and Garbutt's Marine for providing local expert guides and boats for field
571 research. The authors declare that no conflict of interests exists.

572

573 **References**

- 574 1. Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. (2003) Climate change, human impacts,
575 and the resilience of coral reefs. *Science* 301: 929-933.
- 576 2. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. (2007) Coral Reefs under
577 Rapid Climate Change and Ocean Acidification. *Science* 318: 1737-1742.
- 578 3. Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, et al. (2013) Limiting global warming to 2 °C is
579 unlikely to save most coral reefs. *Nature Climate Change* 3: 165-170.
- 580 4. Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O (2005) Global assessment of
581 coral bleaching and required rates of adaptation under climate change. *Global Change Biology*
582 11: 2251-2265.
- 583 5. Chollett I, Mumby PJ, Muller-Karger FE, Hu CM (2012) Physical environments of the Caribbean Sea.
584 *Limnology and Oceanography* 57: 1233-1244.
- 585 6. Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in
586 Caribbean corals. *Science* 301: 958-960.
- 587 7. Jokiel PL, Coles SL (1990) Response of Hawaiian and other Indo-Pacific reef corals to elevated
588 temperature. *Coral Reefs* 8: 155-162.
- 589 8. D'Croz L, Mate JL, Oke JE (2001) Responses to elevated sea water temperature and UV radiation in the
590 coral *Porites lobata* from upwelling and non-upwelling environments on the Pacific coast of
591 Panama. *Bulletin of Marine Science* 69: 203-214.
- 592 9. Aronson R, Precht W, Toscano M, Koltes K (2002) The 1998 bleaching event and its aftermath on a
593 coral reef in Belize. *Marine Biology* 141: 435-447.
- 594 10. Wooldridge S, Done T, Berkelmans R, Jones R, Marshall P (2005) Precursors for resilience in coral
595 communities in a warming climate: a belief network approach. *Marine Ecology Progress Series*
596 295: 157-169.
- 597 11. Donner SD, Knutson TR, Oppenheimer M (2007) Model-based assessment of the role of human-
598 induced climate change in the 2005 Caribbean coral bleaching event. *Proceedings of the*
599 *National Academy of Sciences of the United States of America* 104: 5483-5488.
- 600 12. van Hooedonk R, Maynard JA, Liu Y, Lee S-K (2015) Downscaled projections of Caribbean coral
601 bleaching that can inform conservation planning. *Global Change Biology*: n/a-n/a.
- 602 13. Soto I, Muller Karger F, Hallock P, Hu C (2011) Sea surface temperature variability in the Florida Keys
603 and its relationship to coral cover. *Journal of Marine Biology* 2011.
- 604 14. Oliver TA, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal
605 tolerance? *Coral Reefs* 30: 429-440.
- 606 15. Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, et al. (2013) Genomic basis for coral
607 resilience to climate change. *Proceedings of the National Academy of Sciences* 110: 1387-1392.
- 608 16. Pineda J, Starczak V, Tarrant A, Blythe J, Davis K, et al. (2013) Two spatial scales in a bleaching event:
609 Corals from the mildest and the most extreme thermal environments escape mortality.
610 *Limnology and Oceanography* 58: 1531-1545.
- 611 17. Castillo KD, Ries JB, Weiss JM, Lima FP (2012) Decline of forereef corals in response to recent
612 warming linked to history of thermal exposure. *Nature Climate Change* 2: 756-760.
- 613 18. Carilli J, Donner SD, Hartmann AC (2012) Historical temperature variability affects coral response to
614 heat stress. *Plos ONE* 7: e34418.
- 615 19. van Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, et al. (2012) Climate-change refugia in the
616 sheltered bays of Palau: analogs of future reefs. *Ecology and Evolution* 2: 2474-2484.
- 617 20. Fine M, Gildor H, Genin A (2013) A coral reef refuge in the Red Sea. *Global Change Biology* 19: 3640-
618 3647.

