

1    **Coral bleaching susceptibility is predictive of subsequent mortality within but not between**  
2    **coral species**

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4    Shayle Matsuda<sup>2</sup>, Ariana Huffmyer<sup>2</sup>, Elizabeth A. Lenz<sup>2</sup>, Jen Davidson<sup>2</sup>, Joshua Hancock<sup>2</sup>,  
5    Ariana Przybylowski<sup>1</sup>, Teegan Innis<sup>1</sup>, Ruth D. Gates<sup>2</sup>, Katie L. Barott<sup>1\*</sup>

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7    <sup>1</sup>Department of Biology, University of Pennsylvania, Philadelphia, PA USA

8    <sup>2</sup>Hawai'i Institute of Marine Biology, University of Hawai'i, Kaneohe, HI USA

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10    **\*Correspondence:** Katie Barott, [kbarott@sas.upenn.edu](mailto:kbarott@sas.upenn.edu)

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14

15    **Running Title:** Coral bleaching recovery in Hawai'i

16

17 **Abstract**

18

19 Marine heat waves instigated by anthropogenic climate change are causing increasingly frequent  
20 and severe coral bleaching events that often lead to widespread coral mortality. While  
21 community-wide increases in coral mortality following bleaching events have been documented  
22 on reefs around the world, the ecological consequences for conspecific individual colonies  
23 exhibiting contrasting phenotypes during thermal stress (e.g. bleached vs. not bleached) are not  
24 well understood. Here we describe the ecological outcomes of colonies of the two dominant reef-  
25 building coral species in Kāne'ohe Bay, Hawai'i, *Montipora capitata* and *Porites compressa*,  
26 that exhibited either a bleaching susceptible phenotype (bleached) or resistant phenotype (non-  
27 bleached) following the second of two consecutive coral bleaching events in Hawai'i in 2015.  
28 Conspecific pairs of adjacent bleaching susceptible vs. resistant corals were tagged on patch  
29 reefs in two regions of Kāne'ohe Bay with different seawater residence times and terrestrial  
30 influence. The ecological consequences (symbiont recovery and mortality) were monitored for  
31 two years following the peak of the bleaching event. Bleaching susceptible corals suffered higher  
32 partial mortality than bleaching resistant corals of the same species in the first 6 months  
33 following thermal stress. Surprisingly, *P. compressa* had greater resilience following bleaching  
34 (faster pigment recovery and lower post-bleaching mortality) than *M. capitata*, despite having  
35 less resistance to bleaching (higher bleaching prevalence and severity). These differences  
36 indicate that bleaching susceptibility of a species is not always a good predictor of mortality  
37 following a bleaching event. By tracking the fate of individual colonies of resistant and  
38 susceptible phenotypes, contrasting ecological consequences of thermal stress were revealed that  
39 were undetectable at the population level. Furthermore, this approach revealed individuals that  
40 underwent particularly rapid recovery from mortality, including some colonies over a meter in  
41 diameter that recovered all live tissue cover from >60% partial mortality within just one year.  
42 These coral pairs continue to be maintained and monitored in the field, serving as a “living  
43 library” for future investigations on the ecology and physiology of coral bleaching.

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46

47 **Introduction**

48         Ocean warming due to anthropogenic climate change has caused an increase in the  
49 frequency and severity of coral bleaching, a visually striking stress response where the coral host  
50 loses its endosymbiotic algae (dinoflagellates of the family Symbiodiniaceae) thus revealing the  
51 white coral skeleton beneath the translucent animal tissue (Gates *et al.*, 1992; Putnam *et al.*,  
52 2017). In this nutritional symbiosis, corals are obligate partners that require the algae for the  
53 majority of their energy (Muscatine and Porter, 1977; Muller-Parker *et al.*, 2015). Because of  
54 coral dependence on this partnership, prolonged heat waves that cause sustained coral bleaching  
55 can lead to depletion of the host's energy supply and reserves (Grottoli *et al.*, 2004; Rodrigues  
56 and Grottoli, 2007; Imbs and Yakovleva, 2012; Wall *et al.*, 2019). This stress can elicit a variety  
57 of sublethal effects, including declines in growth and reproduction (Ward *et al.*, 2000; Baird and  
58 Marshall, 2002; Baker *et al.*, 2008; Hughes *et al.*, 2019), and at worst can result in widespread  
59 coral mortality (Loya *et al.*, 2001; McClanahan, 2004; Baker *et al.*, 2008; Eakin *et al.*, 2010;  
60 Hughes *et al.*, 2017; Sully *et al.*, 2019). The loss of live coral cover is often followed by rapid  
61 erosion of the structural framework of the reef (Hughes, Kerry, *et al.*, 2018; Fordyce *et al.*, 2019;  
62 Leggat *et al.*, 2019), reducing habitat complexity (Magel *et al.*, 2019) and negatively impacting  
63 the diversity of the broader reef community (e.g. fish (Pratchett *et al.*, 2011; Darling *et al.*, 2017;  
64 Richardson *et al.*, 2018). Coral mortality following bleaching can also alter the structure of the  
65 coral community itself, as bleaching-susceptible species are lost from the community (Loya *et  
66 al.*, 2001; McClanahan, 2004; Baker *et al.*, 2008; Bahr *et al.*, 2017; Hughes *et al.*, 2017) while  
67 stress-tolerant species remain (Edmunds, 2018; Hughes, Kerry, *et al.*, 2018) and “weedy” genera  
68 that are better suited for rapid recovery following bleaching become dominant (Darling *et al.*,  
69 2012; Edmunds, 2018). These changes in community composition alter the ecological function  
70 of the reef (Alvarez-Filip *et al.*, 2013), which alongside the structural degradation following  
71 bleaching leads to declines in ecosystem goods and services ranging from fisheries production to  
72 coastal protection and tourism (Munday *et al.* 2008).

73         The susceptibility of a reef system to coral bleaching during a marine heat wave depends  
74 on a combination of physical and biological factors (Swain *et al.*, 2016). Differences in the local  
75 microenvironment (e.g. flow, turbidity, surface reflectance, internal waves, etc.) can ameliorate  
76 or exacerbate the magnitude of thermal stress and lead to differential bleaching and mortality on  
77 nearby reefs (Anthony *et al.*, 2007; Wyatt *et al.*, 2019). Local temperature dynamics can also

78 influence coral bleaching by altering the physiological tolerance of coral populations to heat  
79 stress. For example, corals exposed to high diel temperature variability often have higher thermal  
80 tolerance and greater resistance to bleaching than nearby conspecifics in more stable regimes  
81 (Putnam and Edmunds, 2011; Palumbi *et al.*, 2014; Schoepf *et al.*, 2015, 2019; Barshis *et al.*,  
82 2018). These data indicate that environmental history of individuals and populations plays a  
83 significant role in determining coral responses to stress, and is likely driven by a combination of  
84 both acclimatization (Bay *et al.*, 2013; Bay and Palumbi, 2015; Kenkel and Matz, 2016) and  
85 adaptation (Barshis *et al.*, 2013, 2018; Palumbi *et al.*, 2014; Matz *et al.*, 2018). On a global scale,  
86 there is recent evidence that the temperature threshold for coral bleaching has risen in  
87 correspondence with global warming, suggesting widespread acclimatization and/or adaptation  
88 (Coles *et al.*, 2018; DeCarlo *et al.*, 2019). Alternatively, differences in the composition of coral  
89 communities between reefs can also influence bleaching extent due to species-specific  
90 differences in thermal tolerance (Rowan *et al.*, 1997; Berkelmans and Van Oppen, 2006;  
91 Sampayo *et al.*, 2008; Swain *et al.*, 2016; Edmunds, 2018). Indeed, the global loss of many  
92 thermally sensitive coral species from reef communities (e.g. (Loya *et al.*, 2001; McClanahan,  
93 2004; Hughes, Kerry, *et al.*, 2018; Kim *et al.*, 2019) may be a contributing factor in rising  
94 bleaching thresholds. Similarly, intraspecific diversity may also contribute to changes in the  
95 bleaching threshold if tolerant genotypes persist in populations and sensitive genotypes are lost.  
96 While this would promote reef resistance to bleaching, the ecological consequences of  
97 corresponding reductions in genetic diversity remain to be seen.

98 The effect of intraspecific diversity in bleaching susceptibility on downstream ecological  
99 outcomes of individuals with contrasting phenotypes (i.e. bleached vs. not bleached) is not well  
100 understood, despite an abundance of data demonstrating that interspecific differences in  
101 bleaching susceptibility are predictive of mortality such that species resistant to bleaching have  
102 lower mortality than susceptible species (Loya *et al.*, 2001; McClanahan, 2004; Baker *et al.*,  
103 2008; Bahr *et al.*, 2017; Hughes *et al.*, 2017). Kāneōhe Bay, Hawai'i, located on the northeast  
104 coast of Oahu, is an opportune system for investigating this question of how intraspecific  
105 variability in coral responses to thermal bleaching events driven by climate change influence  
106 coral survival. The two dominant reef-building coral species in the bay, *Montipora capitata* and  
107 *Porites compressa*, both exhibit differences in thermal performance within and between species  
108 during bleaching (Grottoli *et al.*, 2006; Cunning *et al.*, 2016; Wall *et al.*, 2019). Differences in

109 symbiont associations and nutritional plasticity are hypothesized to influence bleaching  
110 resistance and resilience between these two species (Grottoli *et al.*, 2006; Cunning *et al.*, 2016;  
111 Wall *et al.*, 2019), while the species of symbionts associated with *M. capitata* contributes to  
112 differences in thermal tolerance (Cunning *et al.*, 2016). However, the influence of intraspecific  
113 variation in bleaching susceptibility on ecological outcomes following bleaching events remains  
114 unexplored. Understanding how intraspecific variation influences differential outcomes  
115 following thermal stress are critical for understanding how the increasing frequency and severity  
116 of coral bleaching events will impact the function of these important ecosystems.

117 In order to better understand how differences in individual colony responses to thermal  
118 stress influences ecological outcomes following a coral bleaching event, we conducted a 2-year  
119 monitoring study to characterize the recovery dynamics of bleaching susceptible and bleaching  
120 resistant coral colonies of *M. capitata* and *P. compressa* following a regional bleaching event in  
121 Kāneōhe Bay in 2015. Hawai'i experienced anomalously high seawater temperatures in late  
122 summer (August – September) of 2015, resulting in widespread coral bleaching throughout the  
123 region (Bahr *et al.*, 2017). This was the first consecutive coral bleaching event ever observed on  
124 Hawaiian reefs, occurring one year following a regional bleaching event in 2014 (Bahr *et al.*,  
125 2015). A total of 22 conspecific pairs of adjacent corals with contrasting bleaching phenotypes  
126 (bleaching susceptible or bleaching resistant) of each species were tagged and georeferenced at  
127 each of two reefs in the bay with different environmental conditions. Coral pigmentation  
128 recovery and mortality were monitored periodically over the following two years to examine  
129 how bleaching influences the ecological trajectories within and between species. These colonies  
130 are maintained on a regular basis for the purpose of establishing these corals as a living library  
131 archived *in situ* for use in future research on coral bleaching mechanisms, thermal physiology,  
132 and climate change resilience.

