

The relative influence of sea surface temperature anomalies on the benthic composition of an Indo-Pacific and Caribbean coral reef over the last decade

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22 Wakatobi,

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32 **Abstract**

33 Rising ocean temperatures are the primary driver of coral reef declines throughout the tropics.
34 Such declines include reductions in coral cover that facilitate the monopolisation of the
35 benthos by other taxa such as macroalgae, resulting in reduced habitat complexity and
36 biodiversity. Long term monitoring projects present rare opportunities to assess how sea
37 surface temperature anomalies (SSTAs) influence changes in the benthic composition of
38 coral reefs across distinct locations. Here, using extensively monitored coral reef sites from
39 Honduras (in the Caribbean Sea), and from the Wakatobi National Park located in the centre
40 of the coral triangle of Indonesia, we assess the impact of global warming on coral reef
41 benthic compositions over the period 2012-2019. Bayesian Generalised Linear Mixed effect
42 Models revealed increases in sponge, and hard coral coverage through time, while rubble
43 coverage decreased at the Indonesia location. Conversely, the effect of sea surface
44 temperature anomalies (SSTA) did not predict any changes in benthic coverage. At the
45 Honduras location, algae and soft coral coverage increased through time, while hard coral
46 and rock coverage were decreasing. The effects of SSTA at the Honduras location included
47 increased rock coverage, but reduced sponge coverage, indicating disparate responses
48 between both systems under SSTAs. However, redundancy analyses showed intra-location
49 site variability explained the majority of variance in benthic composition over the course of
50 the study period. Our findings show that SSTAs have differentially influenced the benthic
51 composition between the Honduras and the Indonesia coral reefs surveyed in this study.
52 However, large intra-location variance which explains the benthic composition at both
53 locations indicates that localised processes have a predominant role for explaining benthic
54 composition over the last decade. The sustained monitoring effort is critical for understanding
55 how these reefs will change in their composition as global temperatures continue to rise
56 through the Anthropocene.

57

58 **Introduction**

59 Coral reefs harbour the highest levels of biodiversity of all marine ecosystems (Fisher et al.
60 2015), performing paramount roles in the stability of ocean life (Oliver et al. 2015; Benkwitt
61 et al. 2020). In addition, the extraordinary complexity of coral reefs sustain a range of key
62 ecosystem services to human wellbeing, including food security, storm protection, and
63 economic benefits relevant to hundreds of millions of people around the globe (Moberg and
64 Folke 1999; Foale et al. 2013; Norström et al. 2016; Woodhead et al. 2019). However, rising
65 ocean temperatures linked to increased anthropogenic emissions of greenhouse gasses have
66 been identified as a key threat for coral reef persistence (Hughes et al. 2017).

67

68 A robust body of evidence has shown that global warming acts as the key driver of coral reef
69 declines throughout the tropics. Pulse events such as marine heatwaves are widely
70 documented to induce bleaching of corals, a process where photosynthetic endosymbionts are
71 expelled from the cnidarian host (Warner et al. 1999; Fitt et al. 2001; Douglas 2003; Boilard
72 et al. 2020; Suggett and Smith 2020). Bleaching is occurring over large spatial scales,
73 resulting in mass mortality of entire coral colonies (Hughes et al. 2018a, 2018b).

74 Additionally, the continued rise in ocean temperatures are preventing coral reefs from
75 recovering before further pulse events occur (Hughes et al. 2018a; Harrison et al. 2019).

76 Rising ocean temperatures also inhibit the recruitment on coral reefs by causing mortality to
77 juvenile corals (Hughes et al. 2019), highlighting the multifaceted process of coral reef
78 decline via global warming. Thus, global warming will continue to transform coral reefs into
79 taxonomically, physically and functionally more homogenous environments (Hughes et al.
80 2018b), reducing biodiversity and impacting ecosystem function (Pratchett et al. 2011; Oliver
81 et al. 2015; Brandl et al. 2019).

82

83 As global warming continues to degrade coral reefs across the globe, monopolisation by other
84 taxa such as macroalgae where reef corals previously resided can occur rapidly (Hughes et al.
85 2007; Graham et al. 2013; Bozec et al. 2019; Fulton et al. 2019). Additionally, other taxa may
86 also monopolise space previously inhabited by hard corals, such as sponges (Bell et al. 2013;
87 Pawlik et al. 2016; Lesser and Slattery 2020) and soft corals (Inoue et al. 2013). Yet these
88 taxa do not provide equal ecological complexity to support biodiversity and provision of
89 ecosystem services as reef building corals (Friedlander and Parrish 1998; Hughes et al. 2017;
90 Woodhead et al. 2019). Furthermore, a combination of biotic interactions and abiotic effects

91 can prevent taxa from monopolising uninhabited space for a period of time, resulting in an
92 increased prevalence of sand or rock across the reef scape, further reducing habitat
93 heterogeneity (Alvarez-Filip et al. 2009). Finally, other non-living benthic components such
94 as coral rubble can inhabit reef space, a clear indication of hard coral mortality, and thus
95 substratum homogenisation. These changes in benthic and taxonomic compositions of coral
96 reefs ultimately represent a phase shifts of coral reefs, which are becoming more common
97 under global warming in the Pacific (Ledlie et al. 2007; Bozec et al. 2019), along the great
98 Barrier Reef (Hughes et al. 2007) and especially in the Atlantic ocean (Roff and Mumby
99 2012).

