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1 **Macroalgal canopies provide corals limited protection from bleaching and impede post-**
2 **bleaching recovery**

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23

24 **Abstract**

25 Coral bleaching, the result of loss of endosymbiotic dinoflagellates, as well as post-bleaching
26 recovery can be exacerbated or mitigated by a range of local factors such as depth,
27 turbidity, and natural or artificial shading providing protection for corals during thermal
28 anomalies. On many reefs, losses in coral cover coincide with increases in upright
29 macroalgae growth. Such shifts in benthic communities are generally viewed as negative,
30 whereby macroalgae can outcompete corals for space, and affect adult coral health and
31 fitness. However, the canopy provided by upright macroalgae could reduce solar irradiance
32 and provide refuge for understorey corals during heat events, decreasing coral bleaching
33 and subsequent mortality. To test this hypothesis, this study manually removed macroalgae
34 from experimental plots on a macroalgae-dominated fringing reef at Magnetic Island in the
35 central inshore region of the Great Barrier Reef, comparing the subsequent bleaching during
36 and recovery following a severe heat stress event. In March 2020, sea surface temperature
37 at Magnetic Island reached 31.4 °C, leading to bleaching. Surveys of coral communities
38 undertaken at the peak of accumulated severe heat stress (DHW of 9.3 °C-weeks) in control
39 and macroalgae removal plots showed that, averaged across coral morphological groups,
40 there was no overall difference in bleaching prevalence in algal-removal and control plots
41 (21.1% and 20.8% of the community bleached; respectively). However, bleaching prevalence
42 varied within morphological groups, with massive morphology corals demonstrating higher
43 probability of bleaching in removal plots compared to controls (0.26 and 0.09, respectively).
44 Bleaching severity (i.e. percent of the colony tissue bleached) was consistent across control
45 and removal plots (83.2% and 80.4% of colony area, respectively, averaged across
46 morphologies), with branching corals demonstrating the lowest severity. Surveys were
47 repeated in July after heat stress had dissipated, with coral communities in algal-removal
48 plots displaying greater recovery than controls (i.e. 86.1% and 75.6% healthy, respectively,
49 model estimated mean averaged across morphologies). Encrusting corals in control plots
50 were the slowest to recover. We conclude that macroalgae provided limited refuge for
51 branching and encrusting corals at the height of the thermal event, likely due to the severity
52 of the accumulated heat stress, while massive corals enjoyed some degree of protection
53 from the canopy. Greater recovery of coral communities in removal plots may potentially be
54 explained by reduced competition with adjacent macroalgae. This study provides important
55 insights into the interactions between these two dominant benthic groups and supports
56 previous work finding macroalgae inhibits coral recovery after severe bleaching events.

57 **1. Introduction**

58 As the global climate continues to warm, coral reefs are under increasing stress. Living near
59 the upper boundary of their thermal niche optimises coral growth and other processes;
60 however, small increases in sea temperatures can cause corals to bleach (Berkelmans and
61 Willis, 1999; Fitt et al., 2001; Woolsey et al., 2015). Coral bleaching, the expulsion of the
62 mutualistic endosymbiotic dinoflagellate community that provides corals with the majority
63 of their nutrition (Muscatine and Cernichiari, 1969; Muscatine and Porter, 1977; Muscatine
64 et al., 1981), can result in mass coral mortality and changes to reef benthic communities
65 (Hughes et al., 2017, 2018). With the escalating frequency and intensity of anomalously-high
66 temperature events (IPCC, 2021), climate-driven coral bleaching and mortality is now

67 reported globally and identified as the major risk to reef ecosystems over the next century
68 (Sully et al., 2019).

69 Global climate change takes place alongside a suite of local conditions which can exacerbate
70 or mitigate bleaching susceptibility (Carilli et al., 2009). For example, nutrient enrichment
71 can increase bleaching frequency or severity (Wooldridge, 2009; Wiedenmann et al., 2013;
72 Vega Thurber et al., 2014; Wooldridge et al., 2017; Burkepile et al., 2020), while turbidity
73 can moderate bleaching through reducing incident light (Sully and van Woesik, 2020). Other
74 factors, such as disease outbreaks, can act in synergy with bleaching by lowering bleaching
75 thresholds and/or leading to increased tissue mortality (Anthony et al., 2008; Brodnicke et
76 al., 2019). Furthermore, local conditions can play a role in subsequent recovery after
77 bleaching, with high nitrate levels prolonging recovery from bleaching (Burkepile et al.,
78 2020) and high macroalgae and/or urchin abundance associated with increased
79 postbleaching mortality (Donovan et al., 2021).

80 While both global and local factors clearly contribute to the dynamics of coral bleaching
81 (Jokiel and Brown, 2004; Carilli et al., 2009), they also combine to shape reef communities
82 more broadly. In the Caribbean, nutrient enrichment, hurricanes, coral bleaching, and
83 overfishing of grazers culminated in a 90% loss of coral cover with a subsequent rise in
84 macroalgae cover throughout the 1970s and 1980s (Hughes, 1994; Lapointe et al., 1997;
85 Idjadi et al., 2006). On the Great Barrier Reef, such dramatic shifts have yet to be realised on
86 a large scale, though combined global (e.g. cyclones, temperature) and local (e.g. water
87 quality) impacts have been implicated in a shift in the dominant reef taxa from corals to
88 fleshy macroalgae on some inner shelf reefs (De'ath and Fabricius, 2010; De'ath et al., 2012;
89 Jackson et al., 2014; Ceccarelli et al., 2020). As anthropogenic influences continue to rapidly
90 increase (IPCC, 2021), community shifts are predicted to become more widespread, with
91 macroalgae proliferation expected (Davis et al., 2021).