133

## 134 **Materials and Methods**

### 135 *Site selection and characterization*

136 This study was initiated during the peak of the 2015 coral bleaching event in Kāneōhe Bay,  
137 Oahu. The lagoon of Kāneōhe Bay consists of a shallow network of fringing and patch reefs  
138 protected by a barrier reef (Bahr *et al.*, 2015), which restricts seawater exchange with the open  
139 ocean leading to regions within the bay with high and low seawater residence times (Lowe *et al.*,

140 2009). Two patch reefs dominated by the reef-building corals *Montipora capitata* and *Porites*  
141 *compressa* from two different regions of the bay were selected for this study: 1) Inner Lagoon  
142 region: patch reef 4 (PR4; 21.4339°N, 157.7984°W), an inshore reef with relatively high  
143 terrestrial influence (e.g. sedimentation, fresh water and nutrient run-off) and long (>30 days)  
144 seawater residence time (Lowe *et al.*, 2009) and 2) Outer Lagoon region: patch reef 13 (PR13;  
145 21.4515°N, 157.7966°W), a seaward reef with less terrestrial influence and short (<24 hour)  
146 seawater residence time (Lowe *et al.*, 2009); Figure 1A,B). Temperature loggers (Onset U22  
147 Hobo; 0.21°C accuracy; 0.02°C resolution) were deployed on the benthos of each reef at ~2 m  
148 depth from October 2015 through October 2016, and seawater temperature was recorded in 15-  
149 minute intervals. The loggers were cross calibrated in an aquarium prior to deployment. Because  
150 these loggers were not deployed until after the peak of the heatwave, data from nearby  
151 monitoring stations within each region were used to determine if there were any differences in  
152 cumulative heat stress between the two regions. These data were collected from PR12, located  
153 ~100 m from PR13 in Outer Lagoon (Figure 1D; Table 1; data courtesy of the Division of  
154 Aquatic Resources of the State of Hawaii<sup>1</sup>), and PR1 (Coconut Island; data from PACIOOS<sup>2</sup>), in  
155 the same Inner Lagoon flow regime as PR4. Degree heating weeks (DHW) were calculated for  
156 the inner and outer lagoon reefs from the PR1 and PR12 data, respectively, according to the  
157 methods described by (Liu *et al.*, 2013).

158

#### 159 *Characterization of benthic community composition and coral bleaching responses*

160 Surveys were performed to assess benthic community composition and coral bleaching responses  
161 during the 2015 bleaching event and periodically thereafter for two years. Four surveys were  
162 conducted at each site for each time point along the reef slope in parallel to the reef crest at a  
163 depth of 2 m ( $\pm 1$  m). Each survey was carried out along a 40 m transect laid parallel to the reef  
164 crest. A photo-quadrat ( $0.33 \text{ m}^2$ ) was placed on the benthos and images were taken every 2 m  
165 along the transect using an underwater camera (Canon PowerShot or Olympus TG5). Images  
166 were analyzed using Coral Point Counts in excel (CPCE; 100 points per image). Corals were  
167 identified to species, and bleaching severity (white, pale, or pigmented) was recorded. Bleaching  
168 prevalence was calculated as the proportion of live coral affected by bleaching (white or pale).

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<sup>1</sup> Division of Aquatic Resources, State of Hawaii: [DLNR.aquatics@hawaii.gov](mailto:DLNR.aquatics@hawaii.gov); <http://dlnr.hawaii.gov/dar/>

<sup>2</sup> <http://www.pacioos.hawaii.edu/weather/obs-mokuoloe/>

169 All other organisms were classified into functional groups (turf algae, crustose coralline algae  
170 (CCA), macroalgae, sediment and sand, sponges).

171

172 *Monitoring of bleaching resistant and susceptible corals*

173 Individual coral colonies of *M. capitata* and *P. compressa* with contrasting bleaching phenotypes  
174 were identified at the peak of the bleaching event from late September through the first week of  
175 November 2015. Bleaching resistant corals were defined as those that remained pigmented  
176 during the bleaching event, while bleaching susceptible corals were defined as those that  
177 appeared completely white. All corals were located along the edge of the reef crest (~1 m depth)  
178 and down the reef slope (up to ~3 m depth). A plastic cattle tag with a unique ID was attached to  
179 each colony, the colony was photographed, and its GPS location was recorded. All tagged  
180 colonies were conspecific pairs of colonies with contrasting bleaching phenotypes that were  
181 located adjacent to one another on the reef (e.g. Figure 4). A total of 22 pairs (44 colonies) of  
182 each species were tagged at each of two reefs (PR4 and PR13; Supplementary Data 1). This  
183 paired design eliminated the potential for differences in the local microenvironment experienced  
184 by one phenotype but not the other (e.g. light intensity, flow) to confound interpretation of  
185 differences in their ecological outcomes. This paired design is also powerful because it can  
186 distinguish between mortality related to thermal stress (both phenotypes) and mortality related to  
187 symbiont loss (bleached phenotypes). Bleaching recovery (where applicable) and partial  
188 mortality of tagged individuals were monitored every ~6 weeks for the first 6 months following  
189 the bleaching event, then once every 6 months up to 24 months following the bleaching event. At  
190 each time point, colonies were photographed and visual observations of their bleaching status  
191 were recorded. Corals in both the benthic surveys and the tagged individuals were given a color  
192 score based on their visual color: 1) white (>80% of colony white with no visible pigmentation);  
193 2) pale (>10% colony affected by pigment loss); or 3) fully pigmented (<10% colony with any  
194 pale coloration). Partial mortality was quantified in 20% intervals (0 - 100%) from the  
195 photographs. The mean color scores and partial mortality for each species were calculated for  
196 each bleaching phenotype and site at each time point. For colonies with a missing observation,  
197 mortality scores were estimated using the mortality score of the previous time point. This is a  
198 conservative estimate of mortality (i.e. minimum possible mortality at that time point), and in  
199 most cases mortality scores did not change surrounding the missing observation. Missing

200 observations of color scores were never interpolated across the time series due to the possibility  
201 for rapid loss or recovery of pigmentation.

202

203 *Statistical analyses*

204 Statistical analyses were conducted in R v. 3.6.1 (R Core Team, 2017). Seawater temperature  
205 means were compared using Wilcoxon rank sum tests. Differences in coral bleaching prevalence  
206 and severity from the benthic survey data were compared between species and reefs using 1- or  
207 2-way ANOVAs. For the tagged colonies, the effect of reef lagoon and bleaching phenotype  
208 (whether a colony was bleached or pigmented in Nov. 2015) on coral pigmentation and tissue  
209 mortality were analyzed at 1.5, 3, 4.5 and 6-months post-bleaching using ANOVAs. In addition,  
210 the rates of pigmentation recovery and the rates of tissue loss during the first three and six  
211 months following bleaching were each compared between bleaching phenotypes and reefs using  
212 2-way ANOVAs. To control for local environment, a 1-way ANOVA was used to test for the  
213 effect of lagoon on the differences in pigmentation score and mortality score between bleaching  
214 phenotypes within each pair (*M. capitata*: PR13, n=22 pairs; PR4, n=21 pairs; *P. compressa*:  
215 PR13, n=20 pairs; PR4, n=21 pairs). For all approaches (all colonies, paired colonies, differences  
216 between pairs, and transect data), Tukey honest significant post hoc tests were used to test for  
217 significant pairwise differences in these main effects. To test hypotheses about the differential  
218 recovery of bleaching susceptible versus bleaching resistant corals, we used a three way  
219 ANOVA model to examine how mean pigmentation and mean tissue loss in each species  
220 differed by time, lagoon and bleaching history (B2015) as factorial fixed effects (Table 2&3).  
221 We also ran models using pigment or tissue loss difference in adjacent coral pairs as the response  
222 variable to account for spatial heterogeneity within sites. Coral pairs with missing measurements  
223 were excluded from paired analyses, but this had no effect on patterns of statistical significance  
224 (Table 2&3 and Supplementary Table1&2). Models for both 3- and 6-month recovery periods  
225 were contrasted in both paired and unpaired analyses (Table 1&2).

226

227 **Results**

228 *Temperature dynamics throughout bleaching and recovery*

229 Seawater temperatures exceeded 30°C across Kāne'ohe Bay in late September 2015 (Figure 1D;  
230 (Bahr *et al.*, 2017). The average maximum daily seawater temperature during the heatwave was

231 0.44°C warmer in the Inner Lagoon (29.08°C) than the Outer Lagoon (28.64°C, Table 1). This  
232 resulted in higher accumulated heat stress, with a total of 5.84 degree heating weeks (DHW) at  
233 Inner Lagoon versus 1.77 DHW at the Outer Lagoon (Table 1). During the recovery period  
234 following the heatwave, temperature dynamics were not significantly different between the two  
235 regions (Figure 1D; Table 1).

236

237 *Benthic community composition*

238 Coral cover was significantly higher at PR13 in the Outer Lagoon (80%  $\pm$  4.2%; Figure 2B) than  
239 at PR4 in the Inner Lagoon (52%  $\pm$  6.0%; Figure 2A) at the initiation of this study (post hoc  
240 p=0.01, Supplementary Table 3). Coral cover did not change significantly at either site over the  
241 course of the two year bleaching recovery period (Figure 2; Supplementary Table 4). The coral  
242 community at PR13 was dominated by *P. compressa* throughout the time series (62-77% of live  
243 coral cover) relative to *M. capitata* (23-38% of live coral cover). The relative abundance of each  
244 species at PR4 was 54-63% for *P. compressa* vs. 37-46% for *M. capitata*. Turf algae were the  
245 second most abundant functional group at both reefs, comprising 6-10% of the benthos at PR13  
246 and 25-40% at PR4. Sediments were also common along the benthos at PR4 (8.5-21%; Figure  
247 2A), but were found in low abundance at PR13 (<1%; Figure 2B). Both reefs had a low  
248 abundance (<5%) of macroalgae, crustose coralline algae (CCA) and sponges. PR4 had an  
249 abundance of small filter feeders (e.g. boring oysters and sponges) that were not readily apparent  
250 on photo-quadrat images but were observed by divers/snorkelers during surveys. This reef also  
251 typically had low visibility (<5 m; Figure 1C), whereas PR13 tended to have higher visibility  
252 (~20-30 m, personal observations; Figure 1B).