100

101 Coral reefs in the Wakatobi National Park (WNP) of Indonesia, and Honduras in the
102 Caribbean, represent two extensively monitored locations since 2012, providing an ideal case
103 study for understanding long term benthic compositional change under sea surface
104 temperature anomalies (SSTAs). At the Honduran reef systems, coral cover has been stable
105 between sites (Titus et al. 2015). Meanwhile, depths between 5 and 15m are associated with
106 divergent responses between hard coral and macroalgae cover, but not sponge and soft coral
107 cover at Utila, an island north of the Honduras coast (Andradi-Brown et al. 2016). At the
108 Indonesia location, fine scale site variability has been reported for key benthic components,
109 such as Sponge dominance on the turbid reefs (Powell et al. 2014; Biggerstaff et al. 2017;
110 Rovellini et al. 2019), while algae coverage shows temporal variability across reefs at this
111 location (Marlow et al. 2020). In contrast hard coral cover has appeared relatively stable at
112 the WNP (Marlow et al. 2020), despite observed general global declines since the turn of the
113 century owing to anthropogenic heating (Bruno and Selig 2007). However, coral community
114 composition did change in the WNP, with a reduction of ~20% in hard coral cover linked to
115 an intense bleaching event in 2010 (Watt-Pringle et al. 2022).

116

117 While previous findings have identified spatial and temporal variations of benthic cover at
118 these extensively monitored locations, the change in benthic composition has not been
119 assessed with satellite derived temperature metrics related to SSTAs. Here we assess the
120 relative role of elevated sea temperatures from remote sensing data for influencing the
121 benthic composition two coral reefs from distinct bioregions from 2012-2019.

122

123

124 **Methods**

125 **Survey locations**

126 Our study aims to compare two major coral reef systems of Honduras and Indonesia (Fig 1)
127 where long term monitoring by Operation Wallacea has been carried out.

128

129 In Honduras, data were collected from multiple reef sites in three distinct locations. Cayos
130 Cochinos Marine Protected Area (CCMPA) is a small archipelago close to the Honduran
131 mainland with an extensive network of gently sloping coral reefs and heavily restricted
132 access (Titus et al. 2015). Utila Island is the smallest of the Bay Islands chain and home to a
133 major dive tourism industry and surrounded by a fringing reef ranging from slopes to steeper
134 walls (Andradi-Brown et al. 2016). Finally, Banco Capiro is a recently discovered reef
135 system in the mainland bay of Tela, comprising an offshore bank that is home to an unusually
136 high percentage cover of live coral for the region (Bodmer et al. 2015) as well as a uniquely
137 high density population of the keystone herbivorous urchin *Diadema antillarum* (Bodmer et
138 al. 2021).

139

140 The study sites in Indonesia were located in the Wakatobi National Park (WNP), South-east
141 Sulawesi. The park encompasses 1.39 million hectares (<https://wakatobinationalpark.id/peta-kerja/>) in the centre of the Coral Triangle, harbouring over 390 species of hard coral, and 590
142 fish species across the 50k hectares of coral reefs (Clifton et al. 2010). Approximately 100k
143 people reside within the WNP, many of which directly rely on coral reefs for their daily
144 livelihoods (Cullen et al. 2007; Exton et al. 2019). Monitoring efforts in the WNP have
145 focused on reefs from the Kaledupa Island, and the smaller adjacent Hoga Island (Fig 1).
146 Surveys were taken across 6 established study sites encompassing various types of coral
147 reefs. Buoy 3 and Ridge 1 are steep walled sites, Pak Kasims, Kaledupa, and KDS are gentle
148 slope reefs, while Sampela is a gentle sloped highly sedimented and turbid reef (Crabbe and
149 Smith 2002; Marlow et al. 2018).

151

152 **Benthic data**

153 Benthic surveys took place during the months of June, July, and August from 2012-2019. The
154 6 reef sites in Indonesia were replicated each year, while multiple sites in Honduras were
155 randomly surveyed throughout the distinct locations over the 8-year study period. Benthic
156 data were collected by trained underwater surveyors using SCUBA. Survey teams were made

157 up of university-level volunteers led by trained experienced scientists in underwater
158 surveying. The standardised methodology required surveyors to perform 50m line intercept
159 transects, where data were collected every 0.25m along the transect, recording data on
160 benthic biotic or abiotic classification under the transect tape at that point. Transects were
161 replicated at 5m, 10m, and 15m at the Honduras location only. Whereas at the Indonesia
162 location, surveys were triplicated at the key reef zones, being the reef crest (~5m), the reef
163 flat (~2-3m) and the reef slope (~12-15m). Using a variety of depths at the Honduras sites,
164 and variety of reef zones at the Indonesia sites which encompasses a wide depth range of
165 shallow reefs (2-15m) allows us generalise the shallow reef benthic compositions at these
166 sites. Categories for the benthic classifications are identified in Table 1.

167

168 **Environmental data**

169 Heat stress was quantified as sea surface temperature anomalies (SSTA) measured in °C over
170 the last 52 weeks preceding surveying at a 5km resolution , extracted from Coral Reef Watch
171 (CRW) v3.1 5km product suite (Liu et al. 2014). The 5km daily SSTA product uses the daily
172 climatology (DC) derived from the monthly mean (MM) climatology interpreted from linear
173 interpolation. The MM value is assigned to the 15th day of each corresponding month, where
174 individual days are derived from the linear interpolation. The SSTA value is thus calculated
175 as follows

176

$$177 \quad SSTA = SST - DC$$

178

179 Where the SST (sea surface temperature) is the value for the day, and DC is the
180 corresponding DC for that specific day of the year.

181

182 The CRW products are highly robust for accurately measuring thermal stress, especially in
183 tropical latitudes (Liu et al. 2014), with many different products utilised for various types of
184 study (e.g. Hughes et al. 2018; McClanahan et al. 2019, 2020). Given the discrepancies in
185 accuracy between satellite derived temperature data, and actual temperature of a given region,
186 small values between -0.2 and +0.2 °C are considered climatologically normal for the SSTA
187 product, exemplifying the robustness of CRW data (Liu et al. 2014). These satellite-derived
188 temperature data are primarily an excellent tool for predicting coral responses to heat stress in
189 shallow water (Sully et al. 2019; Johnson et al. 2022a, 2022b). Additionally, they are also

190 ideal predictors of coral responses of up to 18m depth for changes in coral assemblages
191 (Hughes et al. 2018b), and coral mortality (Donovan et al. 2021).