92 Macroalgae are one of the main competitors for benthic space on coral reefs. When coral
93 cover is low, macroalgae have a competitive dominance over corals, with positive feedback
94 mechanisms reinforcing their establishment. Competitive interactions are widely regarded
95 as negative for corals, with macroalgae inhibiting recruitment of coral juveniles (Webster et
96 al., 2015; Dajka et al., 2019; Smith et al., 2022b), suppressing metamorphosis (Baird and
97 Morse, 2004), reducing juvenile survival and growth (Hughes et al., 2007; Webster et al.,
98 2015), and affecting adult health, fitness, and fecundity (Tanner, 1995; McCook et al., 2001;
99 Foster et al., 2008; Cetz-Navarro et al., 2015; van Woesik et al., 2018; Monteil et al., 2020).
100 In spite of these negative interactions, there is some evidence that macroalgae can have
101 positive interactions with corals, specifically through their ability to shade corals from
102 ultraviolet radiation (Jompa and McCook, 1998). Indeed, a reduction in light penetration by
103 suspended sediments (Sully and van Woesik, 2020), steep reef walls (Fabricius et al., 2004),
104 artificial shade (Coelho et al., 2017), and mangrove canopies (Stewart et al., 2021) have
105 been effective in reducing bleaching incidence, hence an algal canopy may hold similar
106 benefits. However, limited research has been devoted to the positive roles macroalgae play,
107 especially when present in high abundance and alongside global stressors.

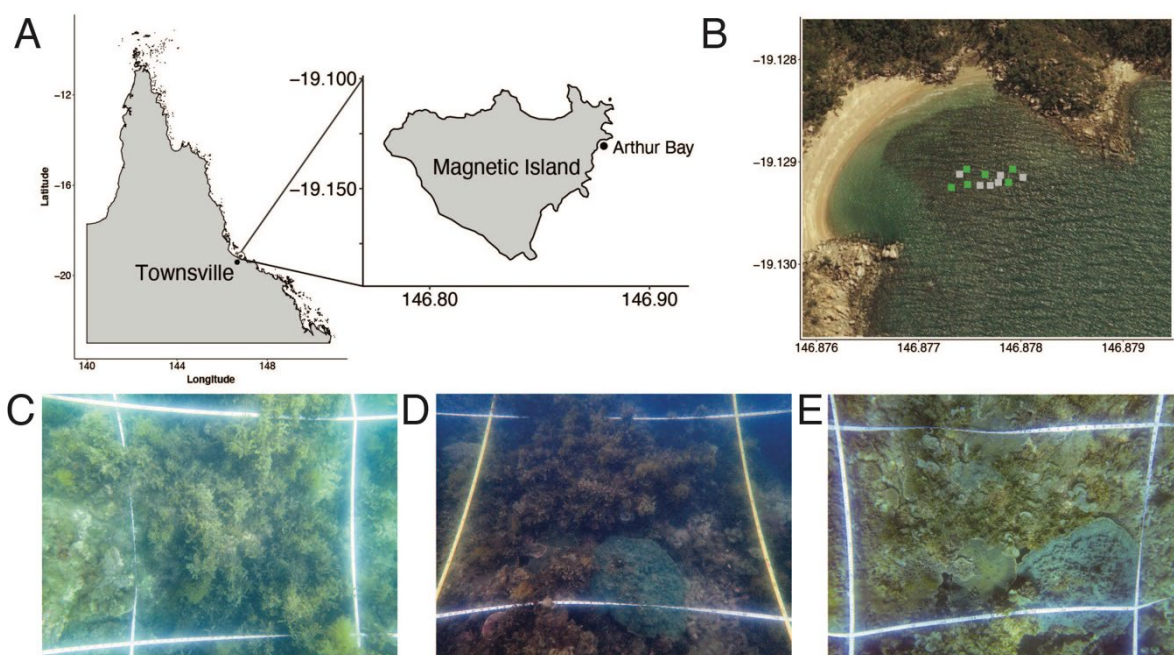
108 Recent work has highlighted macroalgae abundance as a key metric influencing post-
109 bleaching mortality (Donovan et al., 2021). Therefore, investigating how macroalgae affect

110 coral bleaching susceptibility and recovery is vital to inform management and to predict
111 future changes in reef ecosystems impacted by both increased bleaching frequency and
112 higher macroalgal abundances. Herein, we manually removed macroalgae from
113 experimental plots on a fringing reef at Magnetic Island, in the central inshore GBR. Coral
114 bleaching prevalence in control and removal plots was surveyed during the 2020 mass
115 bleaching event by recording the morphology, size, and bleaching severity (% of live tissue)
116 of all bleached colonies. Additional surveys examined the subsequent recovery period by
117 censusing the entire population (morphology, bleaching, partial mortality) within the same
118 experimental plots, to understand how a macroalgal canopy affects bleaching incidence,
119 severity, and recovery.

120 2. Methods

121 2.1. Study site and experimental design

122 Fringing reefs of Magnetic Island (Yunbenun), a continental island in the central inshore
123 GBR, have experienced a decline in coral cover over the last two decades coinciding with
124 increased macroalgae cover (Ceccarelli et al., 2020), and hence these reefs were selected as
125 case study sites to examine the relationship between macroalgal canopy and coral
126 bleaching. The fringing reef of Arthur Bay (19.12925° S, 146.87732° E) is largely macroalgae
127 dominated (40–80% cover), with 10–40% coral cover and 20–30% sand, rubble or rock
128 (Ceccarelli et al., 2020). Twelve 25m² (5 m × 5 m) experimental plots were established in
129 Arthur Bay at 2-3 m depth, avoiding features such as large sand patches or large bommies
130 (Fig. 1). Plots were randomly designated as “control” or “removal” plots ($n = 6$ each
131 treatment), where removal plots were subjected to periodic removal of all macroalgae by
132 hand.



133

134 **Fig. 1.** A) Map of Queensland, Australia showing the location of the study site on Magnetic
135 Island (inset). B) Experimental plot locations within Arthur Bay. Green squares denote algae
136 removal plots, grey squares denote control plots. Note that plot icons are not to scale. C)
137 Representative image of a control plot reef area. D) Representative image of a removal plot
138 reef area prior to removal. E) The same photoquadrat area as shown in panel D, after
139 removal of algal biomass.