- 619 21. Lirman D, Fong P (2007) Is proximity to land-based sources of coral stressors an appropriate measure
620 of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution Bulletin* 54: 779-
621 791.
- 622 22. Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies
623 of reef corals from species traits. *Ecology Letters* 15: 1378-1386.
- 624 23. Grime JP, Pierce S (2012) *The evolutionary strategies that shape ecosystems*: John Wiley & Sons.
- 625 24. Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under
626 multiple stressors. *Global Change Biology* 19: 1930-1940.
- 627 25. Alvarez-Filip L, Dulvy NK, Côté IM, Watkinson AR, Gill JA (2011) Coral identity underpins architectural
628 complexity on Caribbean reefs. *Ecological Applications* 21: 2223-2231.
- 629 26. Greenstein B, Curran H, Pandolfi J (1998) Shifting ecological baselines and the demise of *Acropora*
630 *cervicornis* in the western North Atlantic and Caribbean Province: a Pleistocene perspective.
631 *Coral Reefs* 17: 249-261.
- 632 27. Buglass S, Donner SD, Alemu JB (2016) A study on the recovery of Tobago's coral reefs following the
633 2010 mass bleaching event. *Marine Pollution Bulletin* 104: 198-206.
- 634 28. Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs:
635 region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B:*
636 *Biological Sciences*: rspb20090339.
- 637 29. Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, et al. (2001) Coral bleaching: the winners and the
638 losers. *Ecology Letters* 4: 122-131.
- 639 30. Van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after
640 coral bleaching. *Mar Ecol Prog Ser* 434: 67-76.
- 641 31. Green D, Edmunds P, Carpenter R (2008) Increasing relative abundance of *Porites astreoides* on
642 Caribbean reefs mediated by an overall decline in coral cover. *Marine Ecology Progress Series*
643 359: 1-10.
- 644 32. Cramer KL, Jackson JB, Angioletti CV, Leonard-Pingel J, Guilderson TP (2012) Anthropogenic mortality
645 on coral reefs in Caribbean Panama predates coral disease and bleaching. *Ecology Letters* 15:
646 561-567.
- 647 33. Cramer K. Changes in coral communities and reef environments over the past few centuries in
648 Caribbean Panama; 2010. American Geophysical Union, 2000 Florida Ave., N. W. Washington DC
649 20009 USA.
- 650 34. Cramer KL, Leonard-Pingel JS, Rodríguez F, Jackson JB (2015) Molluscan subfossil assemblages reveal
651 the long-term deterioration of coral reef environments in Caribbean Panama. *Marine Pollution*
652 *Bulletin* 96: 176-187.
- 653 35. Game ET, McDonald-Madden E, Puotinen ML, Possingham HP (2008) Should we protect the strong
654 or the weak? Risk, resilience, and the selection of marine protected areas. *Conservation Biology*
655 22: 1619-1629.
- 656 36. Chin TM, Vazquez J, Armstrong E (2013) A multi-scale, high-resolution analysis of global sea surface
657 temperature. *Algorithm Theoretical Basis Document*, Version 1: 13.
- 658 37. Ginsburg R, Lang J (2003) Status of coral reefs in the western Atlantic: Results of initial surveys,
659 Atlantic and Gulf Rapid Reef Assessment (AGRRRA) program. *Atoll Research Bulletin* 496.
- 660 38. Simons R (2011) ERDDAP—The Environmental Research Division's Data Access Program. Pacific
661 Grove CA: NOAA/NMFS/SWFSC/ERD.
- 662 39. Bell P (1992) Eutrophication and coral reefs—some examples in the Great Barrier Reef lagoon. *Water*
663 *Research* 26: 553-568.
- 664 40. Bell PRF, Elmetri I, Lapointe BE (2014) Evidence of Large-Scale Chronic Eutrophication in the Great
665 Barrier Reef: Quantification of Chlorophyll a Thresholds for Sustaining Coral Reef Communities.
666 *AMBIO* 43: 361-376.