253

254 *Initial coral bleaching prevalence and severity differed between species and reefs*

255 Coral tagging and benthic surveys were initiated during the peak extent of bleaching in  
256 Kāneōhe Bay in late September through October 2015 (Bahr *et al.*, 2017). At that time, there  
257 was a higher prevalence of bleaching and paling corals (proportion of live coral that was white or  
258 pale) for both species at PR4 in the Inner Lagoon: 69%  $\pm$  3% at PR4 vs. 39%  $\pm$  12% at PR13 for  
259 *M. capitata*; 87%  $\pm$  7% at PR4 vs. 45%  $\pm$  5% at PR13 for *P. compressa* (post hoc p<0.05; Figure  
260 3; Supplementary Table 5). Within reefs, the prevalence of completely bleached (white) tissue  
261 was lower for *M. capitata* (26%  $\pm$  6% of all live tissue) than for *P. compressa* (71%  $\pm$  10% of all

262 live tissue) at PR4 ( $p<0.01$ ; Supplementary Table 6; Supplementary Figure 1), whereas there was  
263 no significant difference between species at PR13 (Figure 3; Supplementary Table 6). Bleaching  
264 severity (the proportion of affected tissue that was completely bleached) was higher for *P.*  
265 *compressa* at PR4 ( $80\% \pm 5\%$ ) than for *M. capitata* ( $37\% \pm 7\%$ , Figure 3;  $p<0.01$ ,  
266 Supplementary Table 7). This high level of bleaching severity for *P. compressa* at PR4 was also  
267 higher than this species suffered at PR13 ( $29\% \pm 10\%$ ; post hoc  $p<0.01$ ; Supplementary Table  
268 7), whereas bleaching severity did not differ significantly between sites for *M. capitata* ( $33\% \pm$   
269  $5\%$  at PR13 vs.  $37\% \pm 7\%$  at PR4;  $p>0.05$ ; Supplementary Table 8).

270

271 *Coral bleaching prevalence differs between species and reefs throughout recovery*  
272 Bleaching prevalence rapidly decreased for *P. compressa* at both reefs, with a 97% decrease in  
273 bleaching prevalence observed after 1.5 months of recovery at PR13 to <2% overall prevalence,  
274 and a 89% decrease at PR4 to <10% prevalence (Figure 3). In contrast, bleaching prevalence in  
275 *M. capitata* declined more slowly, with a mean decrease of 67% at the PR4 versus only a 9%  
276 decrease at PR13 after 1.5 months. At that point, <3% of *M. capitata* remained fully bleached at  
277 either site, and 20-33% remained pale. In contrast to peak bleaching, coral bleaching prevalence  
278 was significantly higher for *M. capitata* than *P. compressa* at each time point in the first year of  
279 recovery ( $p<0.01$ ; Supplementary Table 9). Initial differences in bleaching prevalence between  
280 reefs at the peak of bleaching also disappeared beginning at 1.5 months of recovery for *M.*  
281 *capitata* and 3 months of recovery for *P. compressa* ( $p>0.05$ , Supplementary Table 10; Figure 3).  
282 Interestingly, after several months of declining prevalence, the seasonal peak in water  
283 temperatures in September 2016 (Month 10; Figure 1D) corresponded with an increase in the  
284 prevalence of pale *M. capitata* at both reefs (Figure 3A,B). *P. compressa* pigmentation did not  
285 appear affected by this seasonal warming, and bleaching prevalence remained below 2% from  
286 1.5 months of recovery onward (Figure 3C,D).

287

288 *Pigmentation recovery dynamics of individual coral colonies following thermal stress*  
289 Coral pigmentation increased significantly over time for bleached colonies of both *M. capitata*  
290 and *P. compressa*, ( $p < 0.01$ ; Supplementary Table 11), while bleaching resistant individuals  
291 remained pigmented throughout the entire 24 month recovery period (Figures 4&5). The  
292 difference in color scores between bleaching susceptible and resistant coral pairs shrank

293 significantly over time ( $p<0.01$ ; Table 2), indicating significant recovery from bleaching. Over  
294 both 3- and 6-month recovery periods, the temporal trajectory of susceptible and resistant corals  
295 differed significantly between sites in both coral species ( $p<0.05$ ; Table 2); for *M. capitata*,  
296 there was a larger difference between pairs at PR13 than PR4 during the 3-6 month timepoints,  
297 while for *P. compressa* there was not (indicative of a full recovery). The statistical patterns were  
298 robust when analyzing paired differences between susceptible and resistant corals as the response  
299 variable (Supplementary Table 12; Supplementary Figure 2). Mean pigmentation did not differ  
300 between sites in *M. capitata* in the first 6 months ( $p>0.05$ ), but *P. compressa* exhibited greater  
301 overall pigmentation at PR13 than at PR4 ( $p<0.01$ ; Table 2). The timing of pigmentation  
302 recovery of the bleaching susceptible colonies differed between species. Bleaching susceptible  
303 colonies of *P. compressa* remained distinguishable from resistant colonies 1.5 months post peak  
304 bleaching ( $p<0.01$ ), but recovered full visual pigmentation by three months at both reefs ( $p>0.05$ ;  
305 Supplementary Table 11; Figure 5C,D). In contrast, recovery was slower for *M. capitata*, which  
306 on average did not recover full pigmentation within the first 6 months ( $p<0.01$ , Supplementary  
307 Table 11). Only 31% of bleaching susceptible *M. capitata* had fully recovered pigmentation at  
308 PR4 after 3 months, while none had fully recovered at PR13 (Figure 5A,B), resulting in a  
309 significantly smaller mean difference between susceptible and resistant corals at PR4 relative to  
310 PR13 at month 3 ( $p=0.03$ ), which remained so through month 6 of recovery ( $p=0.02$ ;  
311 Supplementary Table 11). There was a decrease in the mean pigmentation score of bleaching  
312 susceptible colonies of *M. capitata* in the late summer of 2016 (month 10), mirroring the  
313 increased prevalence of pale *M. capitata* observed in the benthic survey data (Figure 5A,B). This  
314 seasonal paling was not observed for *P. compressa* colonies of either bleaching susceptibility  
315 phenotype (Figure 5C,D). Full pigmentation recovery for bleaching susceptible *M. capitata*  
316 colonies took as long as 24 months at PR4, going from 25% of individuals with full pigmentation  
317 at 18 months to 94% at 24 months (Figure 5A). At PR13, most bleaching susceptible *M. capitata*  
318 colonies (68%) remained pale for the entire 24-month duration of this study (Figure 5B).  
319

### 320 *Colony mortality following bleaching differs between bleaching phenotypes*

321 Partial mortality increased significantly for both species in the first 6 months following the  
322 bleaching event regardless of bleaching phenotype ( $p<0.02$ ; Table 3; Figure 6). Bleaching  
323 resistant colonies had significantly less cumulative partial mortality than bleaching susceptible

324 colonies across both sites during this same time frame (Table 2;  $p<0.01$ ). Partial mortality also  
325 differed significantly between the two sites, with both species undergoing higher partial  
326 mortality at PR4 ( $p<0.02$ ; Table 2). Differences in tissue loss between susceptible and resistant  
327 colonies remained different between species during the first 6 months of recovery ( $p<0.01$ ; Table  
328 3). The statistical patterns did not differ when analyzing paired differences as the response  
329 variable in all cases except one (Supplementary Table 11). Interestingly, in *M. capitata*, during  
330 the first 3 months there was no significant effect of the three-way interaction of month, lagoon  
331 and bleaching history ( $p>0.05$ ); however, there was when controlling for location (paired  
332 differences) ( $p=0.03$ ; Supplementary Table 12; Supplementary Figure 2), suggesting spatial  
333 location on the reef influences partial mortality following thermal stress.

334 Bleaching susceptible colonies of both coral species had higher rates of tissue loss in the  
335 first three months following the bleaching event than bleaching resistant corals (post hoc  $p <$   
336 0.01; Supplementary Table 12; Figure 6). Site was also a significant factor for the rate of tissue  
337 loss for *M. capitata* but not *P. compressa*, as the rate of tissue loss in the first three months for  
338 *M. capitata* was significantly higher at PR4 than PR13 (post hoc  $p<0.01$ ; Supplementary Table  
339 13; Figure 6A,B). Cumulative partial mortality of bleaching susceptible corals in the first 6  
340 months was relatively low (~17%) for *M. capitata* at PR13 and *P. compressa* at both sites  
341 (Figure 6C,D). This was in contrast to the higher partial mortality of both bleaching resistant and  
342 bleaching susceptible colonies of *M. capitata* at PR4 (20% and 51% mortality, respectively;  
343 Figure 6C,D). Partial mortality in bleaching susceptible colonies of *P. compressa* was  
344 significantly greater than bleaching resistant colonies at PR13 in the first three months following  
345 bleaching (post hoc  $p<0.01$ ), after which there was no difference between lagoons  
346 (Supplementary Table 12). At three months of recovery, bleaching susceptible *M. capitata* also  
347 suffered only ~13% tissue loss at PR13, but had significantly higher partial mortality at PR4  
348 (46% at 3 months (post hoc  $p < 0.01$ ; Supplementary Table 12). Bleaching susceptible *M.*  
349 *capitata* at PR13 did not differ from bleaching resistant colonies at 3 months (post hoc  $p = 0.49$ ),  
350 whereas there was a difference between phenotypes at PR4 (post hoc  $p <0.01$ ; Supplementary  
351 Table 12). During the two year recovery period, only five colonies (one *P. compressa* and four  
352 *M. capitata*) experienced full mortality and all were located at PR4. Tissue loss slowed around 6  
353 months following the bleaching event for bleaching susceptible individuals of both species at  
354 both reefs (Figure 6). While bleaching resistant corals showed very low partial mortality in the

355 first 6 months following the heat wave (<25% for both species at both sites; Figure 6), tissue loss  
356 gradually increased over the following 24 months, with *M. capitata* at PR4 experiencing the  
357 highest loss at 24 months. Of all the corals experiencing partial mortality, *P. compressa* at PR13  
358 was the only group that showed an increase in live tissue within 24 months of the bleaching  
359 event (Figure 6D). For example, *P. compressa* (TagID 225; PR13) suffered ~60% mortality in  
360 the first two months after undergoing bleaching, but had regrown to nearly 100% live tissue  
361 within one year.