140

141 2.2. Seawater temperature data

142 Satellite derived sea surface temperature (SST) data for Arthur Bay were sourced from the
143 CoralTemp satellite SST product from the National Oceanic and Atmospheric Administration
144 (NOAA) Coral Reef Watch (CRW) program (Skirving et al., 2019; coralreefwatch.noaa.gov;
145 $0.05^\circ \approx 5$ km, daily resolution). SST data were used to calculate accumulated heat stress,
146 measured as Degree Heating Weeks (DHW) for the period from 1 December 2019 to 31 July
147 2020. The DHW metric represents the thermal stress accumulation above the expected
148 summertime maximum temperature (the maximum of the monthly mean 'MMM'
149 climatology, 28.8°C at Arthur Bay) on days for which this daily temperature 'HotSpot' is at
150 least 1°C (i.e., SST at or above the localised bleaching threshold of 29.8°C); the
151 accumulation is undertaken over a 12-week period. This measurement is an established
152 predictor for coral bleaching, with thresholds of 4 and 8°C -weeks being associated with
153 significant bleaching and severe coral bleaching and mortality, respectively (Eakin et al.,
154 2010; Liu et al., 2013, 2014; Heron et al., 2016).

155 2.3. Macroalgae removal

156 A mixed community of macroalgal genera was present in the plots, dominated by
157 *Sargassum*. Fleishy macroalgae of all genera were removed from the six designated removal
158 plots on 10 October 2019 in the late Austral spring. Removal of macroalgae was conducted
159 by snorkel and SCUBA divers, assisted by citizen science volunteers from Earthwatch
160 Institute, with particular effort focussed on removing the algal holdfasts. The removed
161 macroalgae were retained in catch bags and the wet biomass was weighed per plot. Benthic
162 surveys were conducted before and after algae were removed to determine the impact of
163 algal removal on algal density and canopy height between treatments. Three replicate 1 m^2
164 quadrats were placed haphazardly within each 25 m^2 plot, within which the number of
165 holdfasts were counted and the height of ten haphazardly selected thalli were measured.
166 Surveys were repeated in February and July 2020. Canopy height and holdfast density data
167 were used to calculate mean macroalgae biomass for each plot and survey time point using
168 a length-weight formula for *Sargassum polycystum* from Orpheus Island (Hoey 2010):

$$169 \quad \text{wet weight (g m}^{-2}\text{)} = 0.5637 \text{ (g cm}^{-1}\text{)} \times \text{height (cm)} \times \text{density (num m}^{-2}\text{)}$$

170 2.4. Coral community data

171 In March 2020, visual reports emerged of coral bleaching on reefs surrounding Magnetic
172 Island, including the Arthur Bay study site. These observations were consistent with the SST
173 data sourced from NOAA's CRW program, which indicated a mass bleaching event taking
174 place on the GBR. Surveys of the coral communities in Arthur Bay were conducted on 10
175 March 2020, near the peak of heat stress.

176 In each experimental plot, all bleached coral colonies over 4 cm in diameter were recorded
177 by genus, morphology, size, and the percent of bleached tissue per colony. Colony size was
178 measured as the widest diameter of each colony and categorised into size classes of 5–20
179 cm, 21–40 cm, 41–60 cm, 61–80 cm, and 81+ cm. Morphological coral groups included
180 branching, encrusting, free-living and massive (Supplementary Table S1). Due to the Covid-
181 19 pandemic, field limitations were introduced while the survey team was onsite. The team
182 was recalled from the field early, allowing only counts of bleached coral colonies to be
183 recorded, rather than the entire coral community. Post-hoc attempts were made to use
184 photo-quadrat images to assess the total number of colonies present during the March
185 surveys, though due to high macroalgae growth in the summer period, canopy effects
186 (Smith et al., 2022a) prevented accurate identification of total coral communities.

187 Coral health surveys were repeated on 28 July 2020, four months following the peak of heat
188 stress and when Covid-19 restrictions had eased. In the July surveys, the entire coral
189 community within each plot was recorded, including healthy colonies. Every coral colony
190 within the 12 plots was counted, measured, identified, and evaluated for health status as
191 previously described, with an additional estimation of mortality. Partial and whole colony
192 mortality was recorded by visually estimating the percentage of recently dead colonies, as
193 identified through minimal algal colonisation, minimal weathering and erosion of skeleton,
194 and intact and identifiable corallites.

195 2.5. Statistical analyses

196 To account for the limitations of the March dataset (i.e. no full community census or counts
197 of healthy colonies), it was assumed that the July colony counts represent the same number
198 of colonies which were present in March. Therefore, the full community census from the
199 July field work was used to standardise the March data. This is considered an appropriate
200 assumption, as it is unlikely that any colonies would have changed size class between the
201 two time points, and surveyor detection error would be consistent across time points. A
202 generalised linear mixed effects model was used to examine differences in bleaching
203 prevalence between control and removal plots in March, where treatment (control, algae
204 removal) and morphology (branching, encrusting, massive) were interactive fixed factors
205 and plot (six replicate plots per treatment) was a random factor. A binomial distribution
206 with logit link was used to model the relationship, using the number of bleached and
207 healthy colonies (total colonies minus bleached colonies) as the response. The model was
208 validated using tests for dispersion and deviation based on simulated residuals. A similar
209 model was used to examine differences in bleaching across dominant genera *Acropora* and
210 *Montipora* (interactive fixed effects of treatment and genus) using a binomial distribution,
211 logit link, and plot as a random factor. Model selection was performed through Akaike's
212 Information Criterion corrected for small sample sizes (AICc). Post-hoc comparisons were
213 made between morphologies using Tukey's tests.