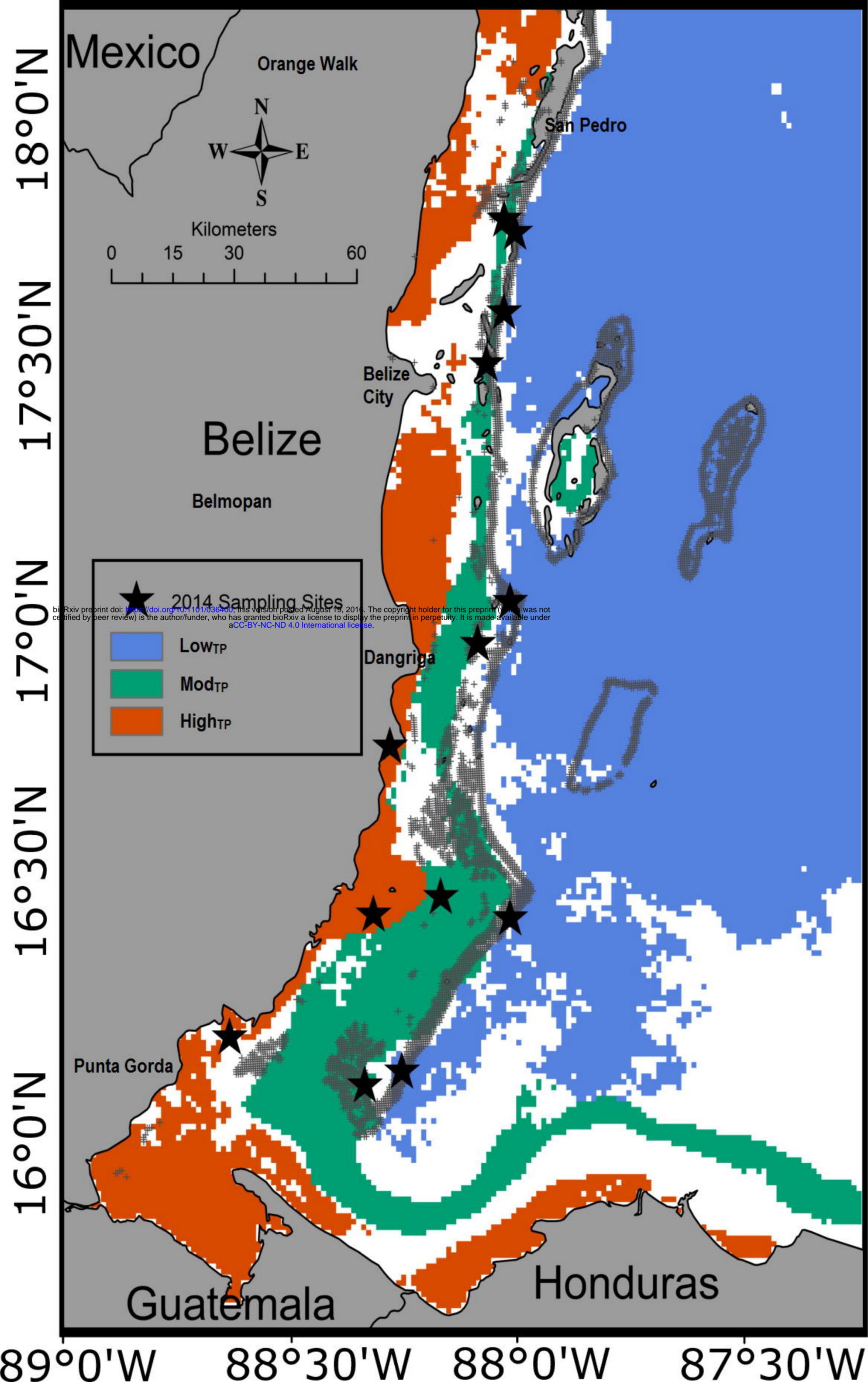
- 667 41. Polónia ARM, Cleary DFR, de Voogd NJ, Renema W, Hoeksema BW, et al. (2015) Habitat and water
668 quality variables as predictors of community composition in an Indonesian coral reef: a multi-
669 taxon study in the Spermonde Archipelago. *Science of The Total Environment* 537: 139-151.
- 670 42. Team RC (2014) R: A language and environment for statistical computing. R Foundation for Statistical
671 Computing, Vienna, Austria, 2012. ISBN 3-900051-07-0.
- 672 43. Gittleman JL, Kot M (1990) Adaptation: statistics and a null model for estimating phylogenetic
673 effects. *Systematic Biology* 39: 227-241.
- 674 44. Dale MR, Fortin M-J (2002) Spatial autocorrelation and statistical tests in ecology. *Ecoscience*: 162-
675 167.
- 676 45. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. (2013) Package ‘vegan’. R Packag ver
677 254: 20-28.
- 678 46. Cortés J (1990) The coral reefs of Golfo Dulce, Costa Rica: distribution and community structure:
679 Citeseer.
- 680 47. Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier
681 Reef. *Coral Reefs* 1: 95-107.
- 682 48. McClanahan T, Maina J (2003) Response of coral assemblages to the interaction between natural
683 temperature variation and rare warm-water events. *Ecosystems* 6: 551-563.
- 684 49. Thompson D, Van Woesik R (2009) Corals escape bleaching in regions that recently and historically
685 experienced frequent thermal stress. *Proceedings of the Royal Society of London B: Biological*
686 *Sciences* 276: 2893-2901.
- 687 50. McClanahan TR, Ateweberhan M, Omukoto J (2008) Long-term changes in coral colony size
688 distributions on Kenyan reefs under different management regimes and across the 1998
689 bleaching event *Marine Biology* 153: 755-768.
- 690 51. Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals.