192
193 The CRW product SSTA values were extracted as a summarised values on a weekly time
194 series. SSTA values were extracted at a 5km resolution for each location over the previous 52
195 weeks from when the benthic surveying commenced (i.e. June 1st-May 31st) for each year
196 from 2012-2019. Benthic surveys where SSTA data were not available were excluded from
197 the analysis, leaving a total of 1,088 surveys over the 8 year time period. While there are
198 potential issues (Ferguson et al. 2017) for using mismatched time series (i.e., values over the
199 last 52 weeks before the commencement of survey) which do not capture fine-scale
200 variability taxa with fast life histories, such as macroalgae and some sponges (Rovellini et al.
201 2021), this approach has been successfully employed for assessing coral responses over the
202 time period used (Donovan et al. 2021), which are indicative of coral reef compositional
203 change. Average SSTA values for each location over the course of the previous 52 weeks are
204 summarised in Fig 2. The number of temperature cells used to extract temperature values for
205 the surveys from CRW at each location are in Table 2.

206

207 **Statistical analyses**

208 Firstly, a Generalised Linear Model (GLM) with a quasi-poisson distribution was used to
209 determine whether the average SSTA was increasing through time at each location, as data
210 were Poisson distributed and over-dispersed.

211

212 *Bayesian generalised linear models*

213 To assess the response of benthic components to rising ocean temperatures, we used Bayesian
214 GLMs from the ‘brms’ package (Bürkner 2017) which utilises the STAN language
215 (Carpenter et al. 2017) in R 4.1.0 (R Core Team 2021). The cover of each benthic component
216 was run as a response variable at each location (Indonesia and Honduras), specified with a
217 beta distribution, as survey data reflected proportions. Time (the year of survey – 2012) and
218 SSTA were the explanatory effects in the model, run with the random effect of site. Priors
219 were fitted for each model using the ‘get_prior’ function in the package ‘brms’ which
220 specifies priors for the beta coefficients, intercept, and random of effects each model
221 (Bürkner 2017). Models were run for 4,000 iterations with 3,000 burnins, across 4 chains. To
222 ensure convergence was achieved trace plots were assessed (Figures S1-14). Posterior

223 predictive checks were also used to assess model performance (Figures S1-14), in addition to
224 each model achieving Gelman-Rubin statistic (Rhat) of 1 (Bürkner 2017).

225

226 *Ordination analysis*

227 To assess the relative influence of our predictors of time and SSTA for predicting benthic
228 composition at each location over the entire survey period (2012-2019) we used Redundancy
229 analysis (RDA) from the ‘vegan’ package (Oksanen et al. 2013) in R. RDA is analogous of
230 ordinary least square regression to the multivariate response variable, which expects a linear
231 response of each benthic component to the environmental variables (Year, SSTA & site).
232 Using RDA allowed us to extract the constrained inertia (variance explained) from each
233 model at the two locations to assess the relative influence of time and SSTA for driving
234 benthic composition.

235

236 Further analysis to assess changes in the benthic components of coral reefs our locations were
237 assessed using non-Metric Multi-Dimensional Scaling (nMDS) from the ‘vegan’ package
238 (Oksanen et al. 2013). Each benthic component was ordinated in 2-dimensional space
239 grouped by the first 4 years of sampling (2012-2015) and the last 4 years of sampling (2016-
240 2019) with a Euclidean dissimilarity matrix. Grouping the composition of coral reefs this way
241 coincided with the 2016-2017 back-to-back bleaching events where marine temperatures
242 were exceedingly high (Hughes et al. 2018a), devastating many corals around the globe
243 (Hughes et al. 2018a; Harrison et al. 2019; McClanahan et al. 2019; Sully et al. 2019), even
244 leading to transformed coral reef assemblages on the Great Barrier Reef (Hughes et al.
245 2018b). To assess the change in composition of each site between the 2 grouped time periods,
246 the entirety of the ordination space occupied by each location were plotted, along with their
247 pairwise distances.

248

249 **Results**

250 **Sea surface temperature anomalies from 2012-2019**

251 The average SSTAs over the last decade were highly divergent between the Honduras and
252 Indonesia locations, with peak SSTAs preceding the survey years of 2016 and 2017 for
253 Honduras (Fig 2). Comparatively, the SSTA peak for Indonesia over the last decade only
254 occurred for one year, preceding 2017 surveying (Fig 2). Overall, the average SSTA was
255 higher for every survey year at the Honduras location compared to the Indonesia location.

256 The SSTA also showed a significant increase through time for both the Indonesia location
257 (GLM, Estimate = 3.644, t = 0.025, p<0.001) and the Honduras location (GLM, Estimate =
258 0.052, t = 3.905, p < 0.001).

259

260 **Response of benthic components to SSTA over the last decade**

261 Changes in the benthic composition between locations varied from 2012-2019 (Fig 3). Thus,
262 as expected, the response of benthic components to sea surface temperature anomalies
263 (SSTA) also varied between locations (Fig 4). Time (year) was a strong predictor of an
264 increase in hard coral cover and sponge cover at the Indonesia location, while also predicting
265 a decrease in coral rubble. At the Honduras location, time predicted an increase in algae and
266 soft coral cover. However, hard coral cover and rock cover are predicted to decrease through
267 time. Over the last decade, SSTA, did not predict any changes in benthic cover at the
268 Indonesia location. Conversely, SSTA predicted an increase in bare rock cover at the
269 Honduras location, while also predicting a reduction in sponge coverage.