362

### 363 **Discussion**

364 *Bleaching susceptibility of a species is not predictive of mortality*

365 *P. compressa* experienced higher bleaching prevalence and severity than *M. capitata* at the inner  
366 lagoon reef, and yet bleaching susceptible individuals of *P. compressa* experienced significantly  
367 less partial mortality than bleaching susceptible individuals of *M. capitata* at this same site.

368 These results are in contrast to the common pattern of greater bleaching prevalence of a species  
369 leading to greater mortality (Baird and Marshall, 2002; Jones, 2008; Hughes, Kerry, *et al.*, 2018),  
370 and may reflect two different species-specific thermal stress response strategies. In the case of *M.*  
371 *capitata*, this species resisted bleaching to a greater extent, but individuals that bleached had  
372 lower resilience following bleaching (slower recovery and higher mortality). *P. compressa*, on  
373 the other hand, was more susceptible to bleaching but had greater resilience following bleaching  
374 (faster recovery and lower mortality). The relatively lower resilience of *M. capitata* following  
375 bleaching observed here contrasts with experimental predictions that *M. capitata* has a higher  
376 capacity to recover from bleaching than *P. compressa* due to its ability to rapidly replace  
377 metabolized energy stores by increasing its heterotrophic feeding rates and recover depleted  
378 tissue biomass more quickly following bleaching (Grottoli *et al.*, 2006; Rodrigues and Grottoli,  
379 2007). Indeed, bleached *M. capitata* recovered pigmentation and biomass more quickly than *P.*  
380 *compressa* following the 2014 coral bleaching event (Wall *et al.*, 2019), indicating that coral  
381 recovery rates following thermal stress may depend on the frequency of thermal stress events. As  
382 our observations describe the responses of these corals to the second of two bleaching events to  
383 occur within the span of one year, the discrepancies between the outcomes we observed and  
384 those of previous studies could be due in part to the recurrent nature of the stress. This pattern

385 has also been observed in other reef systems, where annual repeat bleaching events turn some  
386 coral species from winners into losers (Grottoli *et al.*, 2014).

387

388 *Ecological outcomes differ between bleaching susceptible and resistant phenotypes*

389 Intraspecific differences in bleaching susceptibility had a significant influence on the ecological  
390 outcomes of those individuals in the months following thermal stress. For both *M. capitata* and  
391 *P. compressa*, bleaching susceptible individuals suffered higher partial mortality than bleaching  
392 resistant individuals located on the same reef. This resulted in significant losses of live coral  
393 cover from the reef, which likely has a significant impact on the ecological function of each reef.  
394 From an evolutionary perspective, these differences in partial mortality are likely to negatively  
395 impact reproductive success, as coral reproductive output is positively correlated with colony  
396 size (Hall and Hughes, 1996). Differential partial mortality between susceptible and resistant  
397 phenotypes therefore likely influences individual fitness and thus the genetic composition of  
398 offspring released in subsequent reproductive events. Further exacerbating this loss, corals that  
399 have recently undergone bleaching have a lower likelihood of reproducing at all relative to  
400 bleaching resistant conspecifics, and those that do manage to reproduce tend to release fewer and  
401 less provisioned gametes (Ward *et al.*, 2000; Fisch *et al.*, 2019). Together these factors will  
402 likely limit the evolutionary success of bleaching susceptible genotypes and the ecological  
403 resilience of the reef by reducing the recruitment pool and live coral cover (Fisch *et al.*, 2019;  
404 Hughes *et al.*, 2019). However, the low frequency of complete colony mortality during this  
405 bleaching event indicates the adult gene pool has remained mostly intact, maintaining the genetic  
406 diversity of the current population. Intraspecific differences in coral mortality also affect the  
407 ecological landscape of coral symbionts. In *M. capitata*, for example, bleaching resistant  
408 phenotypes tend to be dominated by *Durusdinium glynii*, whereas bleaching susceptible  
409 individuals are mostly dominated by *Cladocopium* sp. (Cunning *et al.*, 2016), and higher survival  
410 of *D. glynii*-dominated individuals likely increases the relative abundance of *D. glynii* in the  
411 community. As symbiont transmission occurs vertically in this species (Padilla-Gamiño *et al.*,  
412 2012), this would also increase the proportion of larvae inheriting *D. glynii*, potentially altering  
413 the composition of the symbiont community for generations. Furthermore, if thermal stress  
414 events increase in frequency and severity as predicted (Hughes, Anderson, *et al.*, 2018), the  
415 relative growth benefits associated with hosting thermally sensitive symbionts like *Cladocopium*

416 spp. at non-stressful temperatures may fail to make up for the higher costs of these associations  
417 during thermal stress, altering the tradeoffs of the association (Cunning *et al.*, 2015).

418 Mechanisms driving differential thermal performance in *P. compressa* are less well understood,  
419 particularly as symbiont variation in this species is limited (LaJeunesse *et al.*, 2004).

420

421 *Coral bleaching and recovery dynamics differed between inner and outer lagoon reefs*

422 *M. capitata* and *P. compressa* both experienced higher bleaching prevalence and severity at the  
423 inner lagoon reef, which corresponded with higher partial mortality for *M. capitata*. These results  
424 are reflective of coral mortality patterns from baywide surveys, which also observed higher  
425 cumulative coral mortality on reefs in the inner lagoon region (Bahr *et al.*, 2017). Higher rates of  
426 bleaching and mortality within the inner lagoon were likely due to the higher accumulated  
427 thermal stress at this site. However, additional environmental factors were likely involved  
428 because bleaching resistant *M. capitata* also had higher mortality at the inner lagoon reef relative  
429 to either phenotype at the outer lagoon reef. These data suggest that differences in coral  
430 bleaching and mortality between the two reefs were likely due to a combination of environmental  
431 factors, with worse outcomes within the inner lagoon potentially driven by the lower flow rates,  
432 longer seawater residence times (>30 days; (Lowe *et al.*, 2009), and closer proximity to land  
433 relative to the outer lagoon reef. Low flow environments can limit nutrient and waste exchange  
434 in the coral boundary layer, suppressing coral metabolism (Mass *et al.*, 2010; Putnam *et al.*,  
435 2017), and when coupled with higher freshwater and allochthonous nutrient input (Bahr *et al.*,  
436 2015) may have exacerbated the stress of the heat wave, limiting coral recovery and exacerbating  
437 tissue loss. Indeed, pigmentation recovery rates were slower within the inner lagoon, a recovery  
438 pattern that was also observed in 2014 (Cunning *et al.*, 2016; Wall *et al.*, 2019).

439

440 *Coral recovery requires more time between bleaching events*

441 Consecutive annual bleaching events have become a feature of coral reefs around the world  
442 (Grottoli *et al.*, 2014; Bahr *et al.*, 2017; Hughes, Anderson, *et al.*, 2018). Short intervals between  
443 thermal stress events that prevent individual corals from fully recovering energetically from the  
444 first thermal stress prior to exposure to the second are likely to make individuals less resistant to  
445 bleaching and mortality in the second event. The 2015 bleaching event followed here occurred  
446 one year following the previous bleaching event in 2014, and led to higher cumulative coral

447 mortality than either of the two previous bleaching events in the bay (Bahr *et al.*, 2017), which  
448 may have been due in part to the short recovery interval between the two thermal stress events.  
449 Indeed, colonies in Kāneōhe Bay that bleached in 2014 tended to bleach again in 2015 (Ritson-  
450 Williams, 2017), suggesting that these corals had not acclimatized to higher temperatures and  
451 were unlikely to have fully recovered from that event when the 2015 event occurred. Longer  
452 recovery periods are also important for regrowth of tissue lost during a heatwave, and our data  
453 showed that tissue lost due to partial mortality was not replaced by live coral cover in the two  
454 years following the bleaching event. This indicates that corals in Kāneōhe Bay require longer  
455 recovery intervals to replace lost coral cover following bleaching-related mortality. Furthermore,  
456 our data indicate that symbiont recovery rates may take longer following repeat bleaching events,  
457 as *M. capitata* recovered visual pigmentation and symbiont abundance in a span of 1-3 months in  
458 previous bleaching events (Jokiel and Brown, 2004; Cunning *et al.*, 2016; Ritson-Williams,  
459 2017; Wall *et al.*, 2019), while in 2015 we found that it took as much as two years for many  
460 bleached *M. capitata* individuals to fully recover pigmentation. In addition, repetitive bleaching  
461 events may influence the differential success of the major reef building species in Kāneōhe  
462 Bay. We found that *P. compressa* recovered pigmentation faster than *M. capitata* and had a  
463 lower rate of tissue loss. This was similar to patterns of pigmentation recovery and mortality in  
464 these same species at other patch reefs in Kāneōhe Bay during both the 2014 and 2015  
465 bleaching events (Ritson-Williams, 2017), and suggests that *P. compressa* may gain ecological  
466 advantage if bleaching events become more common. Encouragingly, both the 2014 and 2015  
467 events led to low rates of complete colony mortality, with <3% of corals suffering 100%  
468 mortality (*M. capitata* and *P. compressa*; this study) versus <2% of *M. capitata* in 2014  
469 (Cunning *et al.*, 2015). A further testament to the resilience of corals in this system, there were  
470 several colonies that underwent a complete recovery of live tissue cover following significant  
471 (>50%) partial mortality, suggesting that some species are highly resilient and that given a few  
472 years of recovery between stress events can rapidly replace lost tissue when mortality is  
473 incomplete.

474

475 *Individual tracking uncovers low levels of partial mortality following thermal stress*

476 Both bleaching susceptible and bleaching resistant individuals suffered partial mortality in the  
477 months following the bleaching event, indicating that although resistant individuals did not

478 visually bleach, all corals were negatively affected by thermal stress. Interestingly, while  
479 bleaching-susceptible colonies of both species suffered an average of ~20% tissue loss in the first  
480 six months following the bleaching event, these losses did not manifest as significant changes in  
481 live coral cover. This discrepancy could be due in part to the low mortality of bleaching resistant  
482 phenotypes masking the higher mortality of bleaching-susceptible individuals in community  
483 wide surveys. In addition, the high variance of photoquadrat surveys makes it difficult to detect  
484 small changes in benthic cover (Jokiel *et al.*, 2015). Photoquadrat surveys are also commonly  
485 used to quantify recently dead coral cover during or following a bleaching event, however this  
486 method cannot discern whether the coral that died had in fact bleached, whereas individual  
487 colony data revealed the consequences of thermal stress for both bleaching phenotypes. While  
488 these losses in live coral cover were not detected at the community level, the significant partial  
489 mortality observed at the colony level has a negative impact on the ecology and evolution of  
490 coral communities as described above. Loss of susceptible individuals may also lower the  
491 genotypic richness of the population, which in corals can correlate with lower reproductive  
492 success (Baums *et al.*, 2013). That said, the lack of a significant decline in coral cover at these  
493 two reefs is encouraging for reef recovery from this bleaching event.