691 *Nature* 440: 1186-1189.
- 692 52. Anthony K (1999) Coral suspension feeding on fine particulate matter. *Journal of Experimental*
693 *Marine Biology and Ecology* 232: 85-106.
- 694 53. McClanahan TR, Graham NA, Darling ES (2014) Coral reefs in a crystal ball: predicting the future from
695 the vulnerability of corals and reef fishes to multiple stressors. *Current Opinion in Environmental*
696 *Sustainability* 7: 59-64.
- 697 54. Aronson RB, Macintyre IG, Wapnick CM, O'Neill MW (2004) Phase shifts, alternative states, and the
698 unprecedented convergence of two reef systems. *Ecology* 85: 1876-1891.
- 699 55. Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean
700 corals. *Ecology* 81: 2250-2263.
- 701 56. Wild C, Hoegh-Guldberg O, Naumann MS, Colombo-Pallotta MF, Ateweberhan M, et al. (2011)
702 Climate change impedes scleractinian corals as primary reef ecosystem engineers. *Marine and*
703 *Freshwater Research* 62: 205-215.
- 704 57. Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage
705 composition do not ensure persistence of reef functionality. *Scientific reports* 3.
- 706 58. Van Woesik R, Tomascik T, Blake S (1999) Coral assemblages and physico-chemical characteristics of
707 the Whitsunday Islands: evidence of recent community changes. *Marine and Freshwater*
708 *Research* 50: 427-440.
- 709 59. West K, Van Woesik R (2001) Spatial and temporal variance of river discharge on Okinawa (Japan):
710 inferring the temporal impact on adjacent coral reefs. *Marine Pollution Bulletin* 42: 864-872.
- 711 60. Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and
712 synthesis. *Marine Pollution Bulletin* 50: 125-146.
- 713 61. Marubini F, Atkinson MJ (1999) Effects of lowered pH and elevated nitrate on coral calcification.
714 *Marine Ecology Progress Series* 188: 117-121.