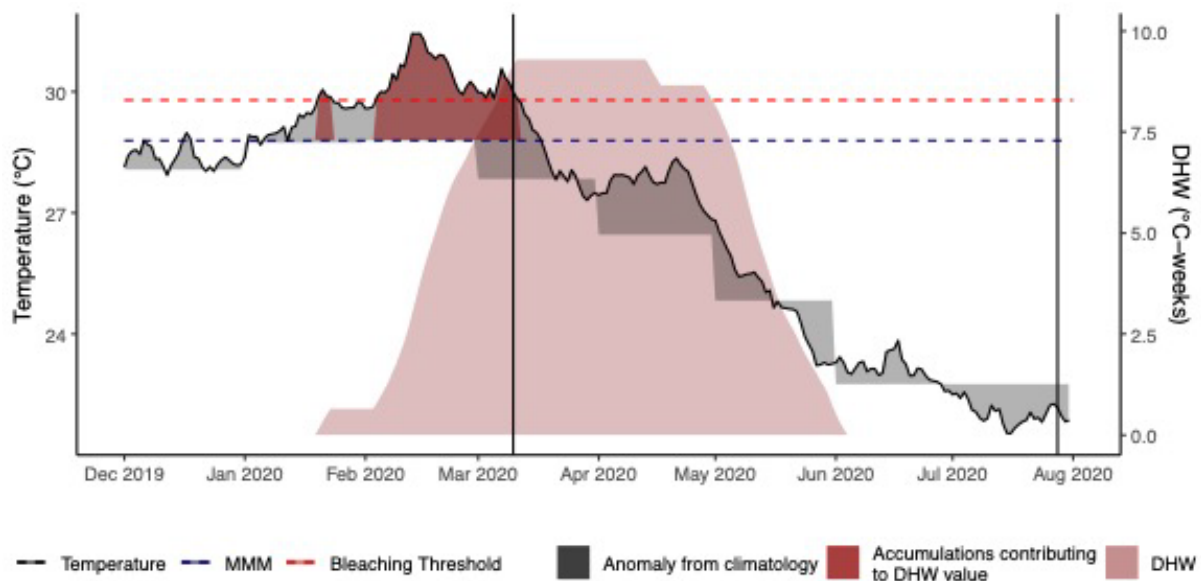
214 Because assessment of recovery of coral communities (July data) included more health
215 categories (i.e. healthy, unhealthy [bleached, partial mortality, bleached + partial mortality],
216 dead), differences in community health between treatments were assessed as the
217 percentage of the coral community within each health category. The generalised linear
218 mixed effect model assessed the response (percent of community) as a function of the fixed
219 factors treatment (control, removal), morphology, and health status, with plot as a random
220 factor. Due to the use of percentage data, the model incorporated a Beta distribution with
221 logit link. Post-hoc comparisons between treatments and health categories were made with
222 Tukey's tests.

223 The severity of bleaching (colony level response, % of live tissue bleached) was examined
224 using March data only, since bleaching severity implies a bleaching score of greater than
225 zero. A generalised linear mixed effects model was used with a Beta distribution (i.e.
226 percent bleaching) and logit link, where a small number (0.00001) was subtracted from fully
227 (100%) bleached colonies to fit the assumptions of a Beta family. The model incorporated
228 fixed factors (treatment, morphology) and plot as a random factor. Model selection using
229 AICc determined that the model including morphology only (not treatment) was most
230 parsimonious. However, because the aim of this study was to determine the role of
231 treatment (algae removal) on bleaching processes, the model incorporating treatment and
232 morphology as fixed factors was used for further analysis. The AICc value for the selected
233 model (treatment + morph) was within two units of the most parsimonious model (morph
234 only), and hence is considered robust. Model validation revealed significant deviation,
235 suggesting that the data do not fit a Beta distribution. However, since no other distribution
236 is considered appropriate to model percentage data, the model was used nonetheless. All
237 analyses were performed in R (version 4.0.5; R Core Team, 2021) using the packages
238 glmmTMB (Brooks et al., 2017), DHARMA (Hartig, 2021), MuMIn (Barton, 2020), emmeans
239 (Lenth, 2021), and ggplot2 (Wickham, 2016).

240 **3. Results**

241 *3.1. Seawater surface temperatures and accumulated heat stress*

242 Satellite-derived SST data indicate the magnitude of the heat stress experienced by coral
243 communities at Arthur Bay (Fig. 2), where the daily SST met or exceeded the thermal stress
244 threshold (i.e. 1 °C above MMM) for five weeks from early February to mid-March 2020,
245 peaking at 31.4 °C. The accumulation of daily heat stress (DHW) from mid- January to mid-
246 April (12-week period) peaked at 9.3 °C-weeks (Fig. 2).



247

248 **Fig. 2.** Satellite derived sea surface temperatures (SST) at Arthur Bay ($0.05^\circ \approx 5$ km
 249 resolution, black line) prior to and throughout the survey period. Heat stress, measured as
 250 DHW (light red shading), accumulates when SST is at or above the bleaching threshold
 251 (dashed red line). Grey shading indicates the difference between observed temperature and
 252 the climatological (long-term) monthly mean SST. Observed SSTs (black line) were
 253 consistently above the climatological monthly means from December 2019 until late May
 254 2020. DHW peaked at 9.3°C-weeks on 11 March 2020. Vertical lines indicate survey dates in
 255 March and July 2020.

256

257 3.2. Study site characteristics and macroalgae removal

258 In the benthic surveys, 16 coral genera were recorded in March, and each of these plus an
 259 additional seven genera were recorded in July (Supplementary Table S1). The coral
 260 community was dominated by encrusting corals (51%), followed by branching (29%) and
 261 massive (20%) morphologies. By genus, encrusting *Montipora* was most dominant (45% of
 262 community and 88% of the encrusting group), followed by branching *Acropora* (28% of
 263 community and 97% of the branching group), with a mix of other genera comprising the
 264 remainder of the community (e.g. *Turbinaria* 4%, *Dipsastrea* 4%, *Porites* 3%; Supplementary
 265 Table 1). The size distribution of corals was similar within control and removal plots, with
 266 both treatments dominated by small corals ≤ 40 cm (Supplementary Fig. S1).