494

495 *Living library: coral pairs are a resource for future research and restoration*

496 By identifying individual coral colonies with distinct thermal stress responses and tracking them  
497 over a multi-year period, we have generated and continue to maintain a live geo-referenced  
498 biological archive in the field as a resource for research on the effects of environmental history  
499 and thermal stress responses on the ecology and physiology of reef-building corals. This resource  
500 will be particularly valuable in light of predicted increases in the frequency and severity of coral  
501 bleaching events, as it allows for prospective sampling of bleaching susceptible vs. resistant  
502 phenotypes before, during, and following a bleaching event. This experimental system allows  
503 researchers to address questions of coral acclimatization and adaptation to changing oceans, such  
504 as examining whether individual coral responses predict tolerance to future stress. In addition, it  
505 allows researchers to identify if repeat events change the ecological outcomes observed in the  
506 current event, potentially altering which species are considered the ecological winners. Finally,  
507 fully recovered corals of known contrasting thermal tolerances can be used to investigate the  
508 interaction of temperature tolerance with coral responses to other stressors, including but not

509 limited to ocean acidification, eutrophication, and pathogens, helping to identify potential  
510 tradeoffs of thermal tolerance in corals and the importance of phenotypic and genetic diversity in  
511 coral reef resilience (Stachowicz *et al.*, 2007; Ladd *et al.*, 2017). This will be useful for  
512 informing coral restoration strategies, particularly in light of the movement towards human  
513 assisted evolution (e.g. assisted gene flow), as it allows assessment of the potential tradeoffs of  
514 propagating thermally tolerant genotypes (Van Oppen *et al.*, 2015, 2017). From a management  
515 perspective, bleaching resistant individuals have the potential to serve as a resource for reef  
516 managers interested in propagating climate change resilient genotypes on damaged or degraded  
517 coral reefs (Van Oppen *et al.*, 2017). Comparing bleaching responses within species  
518 demonstrates the importance of understanding individual colony susceptibility to thermal stress  
519 and trajectories of recovery in the face of ongoing climate change. These questions are important  
520 for understanding the persistence of coral reefs into the future.

521

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537

538 **Author contributions**

539 The study was designed by KB and RG. EL, JD and JH helped collect the data. KB, SM, AP, TI,  
540 and AH collected and analyzed the data. The paper was written by KB and SM, and all authors  
541 edited and approved the final version of the manuscript.

542

543 **Conflict of Interests Statement**

544 The authors declare that the research was conducted in the absence of any commercial or  
545 financial relationships that could be construed as a potential conflict of interest.

546

547 **Data accessibility**

548 The datasets analyzed for this study and R scripts can be found in GitHub:  
549 <https://github.com/BurgessShayle/2015-Coral-bleaching-recovery>. The raw data supporting the  
550 conclusions of this manuscript will be made available by the authors, without undue reservation,  
551 to any qualified researcher.

552

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727

728 **Figure legends**

729

730 Figure 1. A) Map of the southern region of Kāne'ohe Bay, O'ahu. Inset shows the island of  
731 O'ahu, with north indicated by the arrowhead and the red square indicating the southern region  
732 of Kāne'ohe Bay enlarged in detail. Distinct hydrodynamic regimes within the lagoon are  
733 indicated by the polygons: the dashed line surrounds the Inner Lagoon region where seawater  
734 residence times are >30 days; the dash-dot line surrounds the Mid Lagoon region where seawater  
735 residence times are 10-20 days; the solid line surrounds the Outer Lagoon region where seawater  
736 residence times are <10 days (from Lowe *et al.*, 2009). Yellow symbols indicate locations of *in*  
737 *situ* temperature loggers. Representative images of each reef are shown for B) Outer lagoon  
738 (PR13) and C) Inner lagoon (PR4). D) Mean daily temperature at each reef. Shading indicates  
739 daily temperature range. Dashed line indicates local coral bleaching threshold.

740

741 Figure 2. Benthic community composition from the peak of the 2015 bleaching event through 18  
742 months of recovery for A) the Inner lagoon (PR4) and B) the Outer lagoon (PR13) in Kāne'ohe  
743 Bay, O'ahu. Data represent the means of four replicate transects.

744

745 Figure 3. Prevalence of coral bleaching phenotypes for *Montipora capitata* (A-B) and *Porites*  
746 *compressa* (C-D) at the Inner lagoon (left column) and Outer lagoon (right column). Data  
747 represent the means of four replicate transects.

748

749 Figure 4. Representative images of tagged bleached and non-bleached corals. Top row: *M.*  
750 *capitata* pair 5&6; Bottom row: *P. compressa* pair 37&38. Left column shows pairs at the peak  
751 of the bleaching event in November 2015. Center column shows the bleached colony of the pair  
752 after 1.5 months of recovery. Right column shows the same pairs after 3 - 6 months of recovery.

753

754 Figure 5. Average color score of bleaching susceptible versus bleaching resistant colonies of  
755 *Montipora capitata* (A-B) and *Porites compressa* (C-D) at the Inner Lagoon (A,C) and Outer  
756 Lagoon (B,D). Solid lines indicate bleaching resistant colonies; dashed lines indicate bleaching  
757 susceptible colonies. Color scores: 1, white; 2, pale; 3, pigmented. Error bars indicate SEM.

758

759 Figure 6. Average partial mortality of bleaching susceptible versus bleaching resistant colonies  
760 of *Montipora capitata* (A-B) and *Porites compressa* (C-D) at the Inner Lagoon (A,C) and Outer  
761 Lagoon (B,D). Solid lines indicate bleaching resistant colonies; dashed lines indicate bleaching  
762 susceptible colonies. Error bars indicate SEM.

763

764 **Tables**

765 Table 1. Summary of seawater hydrodynamics and temperature conditions within the Inner and  
766 Outer lagoon regions in Kāneōhe Bay, Hawai'i during the peak of the thermal stress event and  
767 the initial recovery period. Asterisks indicate statistical significance ( $p < 0.03$ ; Wilcoxon rank sum  
768 test).

769

	<b>Region:</b>	<b>Inner Lagoon</b>		<b>Outer Lagoon</b>		<b>References</b>
		<b>Patch Reef:</b>	<b>PR 1</b> (Coconut Island)	<b>PR 4</b>	<b>PR 12</b>	<b>PR 13</b>
<b>Physical regime</b>	Dominant physical force	Tide	Tide	Wave	Wave	Bahr et al. 2017; Lowe et al. 2009
	Seawater residence time	>30 days	>30 days	1-5 days	<1 day	Lowe et al. 2009
<b>Thermal stress (July 1 - Oct 1, 2015)</b>	Mean maximum daily temperature (°C)	<b>29.08*</b>	ND	<b>28.64*</b>	ND	Figure 1
	Mean minimum daily temperature (°C)	<b>28.44*</b>	ND	<b>27.94*</b>	ND	Figure 1
	Degree heating weeks (DHW)	5.84	ND	1.77	ND	Figure 1
<b>Initial Recovery (Nov 1, 2015 - Feb 1, 2016)</b>	Mean maximum daily temperature (°C)	25.60	25.59	25.35	25.62	Figure 1
	Mean minimum daily temperature (°C)	25.01	24.80	24.75	24.93	Figure 1

770

771 Table 2. Three-way ANOVA results for pigmentation recovery of bleaching susceptible and  
 772 resistant colonies during the first six months of recovery for *Montipora capitata* and *Porites*  
 773 *compressa* at PR13 and PR4.  
 774