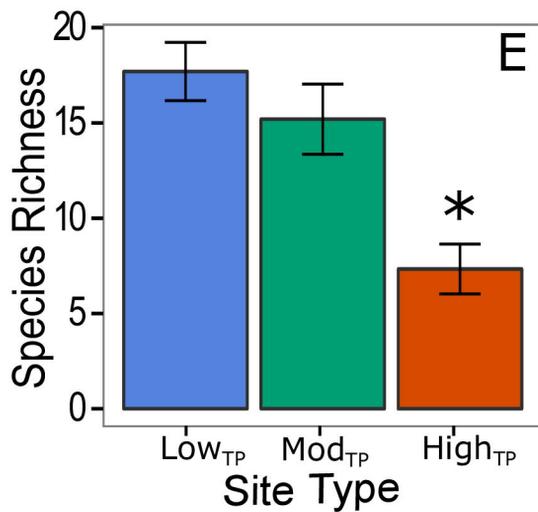
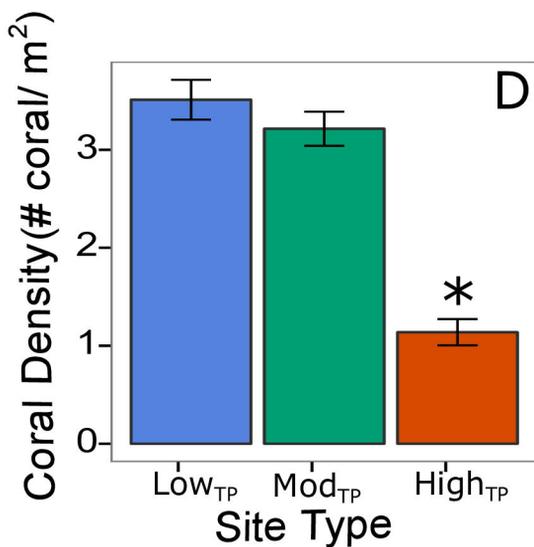
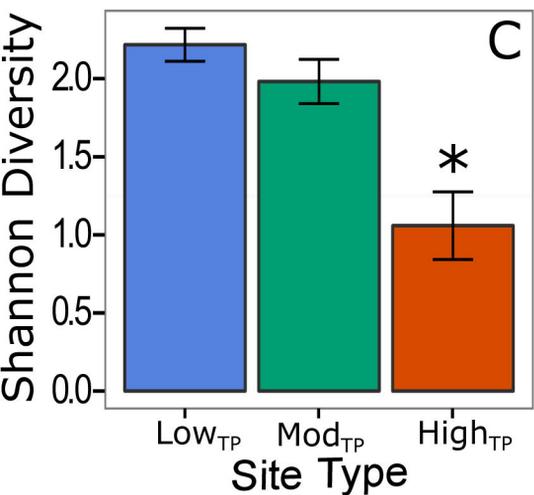
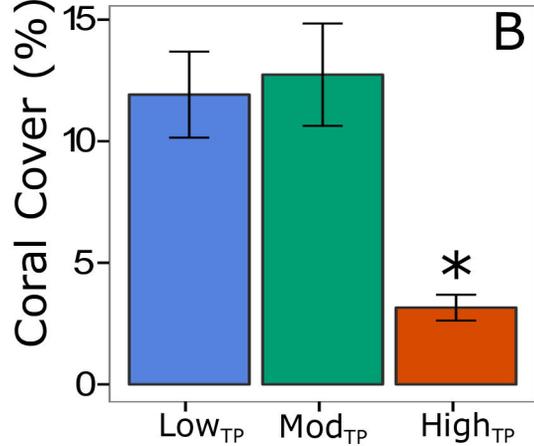
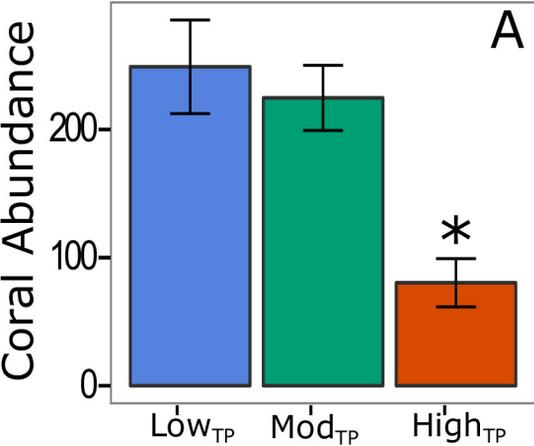
- 715 62. Wooldridge S (2009) A new conceptual model for the enhanced release of mucus in symbiotic reef
716 corals during 'bleaching' conditions. *Marine Ecology Progress Series* 396: 145-152.
- 717 63. Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline?
718 *Estuaries* 25: 743-766.
- 719 64. Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for the
720 inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin* 58: 745-751.
- 721 65. Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, McMinds R, et al. (2014) Chronic nutrient
722 enrichment increases prevalence and severity of coral disease and bleaching. *Global Change*
723 *Biology* 20: 544-554.
- 724 66. Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, McMinds R, et al. (2016) Overfishing and nutrient
725 pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature*
726 *communications* 7.
- 727 67. Paris CB, Cherubin LM (2008) River-reef connectivity in the Meso-American Region. *Coral Reefs* 27:
728 773-781.
- 729 68. Carilli JE, Prouty NG, Hughen KA, Norris RD (2009) Century-scale records of land-based activities
730 recorded in Mesoamerican coral cores. *Marine Pollution Bulletin* 58: 1835-1842.
- 731 69. Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to
732 bleaching. *Plos ONE* 4: e6324.
- 733 70. Torres JL, Morelock J (2002) Effect of terrigenous sediment influx on coral cover and linear extension
734 rates of three Caribbean massive coral species. *Caribbean Journal of Science* 38: 222-229.
- 735 71. Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals.
736 *Marine Biology* 114: 625-631.
- 737 72. Carrillo L, Johns EM, Smith RH, Lamkin JT, Largier JL (2015) Pathways and Hydrography in the
738 Mesoamerican Barrier Reef System Part 1: Circulation. *Continental Shelf Research* 109: 164-176.
- 739 73. Sheng J, Tang L (2003) A numerical study of circulation in the western Caribbean Sea. *Journal of*
740 *Physical Oceanography* 33: 2049-2069.