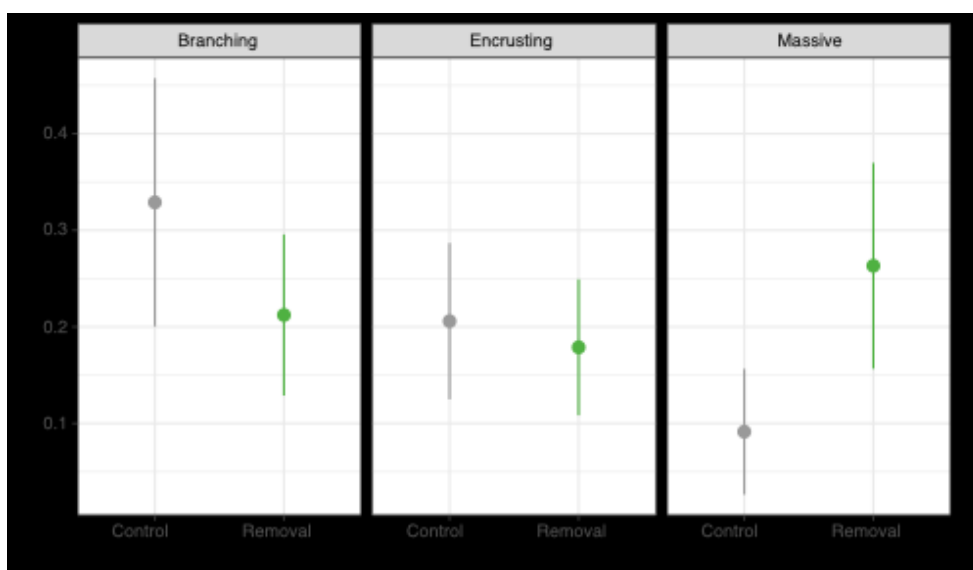
267 Removal of macroalgae in October 2019 yielded 101.5 kg algal biomass (wet weight) across
 268 the six designated removal plots ($16.9 \pm 1.6 \text{ kg plot}^{-1} = 0.68 \pm 0.06 \text{ kg m}^{-2}$;
 269 $\text{mean} \pm \text{SE}$). Prior to removal, mean macroalgal biomass (i.e. holdfast density and thallus
 270 height) did not vary significantly between the treatments ($t = 0.95$, $df = 10$, $p = 0.36$;
 271 Supplementary Fig. S2) though biomass was $\sim 15\%$ higher in control plots (0.34 kg algal
 272 biomass $\text{m}^{-2} \pm 0.04$ SE) compared to algal removal plots ($0.29 \pm 0.03 \text{ kg m}^{-2}$

273 2). Immediately following removal, macroalgae biomass was significantly reduced, being ~71%
274 lower than pre-removal ($0.08 \pm 0.01 \text{ kg biomass m}^{-2}$; $t = 7.7$, $df = 5.7$, $p < 0.001$;
275 Supplementary Fig. S2). In February 2020, during the peak algal growth period (Vuki and
276 Price, 1994), macroalgae biomass remained significantly lower (by ~63%) in the removal
277 plots ($0.25 \pm 0.06 \text{ kg m}^{-2}$) than in control plots ($0.68 \pm 0.16 \text{ kg m}^{-2}$; $t = 2.52$, $df = 10$, $p =$
278 0.03 ; Supplementary Fig. S2). Furthermore, the canopy height of macroalgae in removal
279 plots was approximately half the height of the canopy in control plots (mean height $30.9 \pm$
280 6.3 cm in control plots, $17.7 \pm 4.2 \text{ cm}$ in removal plots).

281 3.3. Community bleaching prevalence

282 More individual coral colonies were observed in removal plots (133 ± 18 colonies per plot;
283 mean \pm SE) than in control plots (92 ± 20 colonies per plot), though this difference was not
284 statistically significant ($t = -1.56$, $df = 10$, $p = 0.15$). While the higher number of colonies
285 counted in removal plots may be an artefact of detectability of corals below the macroalgal
286 canopy (Smith et al., 2022a), benthic survey methods were chosen instead of photo-
287 quadrats to minimise such canopy effects.

288 In March, the probability of bleaching was different between removal and control
289 treatments only for massive corals, for which removal plots (estimated marginal mean
290 probability of bleaching \pm SE; 0.26 ± 0.57) showed a significantly higher probability than
291 controls (0.09 ± 0.60 ; $t = -2.69$, $p = 0.01$; Fig. 3; Supplementary Table S2, Supplementary
292 Table S3). In contrast, bleaching prevalence for branching corals was statistically
293 indistinguishable in removal and control plots (0.21 ± 0.56 and 0.33 ± 0.57 , respectively; $t =$
294 1.58 , $p = 0.12$; Fig. 3; Supplementary Table S3). Encrusting morphology corals for the two
295 treatments were similarly indistinguishable (0.18 ± 0.56 removal, 0.21 ± 0.56 control; $t =$
296 0.51 , $p = 0.61$). The model moderately explained the variance in bleaching, with 39% of
297 variation explained by the fixed factors (marginal delta $R^2 = 0.39$, conditional delta $R^2 =$
298 0.74 ; (Nakagawa et al., 2017)).