270

271 Redundancy analysis identified low variance explained from the effects of time (year of
272 survey) and SSTA at the Indonesia (5.9%) and Honduras (4.7%) location. However, when
273 adding site in the RDA model (Fig 5), 69.5% of the variance is explained at the Indonesia
274 location while 81.8 is explained at the Honduras location, indicating site variability is the
275 strongest predictor of benthic composition at both these locations.

276

277 **Change in the benthic community composition from 2012-2019**

278 The relative contribution of individual benthic components to the reef benthic composition
279 are shown from 2012-2015 (Fig 6a) and 2016-2019 (Fig 6b), with only slight changes to the
280 benthic components at the Indonesia sites between these time groups. Furthermore, potential
281 simplification/stabilisation of the benthic composition at the Indonesia location can be
282 observed based on the entirety of the ordination space occupied pre-2016 compared to 2016-
283 2019 (Fig 6c). However, at the Honduras location a drastic change in the benthic components
284 which drives the community composition was observed from 2012-2015 compared to 2016-
285 2019 (Fig 6d,e). This coincided with a shift in the ordination space occupied by each site (Fig
286 6f).

287

288 **Discussion**

289 Our findings reveal dichotomous responses between the two locations of coral reef sites of
290 the Honduras and Indonesia location under SSTAs from 2012-2019. Benthic composition
291 varied over time at both locations, but the changes in benthic composition were location
292 specific. Meanwhile, intra-location variability (i.e. the composition at each site) explained the
293 largest proportion of variance for the benthic composition at both the Indonesia and Honduras
294 locations, indicating fine-scale variability as a key factor for explaining the benthic
295 composition of these coral reefs.

296

297 **The relative role of SSTA for driving compositional change**

298 Elevated sea surface temperatures appear to predict coverage of benthic components at the
299 Honduras location only, and not the Indonesia location, indicating that the Honduran reefs
300 surveyed in this study are more susceptible to compositional change under marine heatwaves.
301 This can be seen with the increase in bare rock coverage at the Honduras location and a
302 decrease in sponge coverage in association with SSTAs (Fig 4), but note temporal variations
303 in cover (Fig 3). The increase in bare rock coverage associated with temperature could
304 indicate global warming driving biotic declines of the reef scape through direct and indirect
305 cascading processes (Alvarez-Filip et al. 2009). Meanwhile, the decrease in sponge coverage
306 identified at the Honduras location is convoluted in the literature. Coral loss attributed to
307 global warming leads to increase in seaweed abundance, which results in an increased
308 production of dissolved organic carbon (DOC) that is consumed by sponges. Consequently,
309 nutrients released by sponges enhance seaweed abundance, further inhibiting coral cover
310 (Pawlik et al. 2016). Yet, this process is likely constrained in the long term owing to
311 cascading trophic processes (Lesser and Slattery 2020). Our findings suggest that this
312 increase will not occur at this location under rising sea temperatures. At the Indonesia
313 location, none of the benthic components were predicted to either increase or decrease from
314 the effect of SSTA, suggesting other factors are driving the benthic composition of these
315 reefs.

316

317 In contrast to the effects of SSTAs, temporal patterns of variation predicting the benthic
318 composition of reefs at both the Indonesia and Honduras location are prominent. These
319 temporal patterns which predict compositional changes at the Indonesia location have been
320 previously recorded for sponges, which showed the strongest temporal increase of all the
321 benthic components. This stark increase is most strongly related to the Sampela site where
322 high sedimentation has driven sponge dominance (Biggerstaff et al. 2017). However, fine

323 scale temporal variation in sponge and algae coverage on the coral reefs of the WNP are well
324 documented (Rovellini et al. 2019; Marlow et al. 2020), along with interannual variability of
325 algae coverage (Marlow et al. 2020; Rovellini et al. 2021) which are likely overlooked based
326 on our findings (e.g. Fig 3). The increase in hard corals at the Indonesia location contradicts
327 the assumed temporal stability of hard coral at this reefs (Marlow et al. 2020; Rovellini et al.
328 2021), but may be a consequence of recovery from a lower baseline because of the 2010
329 bleaching event (Watt-Pringle et al. 2022), or a natural cycle where hard corals are increasing
330 owing to temporal variation (Rovellini et al. 2021). This is also indicated by a decrease in
331 coral rubble at the Indonesia location through time, suggesting hard coral cover has displaced
332 dead corals over time. At the Honduras location, increased algae coverage and decreased hard
333 coral cover conform to previous to the expectation of decline for coral reefs in this region
334 where multiple stressors are compounding coral reef transitions into alternative states
335 (Contreras-Silva et al. 2020). The decrease in bare rock cover at this location likely relates to
336 the observed increased in algae monopolisation, and the increase in soft coral cover through
337 time. Soft corals are a taxa assumed to increase on reefs under global warming, as reduction
338 in hard corals from warming and acidification should allow for soft corals to outcompete hard
339 corals (Inoue et al. 2013), which may be occurring at these Honduran reefs.

340

341 **Other drivers of reef composition**

342 Given that intrinsic site variability between these two locations appears to be the strongest
343 predictor of benthic composition compared to SSTA and time, it is critical to note other
344 potential drivers of composition at these locations. Firstly, the use of mismatched time series
345 methodology does not capture fine-scale temporal dynamics of species with faster life
346 histories, such as macroalgae and some sponges (Rovellini et al. 2021). These faster life
347 history traits will also influence rock coverage as bare substrate will be quickly monopolised
348 by these taxa, yet grazing and/or displacement could occur before sampling between years
349 takes place. However, the general effects of using SSTA over the 52 week period have been
350 well validated for coral cover (Donovan et al. 2021) which is the most important component
351 for coral reef complexity. The influence of depth was also not considered within our models
352 owing to the dearth of sufficient data. Yet, coral and algae cover at the Honduras location
353 vary by depth (Andradi-Brown et al. 2016), which is also often assumed to be refuge for
354 some corals under warming oceans (Bridge et al. 2014). Surveying at both locations
355 encompassed a variety of reef types, zones, and depths, but these data were not specifically
356 recorded during collection so were not included in analyses. However, for corals specifically,