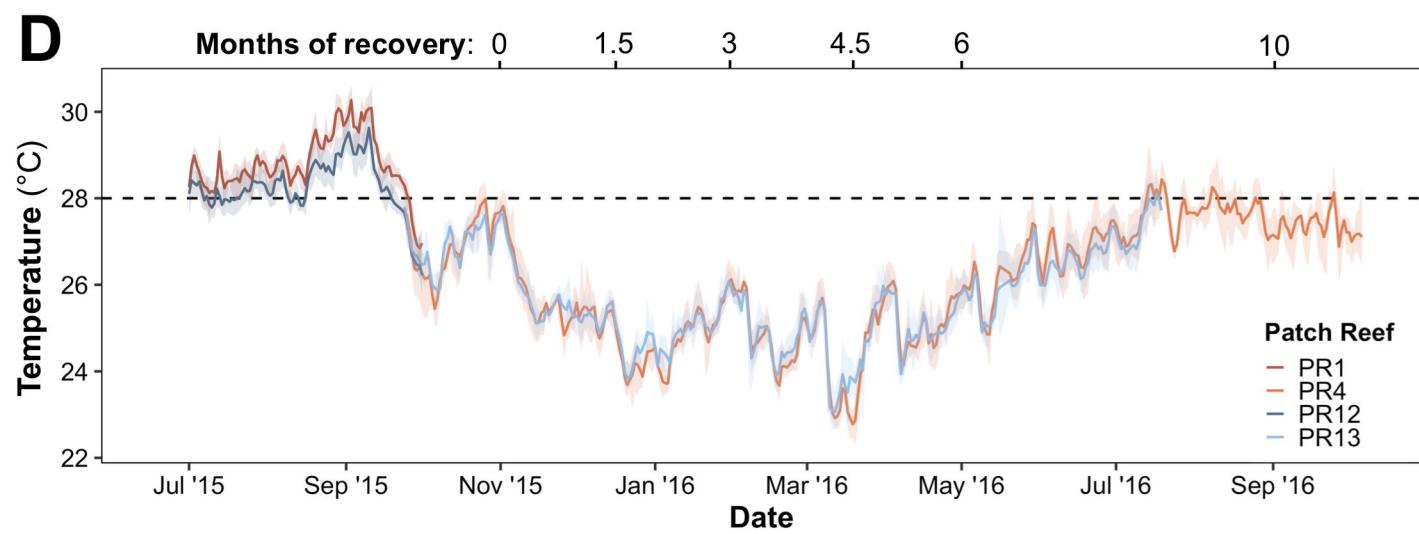
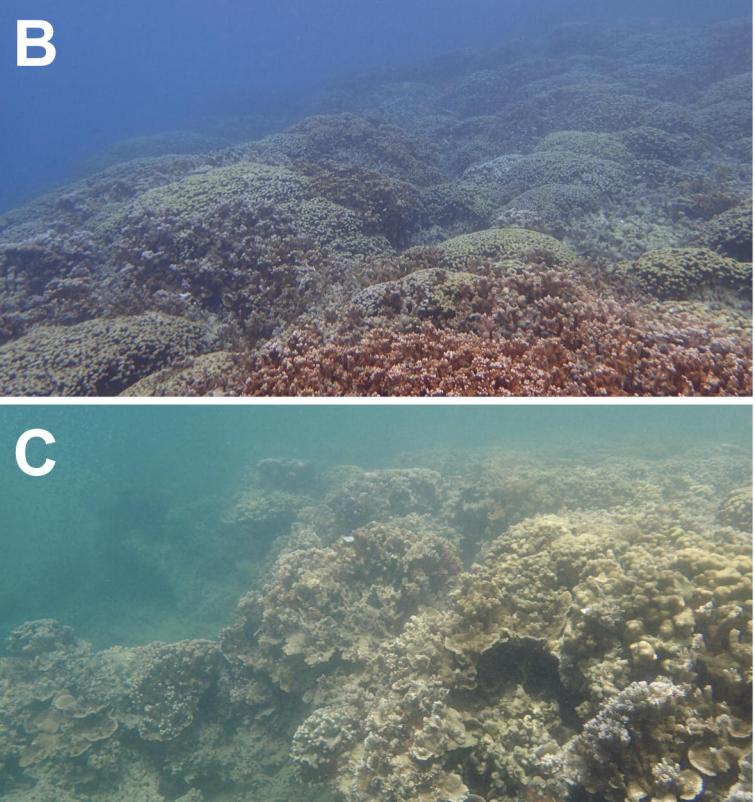
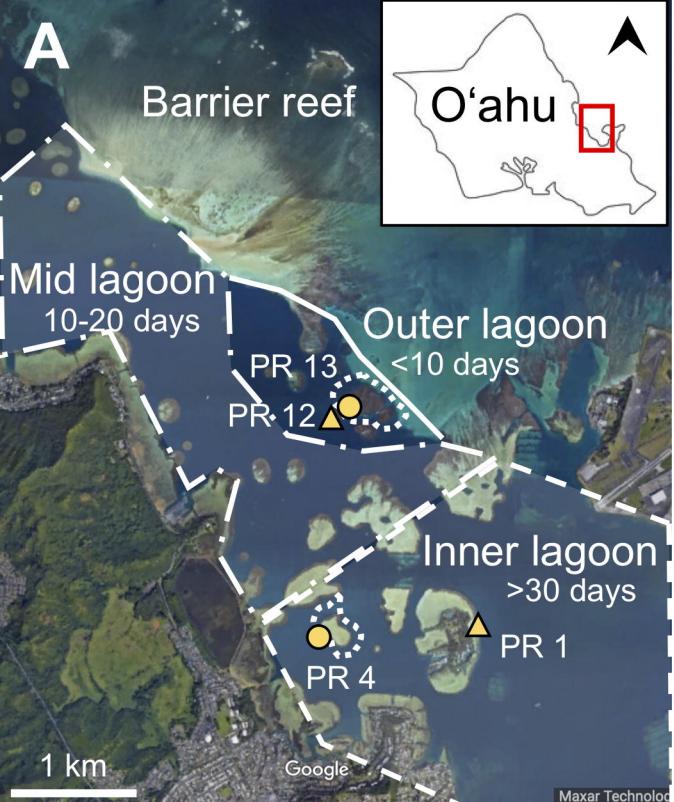
		<i>Months 0-3</i>				<i>Months 0-6</i>			
		Df	Sum Sq	F val	p	Df	Sum Sq	F val	p
<i>Montipora capitata</i>	Month	2	14.31	68.97	<0.01	4	20.55	41.04	<0.01
	Lagoon	1	0.05	0.51	0.48	1	0.24	1.89	0.17
	B2015	1	100.16	965.73	<0.01	1	101.97	814.53	<0.01
	Month:Lagoon	2	0.36	1.74	0.18	4	1.21	2.42	<0.05
	Month:B2015	2	11.92	57.49	<0.01	4	22.85	45.63	<0.01
	Lagoon:B2015	1	0.05	0.49	0.49	1	0.91	7.27	<0.01
	Month:Lagoon:B2015	2	0.76	3.67	0.03	4	1.54	3.09	0.02
	Residuals	221	22.92				351	43.94	
<i>Porites compressa</i>	Month	2	46.55	196.59	<0.01	4	67.20	196.45	<0.01
	Lagoon	1	0.48	4.01	<0.05	1	0.68	8.00	<0.01
	B2015	1	34.50	291.46	<0.01	1	20.91	244.52	<0.01
	Month:Lagoon	2	0.33	1.39	0.25	4	0.55	1.60	0.17
	Month:B2015	2	35.49	149.89	<0.01	4	49.10	143.54	<0.01
	Lagoon:B2015	1	0.03	0.28	0.60	1	0.02	0.26	0.61
	Month:Lagoon:B2015	2	1.63	6.87	<0.01	4	1.64	4.79	<0.01
	Residuals	228	26.99			375	32.07		

775

776 Table 3. Three-way ANOVA results for partial mortality over the first six months post peak  
777 bleaching for bleaching susceptible and resistant colonies of *Montipora capitata* and *Porites*  
778 *compressa* at PR13 and PR4.  
779

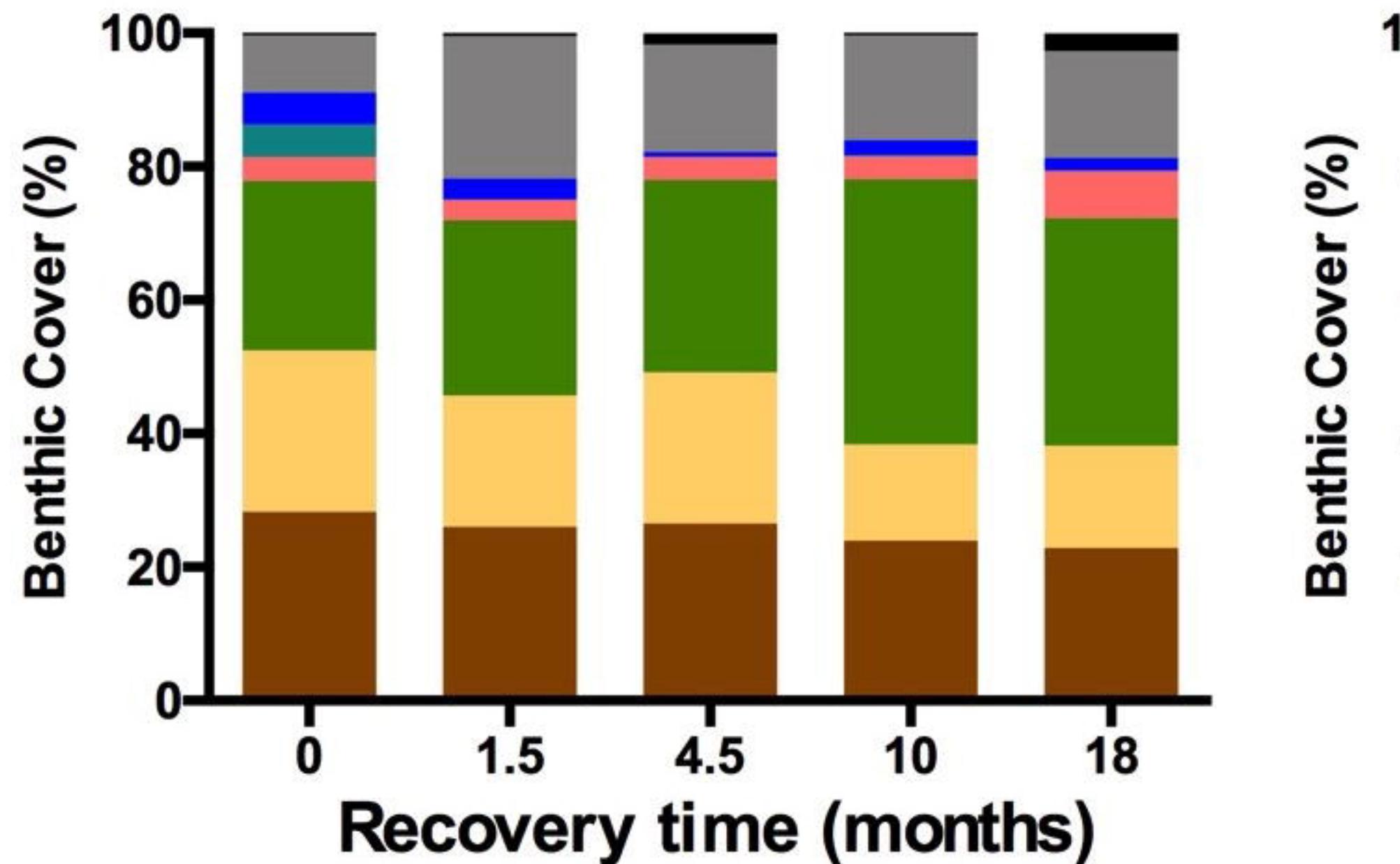
		<i>Months 0-3</i>				<i>Months 0-6</i>			
		Df	Sum Sq	F val	p	Df	Sum Sq	F val	p
<i>Montipora capitata</i>	Month	2	1.06	18.15	<b>&lt;0.01</b>	4	2.63	18.26	<b>&lt;0.01</b>
	Lagoon	1	0.72	25.15	<b>&lt;0.01</b>	1	2.55	70.88	<b>&lt;0.01</b>
	B2015	1	1.18	41.18	<b>&lt;0.01</b>	1	2.93	81.49	<b>&lt;0.01</b>
	Month:Lagoon	2	0.43	7.39	<b>&lt;0.01</b>	4	0.97	6.75	<b>&lt;0.01</b>
	Month:B2015	2	0.40	6.93	<b>&lt;0.01</b>	4	0.63	4.39	<b>&lt;0.01</b>
	Lagoon:B2015	1	0.27	9.33	<b>&lt;0.01</b>	1	0.53	14.58	<b>&lt;0.01</b>
	Month:Lagoon:B2015	2	0.15	2.59	0.08	4	0.17	1.15	0.33
	Residuals	237	6.81			370	13.32		
<i>Porites compressa</i>	Month	2	0.08	2.63	0.07	4	0.22	2.87	<b>0.02</b>
	Lagoon	1	0.20	13.35	<b>&lt;0.01</b>	1	0.11	5.73	<b>0.02</b>
	B2015	1	0.65	44.02	<b>&lt;0.01</b>	1	1.36	72.17	<b>&lt;0.01</b>
	Month:Lagoon	2	0.01	0.48	0.62	4	0.11	1.47	0.21
	Month:B2015	2	0.05	1.63	0.20	4	0.08	1.02	0.40
	Lagoon:B2015	1	0.27	18.24	<b>&lt;0.01</b>	1	0.35	18.41	<b>&lt;0.01</b>
	Month:Lagoon:B2015	2	0.03	0.96	0.39	4	0.04	0.51	0.73
	Residuals	234	3.43			385	7.28		