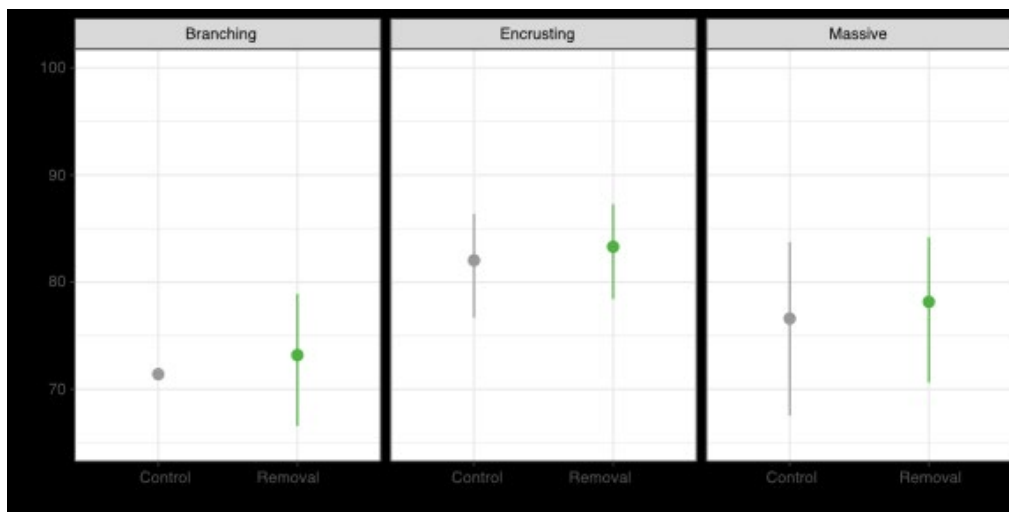


300 **Fig. 3.** Model estimated mean bleaching probability among dominant morphological groups
301 and treatments; grey represents control and green represents removal, lines represent 95%
302 confidence intervals.

303

304 These patterns were replicated in the analysis of bleaching prevalence in dominant genera,
305 where there was no significant difference in the probability of bleaching in control versus
306 removal plots for *Acropora* (model estimated mean probability of bleaching \pm SE: 0.34 ± 0.58
307 control, 0.18 ± 0.57 removal; $t = 1.94$, $p = 0.07$; Supplementary Fig. S3; Supplementary Table
308 S4) nor *Montipora* (0.21 ± 0.57 control, 0.15 ± 0.57 removal; $t = 0.95$, $p = 0.35$;
309 Supplementary Fig. S3; Supplementary Table S4).

310 Bleaching severity (i.e. percent of colony tissue bleached) was consistent across control and
311 removal plots ($z = 0.53$, $p = 0.60$), though varied between morphologies. Specifically,
312 branching colonies had lower bleaching severity than encrusting colonies ($t = -3.38$, $p =$
313 0.001), though all other pairwise comparisons were not statistically significant (Fig. 4,
314 Supplementary Table S6).



315

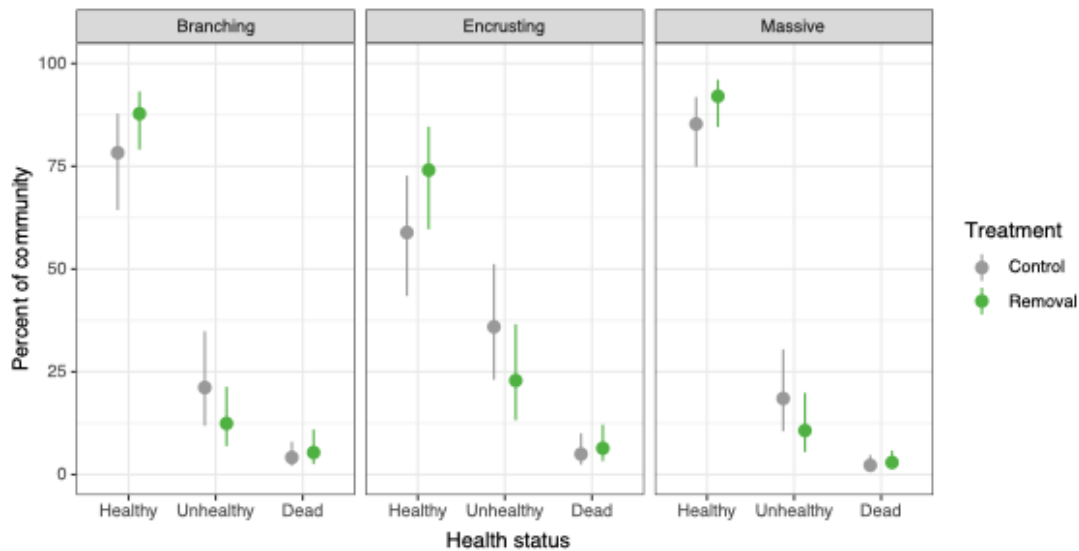
316 **Fig. 4.** Model estimated mean bleaching severity among dominant morphological groups
317 and treatments; grey represents control and green represents removal, lines represent 95%
318 confidence intervals.

319

320 3.4. Impact of macroalgae removal on coral recovery

321 In-water surveys of coral health status in July 2020 found that visual signs of bleaching were
322 still apparent in both control and removal plots four months after the peak heat stress. Signs
323 of poor health (bleaching, partial mortality, combined bleaching plus partial mortality) were
324 observed across all morphologies. Recent full mortality was observed in branching and
325 encrusting corals, though no massive morphology corals were observed as recently dead.
326 Averaged across morphologies, the representation of healthy colonies in the community

327 was significantly higher in removal plots ($86.1 \pm 3.0\%$, model estimated mean \pm SE)
 328 compared to controls ($75.6 \pm 4.3\%$; $t = 1.92$, $p = 0.04$; Fig. 5). Averaged across treatments,
 329 encrusting morphology corals had significantly lower representation of healthy colonies
 330 than both branching ($t = 2.32$, $p = 0.02$) and massive morphology corals ($t = -3.41$, $p <$
 331 0.001 ; Fig. 5). Unhealthy corals were more common in control plots than removal for all
 332 morphologies, but this difference was not statistically significant ($t = 1.92$, $p = 0.058$).



333

334 **Fig. 5.** Patterns of community health in July 2020, after the heat stress event had dissipated.
 335 Points are the model estimated means and lines are 95% confidence intervals.