357 depth certainly does not equal refuge, as temperature sensitivity increases with depth
358 (Bongaerts et al. 2017). Furthermore, at the Honduras location, the impacts of grazing
359 herbivores such as *Diadema antillarum* which support ecosystem function by reducing algae
360 coverage, thus facilitating coral cover increase, was not considered as a driver of benthic
361 composition in this study despite their known positive impacts (Bodmer et al. 2015, 2021).
362 Our analysis also did not consider prevailing ocean currents, such as the influence of the
363 Banda and Flores Sea (Gordon et al. 1994), which at the Indonesia location, is hypothesised
364 to provide cooling waters to corals of the WNP, potentially alleviating bleaching during
365 thermal stress. Finally, lack of information on at the level of coral reef species are also not
366 available from monitoring data, which are likely to be an influential factor for assessing
367 changes to the benthic composition under SSTAs. However, data at this resolution on coral
368 reefs are unlikely feasible with citizen science techniques, therefore a trade-off between
369 accuracy and resolution must be considered (Done et al. 2017; Gouraguine et al. 2019).

370

371 **Conclusions**

372 In conclusions, our analyses reveal the composition of reefs at both locations have changed
373 over the last decade, with increased evidence of changes at the Honduras during SSTAs
374 compared to the Indonesia location. At the Indonesia location, temporal variation predicts
375 changes in the benthic composition far more than the effect of elevated sea surface
376 temperatures. However, high variance explained of the benthic composition by adding site to
377 RDA models indicates other fine-scale inter-location factors are likely driving the benthic
378 composition of both these locations. Consequently, continued monitoring of these reefs with
379 higher taxonomic resolution of data may be beneficial, along with in-situ temperature
380 recordings. Ultimately, however, the monitoring effort is critical for understanding local scale
381 composition dynamics of these coral reefs, and how they will change under anthropogenic
382 heating.

383

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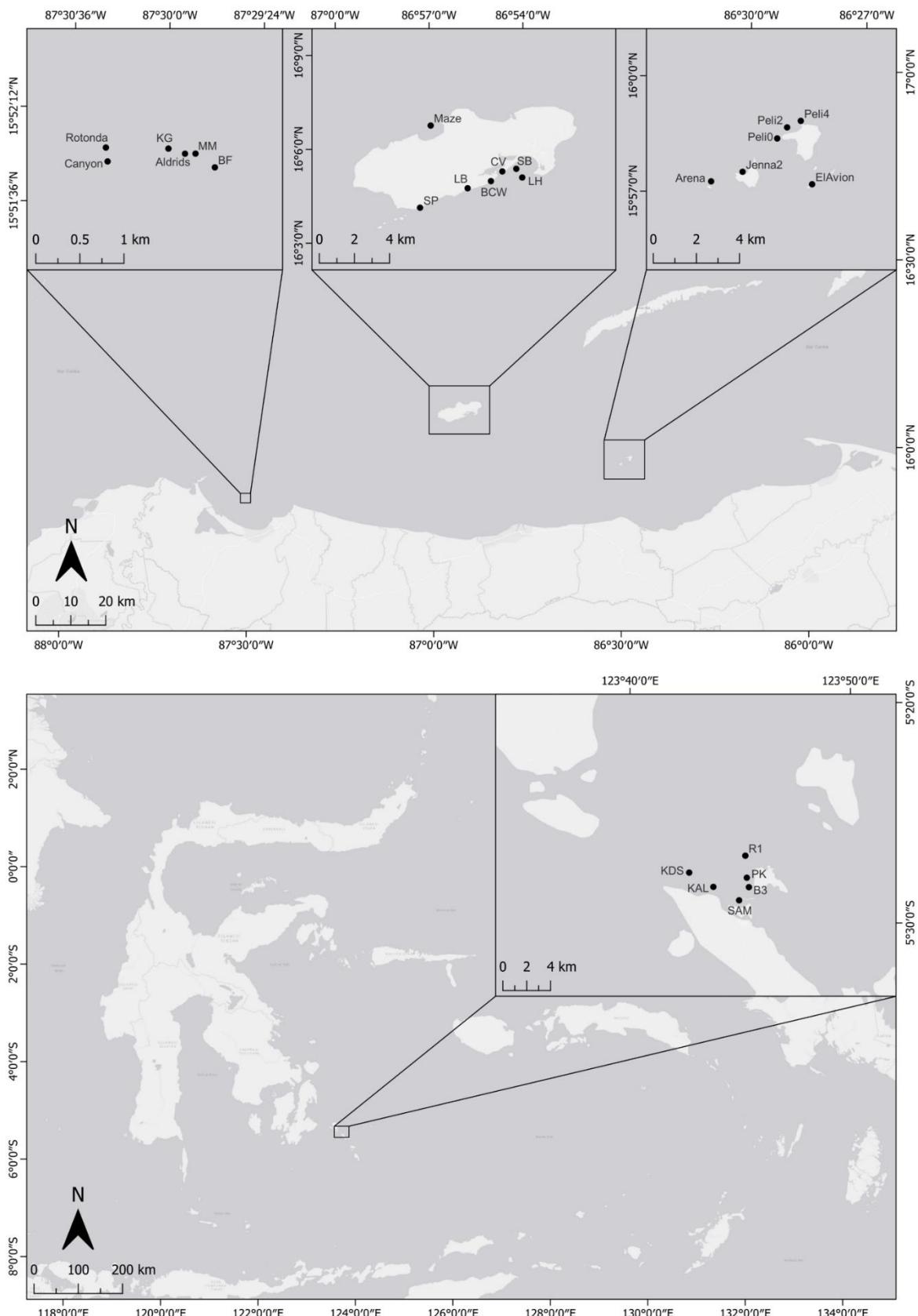
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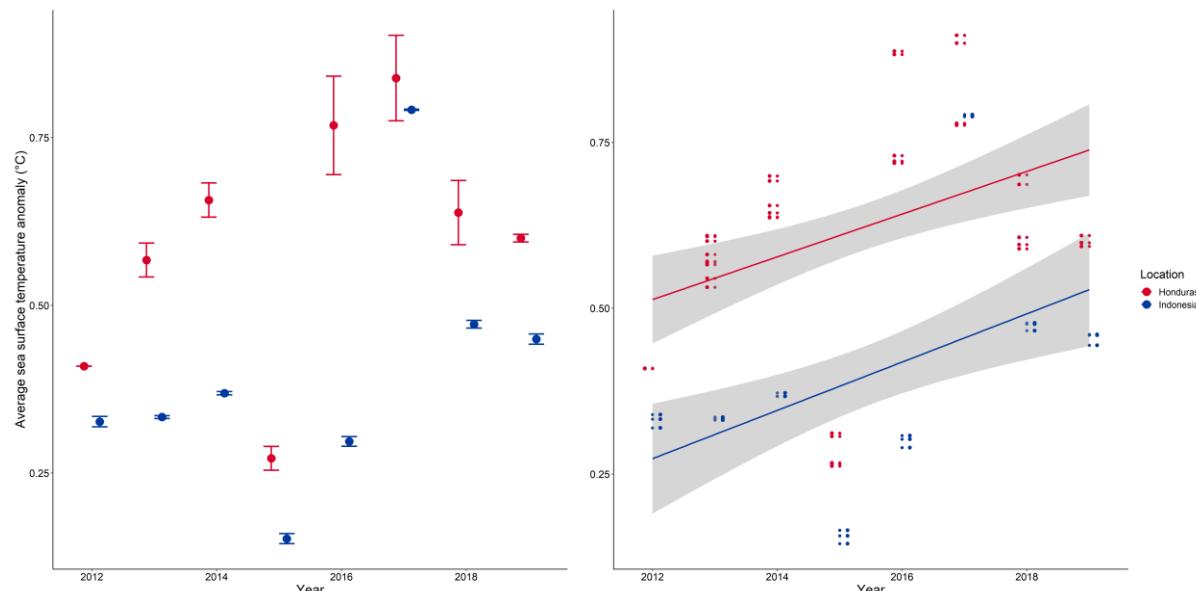
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- 558
- 559
- 560 **Figure legends**