780

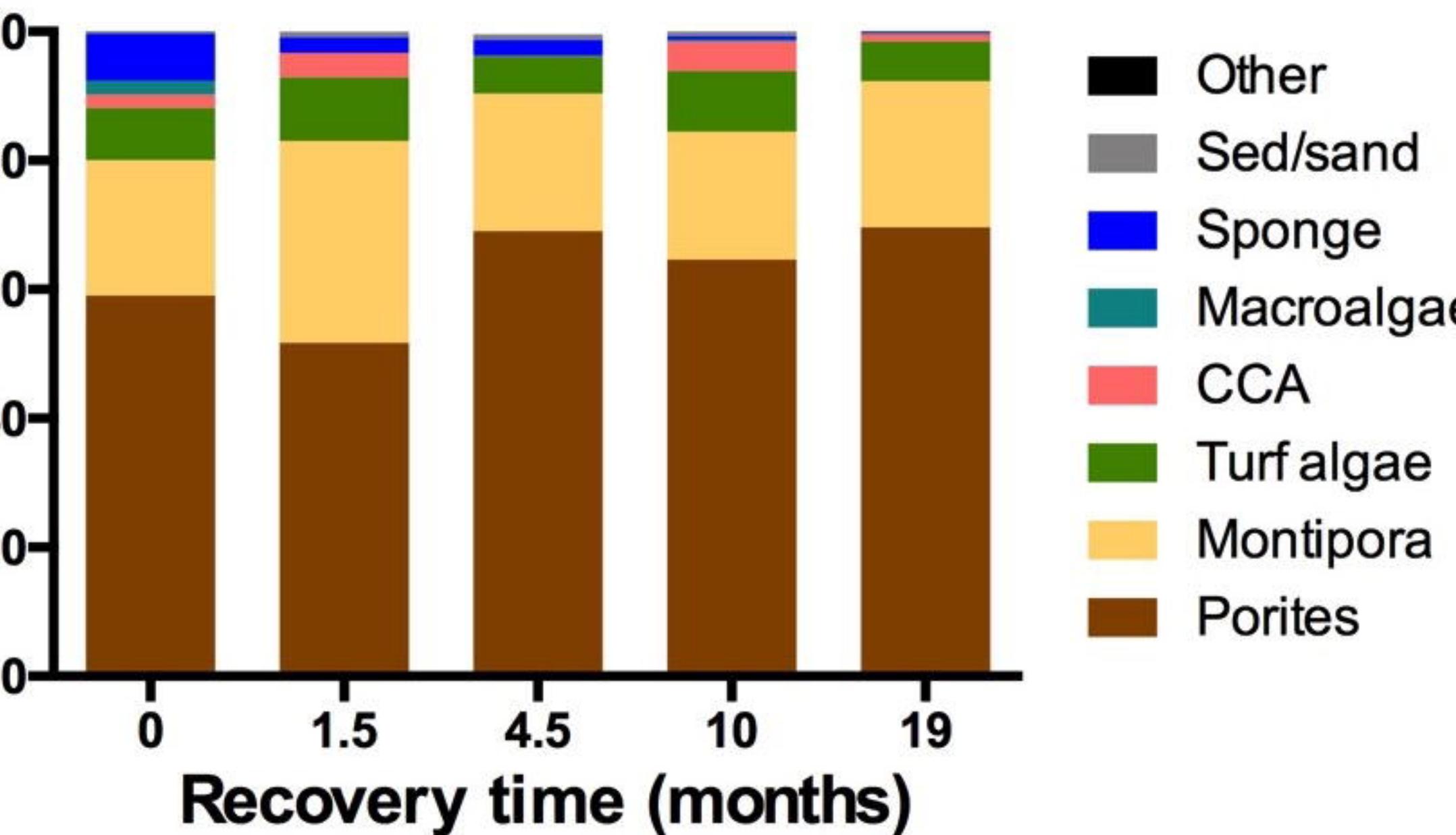


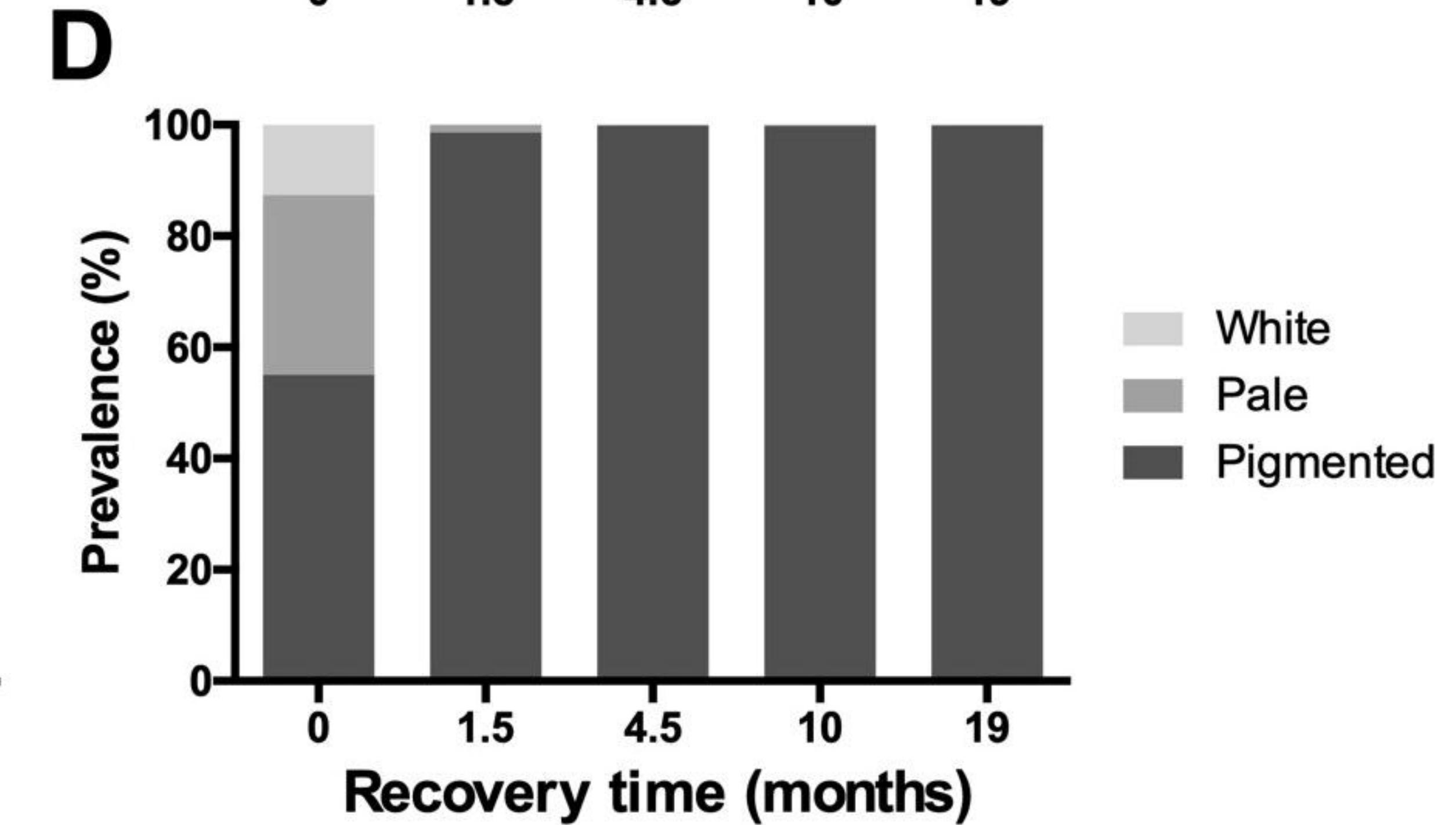
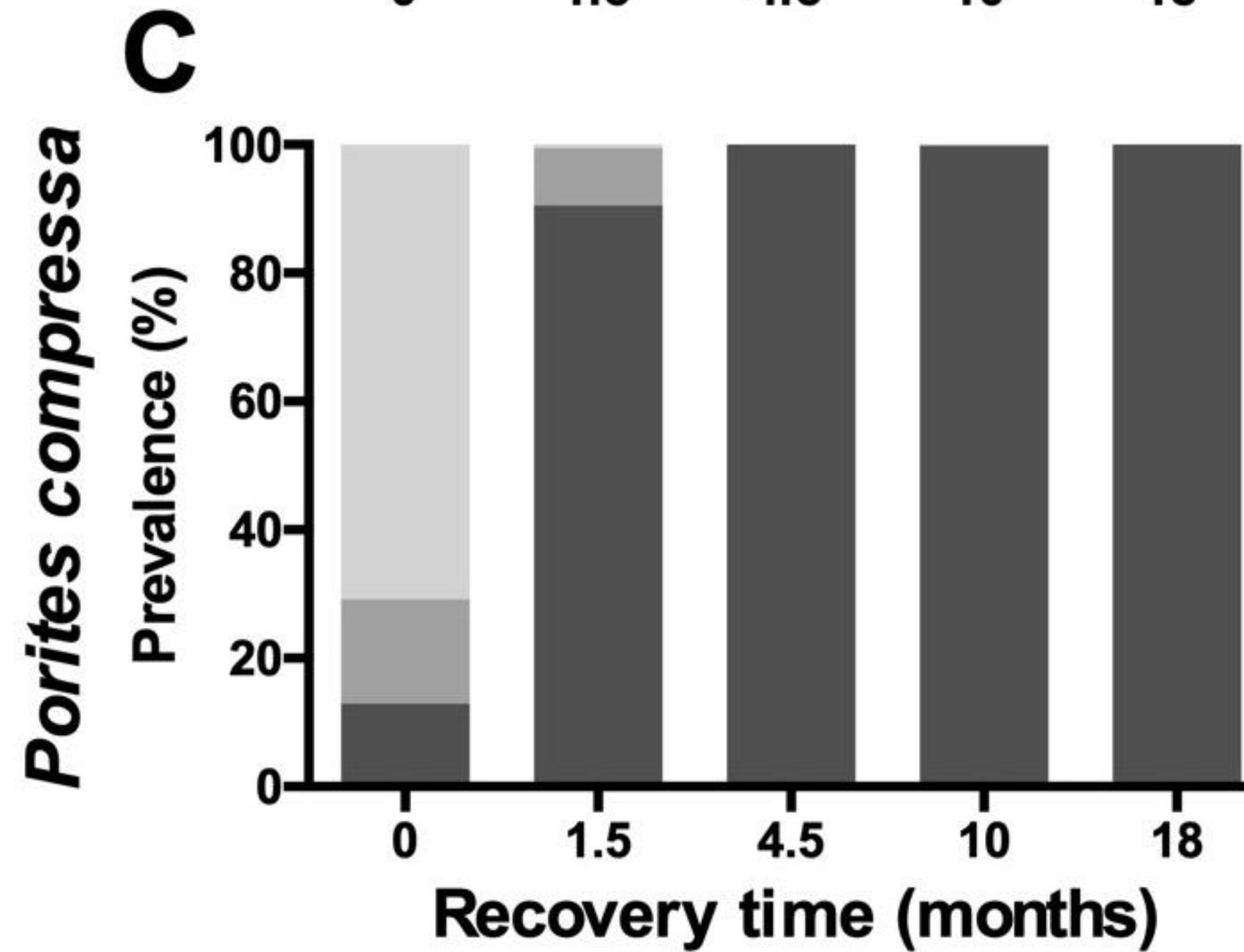
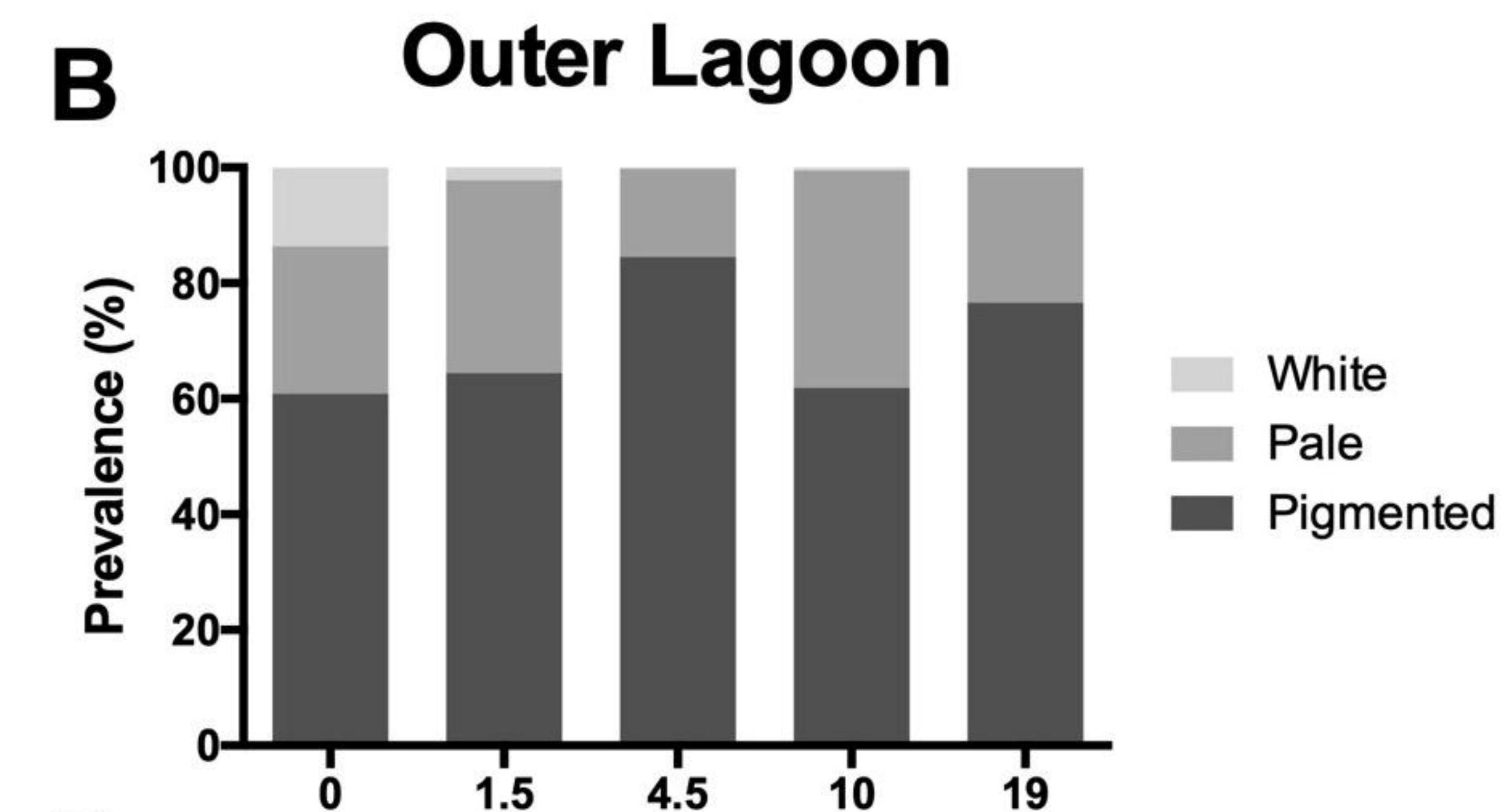
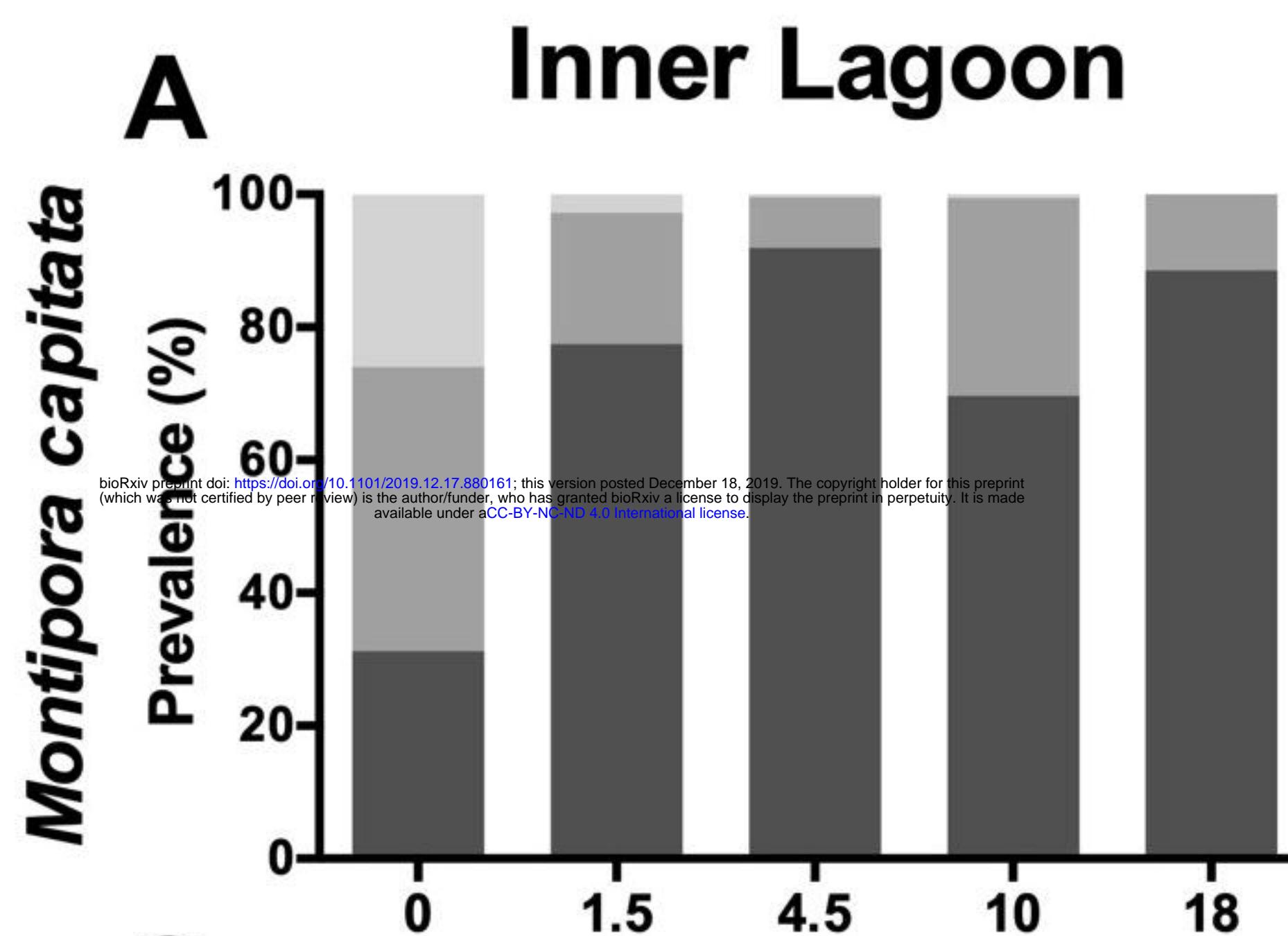