336

337 4. Discussion

338 Coral bleaching was widespread in Arthur Bay in March 2020, affecting corals of all
 339 morphologies and sizes. Sea surface temperatures were extreme, culminating in DHW
 340 values exceeding those at this location during the GBR's most extreme mass bleaching
 341 events on record (e.g. 5.05 °C-weeks and 7.67 °C-weeks in the 2016 and 2017 mass
 342 bleaching events, respectively) (Hughes et al., 2019). A macroalgal canopy offered little
 343 protection to resident branching and encrusting morphology corals, with no discernible
 344 difference in bleaching prevalence between control and removal plots. Massive corals,
 345 however, appeared to benefit from macroalgal canopies, showing lower bleaching
 346 prevalence in control plots compared to removals. Following the thermal event, the
 347 presence of an algal canopy was associated with decreased recovery, with coral
 348 communities in control plots showing significantly lower percentages of healthy corals four
 349 months after the thermal peak.

350 Overall, patterns of bleaching were similar between control and removal plots, with
 351 approximately 20% of the coral community (averaged across morphologies) experiencing
 352 bleaching across both control and algal removal plots. Additionally, there were no
 353 differences in the severity of bleaching across treatments, with affected colonies
 354 experiencing approximately 80% of the colony tissue bleached (averaged across

355 morphologies). A number of factors could have contributed to the similarities in observed
356 bleaching patterns between control and treatment plots. For example, algal removal had
357 been conducted four months prior to the bleaching event, allowing for thallus regrowth
358 during the peak summer growth season (Vuki and Price, 1994). Dense algal canopies have
359 the potential to reduce light penetration, with one species of *Sargassum* reducing
360 photosynthetically active radiation (PAR) by 97% below thick canopies (Critchley et al.,
361 1990). While algal surveys detected significantly reduced algal canopy and biomass in
362 removal compared to control areas four months after removal at peak DHW, the regrowth
363 in the preceding months may have been enough to provide equivalent solar protection
364 across control and removal plots. Indeed, a reduction of light intensity through a variety of
365 mechanisms including cloud cover (Pratchett et al., 2013), depth (Baird et al., 2018),
366 turbidity (Sully and van Woesik, 2020), artificial shading (Coelho et al., 2017), and canopies
367 (Jompa and McCook, 1998; Stewart et al., 2021) has been associated with reduced bleaching
368 incidence and intensity. Alternately, it is possible that any protection provided by the
369 canopy was overcome by the severity of this thermal event.

370 Importantly, there were differences in bleaching response (susceptibility and severity)
371 among and between morphological groups. Massive morphology corals bleached
372 significantly more in removal plots, while branching and encrusting morphology corals
373 showed similar levels of bleaching in control and removal plots. Massive morphology corals
374 are generally more tolerant to simultaneous stressors (Darling et al., 2013), and hence may
375 be less likely to experience stress directly from macroalgal competition, which could explain
376 their tolerance to bleaching in control plots. The higher incidence of bleaching in removal
377 plots, however, suggests that the combined stress of heat with increased light intensity from
378 the canopy reduction pushed these corals beyond their tipping point (Smith and Birkeland,
379 2007). In contrast, branching corals are generally more susceptible to stress (Loya et al.,
380 2001; Mizerek et al., 2018), and the thermal extreme was likely sufficient to induce
381 bleaching across both control and removal plots, regardless of light intensity. However,
382 while not statistically significant, branching corals did display 1.5-fold lower bleaching levels
383 in removal plots. While considered to be susceptible to stress, branching corals also
384 generally display high phenotypic plasticity and acclimatisation potential (Palumbi et al.,
385 2014; Putnam et al., 2016). It is possible that the removal of algae well in advance of
386 bleaching triggered an acclimatory response to irradiance in branching morphology corals
387 that resulted in lower bleaching impact. Interestingly, branching morphology corals also
388 displayed the lowest severity, with significantly less tissue affected compared to encrusting
389 colonies (but not massives), which lends support to the hypothesis that these colonies
390 experienced acclimatisation. However, the severity of bleaching within branching colonies
391 was still high (over 70%), and hence any acclimatory response triggered was insufficient to
392 entirely prevent bleaching. Importantly, the taxonomic diversity within the massive
393 morphology group ($n = 13$ genera) was higher than the encrusting ($n = 7$ genera) and
394 branching ($n = 2$ genera) groups, and the patterns detected may be confounded by species-
395 level differences in susceptibility. Further research focussed on bleaching response of
396 individual massive-morphology genera would be valuable. For encrusting corals, while there
397 was no difference in bleaching susceptibility between control and removal plots, this
398 morphological group experienced on average the lowest overall probability of bleaching. It
399 is possible that these corals, which grow closely along the benthos, experienced the greatest
400 coverage of algal canopy, and that even the minor regrowth of algae in removal plots

401 offered some refuge. However, encrusting corals also experienced the highest severity of
402 bleaching, suggesting that protection from the canopy may have been patchy. Finally, the
403 small sample sizes across analyses may have prohibited statistical detection of an effect due
404 to low statistical power.

405 Macroalgae affected coral recovery four months after the peak of heat stress. In July 2020,
406 there were significantly higher proportions of healthy corals in removal plots compared to
407 control plots across all morphologies. Conversely, the representation of unhealthy corals
408 (those experiencing bleaching and/or partial mortality) was 1.7-fold higher in control plots
409 than in removal plots, though this difference was not statistically significant. Interestingly,
410 between morphologies, the encrusting group had the lowest proportion of healthy corals in
411 July, and this was significantly lower than both branching and massive morphotypes. Just as
412 their low profile on the benthos may have afforded these corals some protection during the
413 bleaching, it is possible that their low-lying morphologies increased their susceptibility to
414 mortality during the recovery phase due to increased competition with macroalgae. This
415 pattern has been observed in previous studies, where macroalgal competition can prevent
416 the recovery of coral communities after bleaching (Wilson et al., 2012; Donovan et al.,
417 2021). While the exact mechanism of impaired recovery remains to be elucidated, a re-
418 allocation of resources toward competition rather than repair from bleaching is one likely
419 explanation. Macroalgal competition is known to affect other metrics of coral fitness (e.g.
420 growth, fecundity), with these impacts also being explained as potential resource
421 reallocation toward competition (Tanner, 1995; Monteil et al., 2020; Fong and Todd, 2021;
422 Röfller et al., 2021).