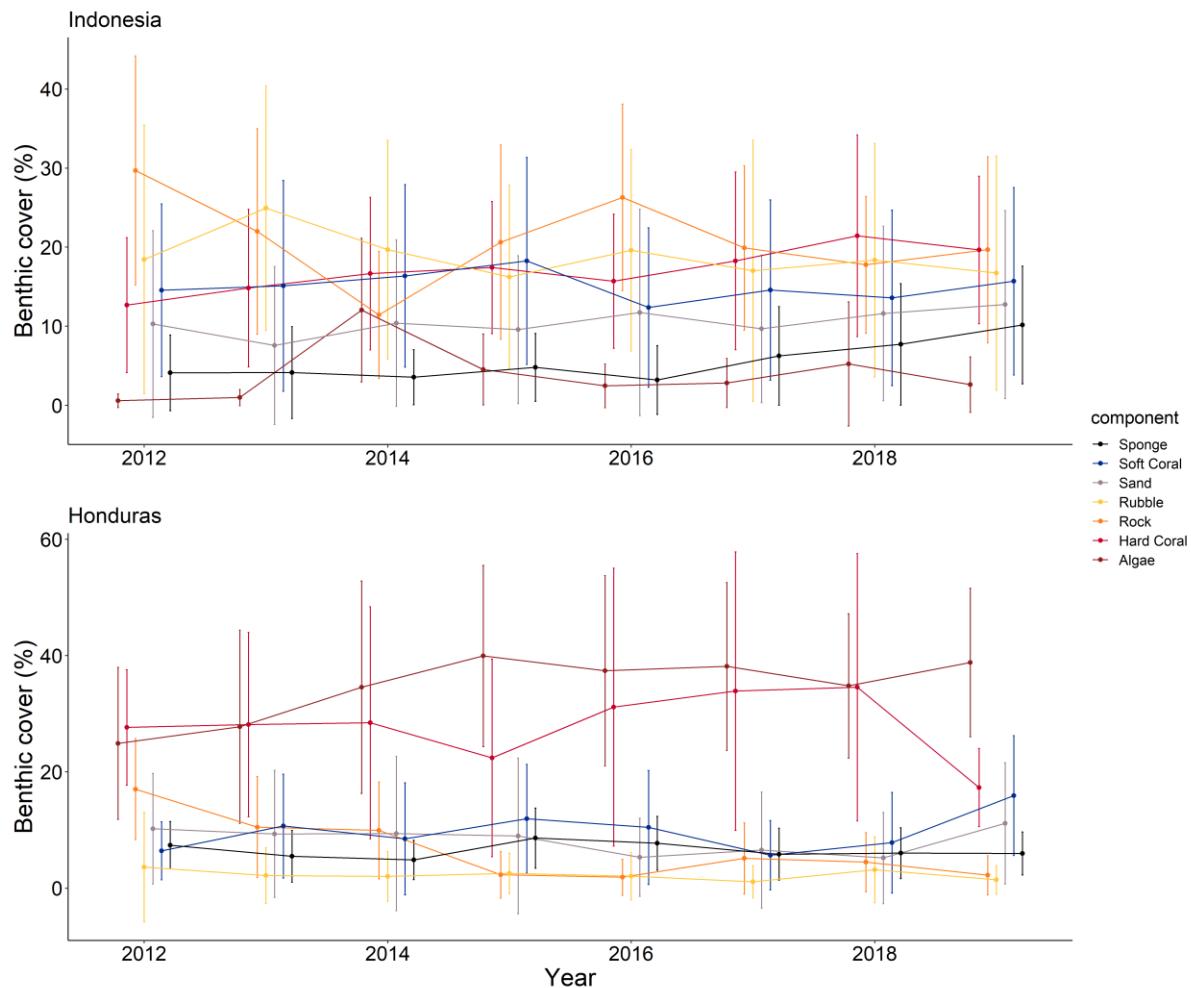
561

562 **Fig 1.** Locations of reefs where field surveys were undertaken for benthic data collection by
563 Operation Wallacea citizen scientists. The top panel shows the location of surveyed reef sites

564 from Honduras, the bottom pannel shows the surveyed reef sites of Indonesia, located in the
565 Wakatobi National Park.