**A**

# Inner Lagoon

**B**

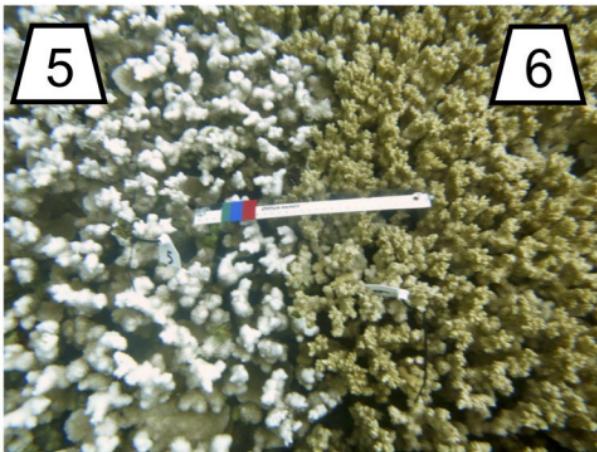
# Outer Lagoon





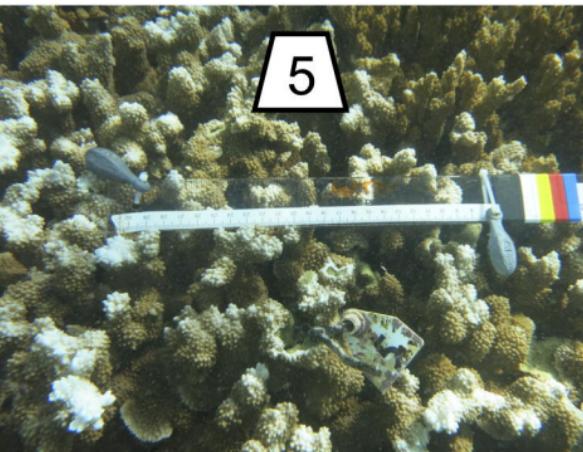
## Bleaching

0 months



## Recovery

1.5 months



3 – 6 months