- 741 74. Tang L, Sheng J, Hatcher BG, Sale PF (2006) Numerical study of circulation, dispersion, and
742 hydrodynamic connectivity of surface waters on the Belize shelf. *Journal of Geophysical*
743 *Research: Oceans* 111.
- 744 75. Sheng J, Tang L (2004) A two-way nested-grid ocean-circulation model for the Meso-American
745 Barrier Reef System. *Ocean Dynamics* 54: 232-242.
- 746 76. Paris CB, Chérubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on
747 population connectivity. *Marine Ecology Progress Series* 347: 285-300.
- 748 77. Andrefouet S, Mumby PJ, Mcfield M, Hu C, Muller-Karger RE (2002) Revisiting coral reef connectivity.
749 *Coral Reefs* 21: 43-48.
- 750 78. Prouty N, Hughen K, Carilli J (2008) Geochemical signature of land-based activities in Caribbean coral
751 surface samples. *Coral Reefs* 27: 727-742.
- 752 79. Cooper TF, Uthicke S, Humphrey C, Fabricius KE (2007) Gradients in water column nutrients,
753 sediment parameters, irradiance and coral reef development in the Whitsunday Region, central
754 Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 74: 458-470.
- 755 80. Brown BE (1997) Coral bleaching: causes and consequences. *Coral Reefs* 16 suppl: s129-s138.
- 756 81. Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. (2001) Historical overfishing and
757 the recent collapse of coastal ecosystems. *Science* 293: 629-637.
- 758 82. Burke LM, Maidens J, Spalding M, Kramer P, Green E (2004) *Reefs at Risk in the Caribbean*: World
759 Resources Institute Washington, DC.
- 760 83. Perry C, Larcombe P (2003) Marginal and non-reef-building coral environments. *Coral Reefs* 22: 427-
761 432.

- 762 84. Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, et al. (2012) Climate-change refugia in the
763 sheltered bays of Palau: analogs of future reefs. *Ecology and evolution* 2: 2474-2484.
764 85. Graham NAJ, Cinner JE, Norström AV, Nyström M (2014) Coral reefs as novel ecosystems: embracing
765 new futures. *Current Opinion in Environmental Sustainability* 7: 9-14.
766 86. Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecological*
767 *Economics* 29: 2151-2233.

768

769





NMDS2

k=20

stress=0.0183996

adonis p=0.006

Site Type

- LOW_{TP}
- ▲ Mod_{TP}
- High_{TP}

NMDS1