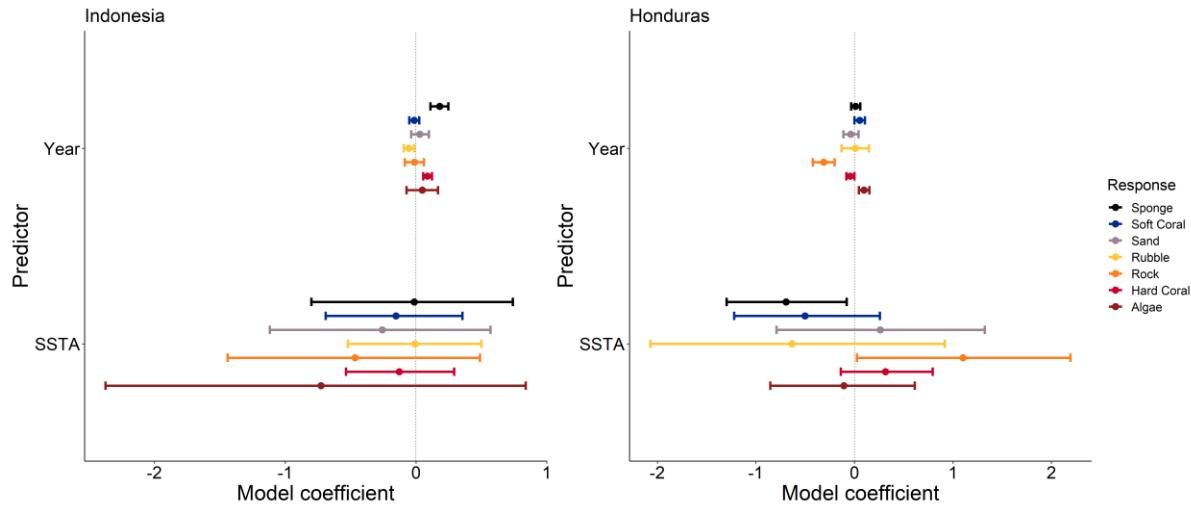


566
567 **Fig 2.** Average sea surface temperature anomaly (SSTA) in °C and standard errors (whiskers)
568 from 2012-2019 at the Indonesia and Honduras sites surveyed in this study. Temperatures
569 were quantified from the 52 weeks preceding the survey period which began at the 1st of
570 June for each site, each year. Points represent the mean SSTA, while error bars are standard
571 error.



572

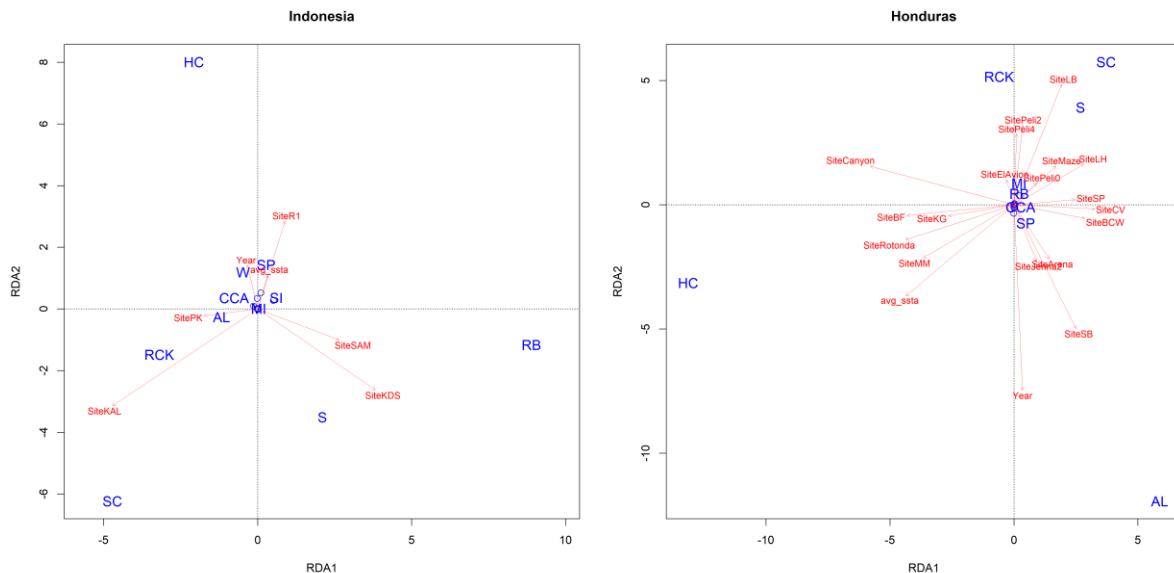
573 **Fig 3.** Temporal dynamics of each benthic cover for each category at the Indonesia (top) and
574 Honduras (bottom) location.