423 While direct competitive interactions may explain patterns of bleaching and recovery in
424 control and removal plots, it is also possible that indirect mechanisms occur. Canopy-
425 forming macroalgae have the potential to alter hydrodynamic patterns, especially in the
426 boundary layer, such that resident corals experienced reduced flow regimes (Denny, 1988;
427 Duggins et al., 1990). High flow conditions have been observed to mediate impacts of heat
428 stress (Page et al., 2021). During the bleaching event, decreased flow rate in control plots
429 with abundant macroalgae may have created stagnant hot water, potentially causing
430 increased bleaching (though herein not statistically significant) in branching colonies
431 (Nakamura et al., 2003). During the recovery phase, higher flow rates in removal plots may
432 have similarly contributed to increased recovery (Nakamura et al., 2003).

433

434 In addition to altering flow regimes, macroalgae can alter surrounding seawater chemistry
435 through release of dissolved organic carbon (DOC). Fleshy macroalgae such as *Sargassum*
436 release DOC that is enriched in labile sugars, which supports growth of copiotrophic and
437 virulent microbial biomass (Haas et al., 2016), creating a positive feedback loop for
438 macroalgae growth and reinforcing reef degradation (Kline et al., 2006; Cárdenas et al.,
439 2018). While it is unlikely that bulk seawater chemistry at the experimental site would have
440 been altered by the relatively small scale of macroalgae removal, it is possible that fine-
441 scale differences in seawater and associated microbial communities in control versus
442 removal plots may have contributed to the bleaching patterns observed herein. Indeed,
443 enriched labile DOC has been implicated in increasing coral bleaching even in the absence of
444 heat or light stress (Pogoreutz et al., 2017). However, further research is needed to

445 determine the scale at which removal of macroalgae has the potential to alter surrounding
446 seawater chemistry and downstream microbial loops, and hence the role of macroalgae in
447 mitigating or exacerbating bleaching prevalence.

448 These results have several implications for management, particularly in the lens of
449 increasing reef restoration efforts worldwide. Novel interventions are being developed
450 globally to help corals resist the impacts of climate change. One important focus of such
451 interventions is reducing thermal and irradiance stress during summer heat waves.
452 Interventions such as reflective surface films, cloud brightening or seeding, seawater
453 fogging, and subtidal fans and shade cloths all aim to cool and/or shade resident corals to
454 prevent or reduce coral bleaching (Hardisty et al., 2019). The interactions of shading and
455 bleaching are complex, and herein we found little evidence of shading from canopy-forming
456 *Sargassum* mediating coral bleaching, despite previous reports of up to a 97% reduction in
457 light penetration by *Sargassum* canopies (Critchley et al., 1990). How the proposed
458 engineered solutions mitigate light and thermal stress, which drive the coral bleaching
459 response, will be critical to evaluate their potential benefit to reef ecosystems.

460 Because of the known negative interactions between corals and macroalgae, manual
461 removal of macroalgae has been proposed as one low-tech intervention option for boosting
462 local resilience. Proponents of the method suggest that reducing benthic macroalgae could
463 relieve competition for benthic space and reduce impacts on adult coral health and fitness
464 (Smith et al., 2022b). However, concerns have been raised that removing the canopy could
465 expose understory corals to excessive solar irradiance, especially if they are adapted to low-
466 light conditions. The results of this study suggest that the removal of canopy-forming
467 macroalgae does not significantly affect bleaching susceptibility. However, this study took
468 place several months after the removal of algae, allowing considerable regrowth, which may
469 have afforded some protection. Additionally, the regrowth period should have given
470 resident corals a chance to acclimatize to changes in light levels prior to warming waters,
471 though this did not appear to have significantly aided corals in removal plots (though
472 branching corals may have received some benefit) and may point to the severity of the
473 thermal event. It is also possible that the low sample size in this study may have lacked the
474 statistical power to detect a biological effect. Additionally, this study experienced
475 roadblocks due to the Covid-19 pandemic and would have benefitted from full community
476 censuses at multiple time points. Herein, bleaching observations were only made at the
477 peak of severe thermal stress. Especially during the onset of bleaching, differences in
478 susceptibility between control and removal plots, as well as between morphological groups,
479 may play out more clearly with multiple temporal observations, and could help support or
480 refute the hypothesis that pre-conditioning leads to reduced bleaching (Ainsworth et al.,
481 2016). Hence further study should examine if removing algae closer to the thermal
482 maximum results in changes to bleaching susceptibility. Studies across the full spectrum of
483 bleaching severity are also warranted, with the canopy potentially mitigating bleaching
484 under low to moderate heat stress periods. Future work on this topic should also be
485 focussed on coral juveniles, which may be more vulnerable to both thermal stress and
486 macroalgal competition. It is possible that adult corals are more robust, while recruits may
487 depend on shading during heat waves to survive early life phases. As managers look toward
488 novel approaches to boost coral reef resilience, benefits of removing macroalgae on the
489 GBR may be maximised by timing removal events before the annual mass spawning period

490 (September/October) to reduce competition for substrate for early life stages of coral, while
491 allowing regrowth of canopy prior to the summer thermal maxima (February/March).

492 **CRedit authorship contribution statement**

493 **Hillary A. Smith:** Conceptualization, Data curation, Formal analysis, Funding acquisition,
494 Investigation, Methodology, Project administration, Validation, Visualization, Writing –
495 original draft, Writing – review & editing. **Tara Prenzlau:** Conceptualization, Data curation,
496 Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Taylor**
497 **Whitman:** Investigation, Writing – review & editing. **Stella E. Fulton:** Investigation,
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501 Conceptualization, Funding acquisition, Project administration, Supervision, Writing –
502 review & editing.

503 **Declaration of Competing Interest**

504 The authors declare that they have no known competing financial interests or personal
505 relationships that could have appeared to influence the work reported in this paper.

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