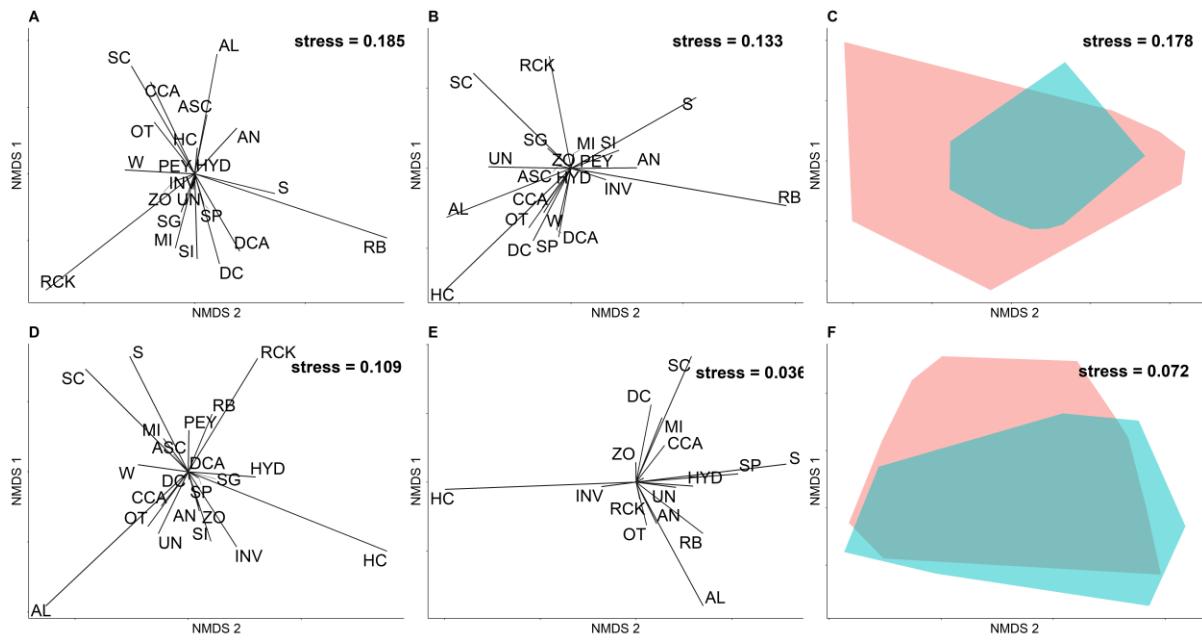
575

576 **Fig 4.** Bayesian GLM coefficient estimates for the response of selected major benthic
577 components under elevated sea surface temperatures (SSTA) and time (Year). Coloured
578 points correspond to the specified benthic component, representing the mean model

579 coefficient. Horizontal bars represent 95% credible intervals, which are considered
 580 ‘significant’ when they do not cross zero (grey line). The models ran separately for Indonesia
 581 and Honduras locations. The components were selected based on preliminary analysis as the
 582 most dominant components of reefs from the field surveys undertaken by Operation Wallacea
 583 volunteers from the years of 2012-2019. Colours are from *Centropyge loricula* using the
 584 ‘fishualize’ package (Schiettekatte et al. 2022).



585
 586 **Fig 5.** Redundancy analysis of the benthic community composition at each location and their
 587 relationship with environmental variables. The left plot are data from Indonesia, while
 588 Honduras is shown on the right. The blue text within the plots indicates the individual benthic
 589 components (Table 1), while the red text specifies the environmental drivers considered in the
 590 model which includes individual sites. The arrows correspond to the relative influence of
 591 environmental variables.



592

593 **Fig 6.** nMDS analysis of the benthic community composition at the Indonesia sites (A-C) and
 594 Honduras sites (D-F). A. and D. are the composition of individual benthic components from
 595 2012-2015. B. and E. are response of individual benthic components from 2016-2019 (i.e.
 596 showing the response of the global marine heatwaves which took place in 2016/2017 (Fig.
 597 2)). Letters represent the individual taxa which are specified in Table 1. C. and F. represent
 598 the entire ordination space of the benthic composition at each individual reef, where the red
 599 polygon bounds the sites from 2012-2015, while the blue polygon bound sites from 2016-
 600 2019.

601

602 **Tables**

603 **Table 1.** Categorisation of biotic and abiotic benthic components collected from benthic
 604 transect surveys

Code	Benthic category
AL	Algae
AN	Anemone
ASC	Ascidian
CCA	Coralline Crustose Algae
DC	Dead Coral
HC	Hard Coral
HYD	Hydroids

INV	Other Invertebrate
MI	Millipora
PEY	Peysonnellia
RB	Rubble
RCK	Rock
S	Sand
SC	Soft Coral
SG	Sea Grass
SI	Silt
SP	Sponge
UN	Unknown
W	Water
ZO	Zooanthid

605

606 **Table 2. The Coral Reef Watch (CRW) temperature cells used for each site at each
607 location in the study.**

608

Location	Sties sharing a CRW cell
Indonesia	B3 & PK
	Sampela, KDS, & KAL
	R1
Honduras	BCW, CV, LB, & SB
	LH
	El Avion, Peli0, Peli2, & Peli4
	SP
	Maze
	BF, KG, MM, Aldrids
	Canyon, Rotanda
	Arena
	Jenna 2

609

610

611

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614 volunteers who contribute to the data collection with Operation Wallacea, and Operation
615 Wallacea for sharing their data. We also thank Coral Reef Watch for the maintenance and
616 open access use of their database.

617

618 **Data Accessibility Statement**

619 Data are permanently deposited in Dryad (<https://doi.org/10.5061/dryad.w3r2280tt>) with all
620 code available on our Github page
621 (https://github.com/JackVJohnson/Disparity_between_Indo_Pac_and_Caribbean).

622

623 **Authors' Contributions and Conflict of Interest**

624 JVJ, DAE, and DPD designed the study. DAE provided the data, JVJ analysed the data, JVJ
625 and JO created the figures. All authors contributed to manuscript writing and revisions and
626 declare no conflict of interest.

627

628