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2 **The benefits of herbivory outweigh the costs of bioerosion in a eutrophic coral**

3 **community**

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14 **Running Head:** Urchin herbivory benefits corals

15 **Abstract**

16 Herbivores play an integral part in maintaining the health of coral reefs by suppressing the  
17 growth of algae and accumulation of sediment and facilitating coral growth. However, in  
18 predator-depleted systems where densities of herbivores are unnaturally high, grazing can  
19 have detrimental effects on corals through excessive bioerosion. Yet, these benefits and costs  
20 are rarely investigated concurrently, especially in eutrophic systems where grazers may play  
21 a disproportionate role. We used a year-long exclusion experiment to elucidate the effect of  
22 natural densities of the dominant herbivore (the sea urchin *Diadema setosum*) on coral  
23 communities in a heavily fished and eutrophic system (Hong Kong, China). To assess benthic  
24 community response to grazing, we monitored the survival and growth of three locally  
25 abundant coral species (*Pavona decussata*, *Platygyra carnosus* and *Porites* sp.), algal and  
26 sediment accumulation, and bioerosion of coral skeletons across seasons. We found that  
27 urchins maintained our experimental coral assemblages, and when excluded, there was a 25  
28 to 75-fold increase in algal-sediment matrix accumulation. Contrary to predictions, there was  
29 no general response of corals to urchin presence; *Porites* sp. survivorship increased while *P.*  
30 *decussata* was unaffected, and growth rates of both species was unchanged. Surprisingly, *P.*  
31 *carnosus* experienced higher mortality and bioerosion of up to 33% of their buoyant weight  
32 when urchins were present. Therefore, under natural densities, sea urchins clear substrate of  
33 algae and sediment, increase survival, maintain growth rates and health of coral assemblages,  
34 yet can accelerate the bioerosion of species with porous skeletons following mortality.

35

36 **Key words:** Herbivore-coral interaction, coral reef herbivory, ecosystem function,  
37 bioerosion, sea urchin exclusion, coral survival

## 38 **Introduction**

39 Coral reefs are highly diverse and productive systems, providing habitat and resources for  
40 25% of the world's marine fauna (Molberg and Folke 1999). Herbivores have been well  
41 documented to facilitate healthy coral reefs (Hughes 1994, Jackson et al. 2001, Carpenter and  
42 Edmunds 2006, Hughes et al. 2007), keeping faster-growing algae in check thereby  
43 preventing corals from being overgrown and reducing sediment accumulation (Sammarco  
44 1980, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Hughes et al. 2007).  
45 Benthic grazers increase reef complexity, providing habitat for fish and invertebrates (Hughes  
46 1994), and increasing habitat suitability for coral larvae settlement by clearing substrate of  
47 algal turfs (Sammarco 1980, Davies et al. 2013, Nozawa et al. 2020). Grazing also promotes  
48 growth of crustose coralline algae (CCA), which acts as a chemical cue for coral larvae to  
49 settle (Heyward and Negri 1999, Harrington et al. 2004, Gómez-Lemos et al. 2018).  
50 Furthermore, a healthy grazer community increases ecosystem functions and services  
51 (Molberg and Folke 1999), and resilience of reefs to disturbances (Hughes et al. 2007,  
52 Graham et al. 2015, Holbrook et al. 2016). The detrimental effects of the loss of grazers on a  
53 reef, shifting from of algal dominance to ecosystem collapse, is well documented (Jackson et  
54 al. 2001, Hughes, 1994, Bellwood et al. 2004, Carpenter and Edmunds 2006, Mumby et al.  
55 2006). Therefore, with increasing disturbances, such as tropical cyclones and ocean warming-  
56 derived bleaching events, replete grazer communities are likely to be essential for coral reefs  
57 to persist.

58 Yet, not all herbivores have the same effects on clearing algae and benefiting corals, as  
59 urchins remove more algae than fishes and contribute to higher coral survival rates (Lirman  
60 2001, Mumby et al. 2006, Burkepile and Hay 2008, Reverter et al. 2020). The die-off of the  
61 sea urchin *Diadema antillarum* in the Caribbean, during which urchin populations decreased  
62 by up to 99% (Lessios et al. 1984, Carpenter 1988), in combination with over-fishing on

63 many reefs (Jackson et al. 2001), led to a shift in reef composition where hard corals were  
64 replaced by macroalgae (Edmunds and Carpenter 2001; Carpenter and Edmunds 2006).  
65 Conversely, an overabundance of grazers, generally attributed to the removal of predators,  
66 can have detrimental effects on ecosystems. Sea otter extirpation from the Aleutian Islands  
67 released sea urchins from predation pressure and urchin populations increased, reducing kelp  
68 forests to urchin barrens (Estes and Palmisano 1974). In New Zealand, overfishing of spiny  
69 lobsters and snapper lead to urchin barrens devoid of most algae; however, this trend was  
70 reversed once the top predators returned with the implementation of a no-take marine reserve  
71 (Shears and Babcock 2003). In tropical marine ecosystems, an overabundance in herbivores  
72 can lead to coral bioerosion. Epilithic bioeroders, like fishes and urchins, target algae  
73 growing on the exposed skeleton of corals and scrape away calcium carbonate to eat the algae  
74 (Glynn 2015, Alvarado et al. 2017). While coral bioerosion is a natural process - essential for  
75 algae removal, coral recruitment, and reef accretion - excessive rates of bioerosion can  
76 undercut and topple corals and, on very rare instances, destroy reefs (Bellwood et al. 2004,  
77 Glynn 2015). Additionally, eutrophic environments further exacerbate bioerosion rates, as  
78 these conditions favour endolithic bioeroders (Barkley et al. 2015, Rice et al. 2020), yet the  
79 benefits of herbivory in such systems is less well studied.

80 The waters around Hong Kong are eutrophic and, as such, conditions have already caused  
81 significant loss to local coral abundance and diversity (Duprey et al. 2016, Cybulski et al.  
82 2020). Further, Hong Kong has been extensively overfished and most large predatory and  
83 herbivorous fishes found elsewhere in the South China Sea are absent (Cheung and Sadovy  
84 2004, Lai et al. 2016). Consequently, urchins are the primary herbivores which maintain  
85 ecosystem functions, as was the case in the Caribbean before the urchin die-off (Jackson et al.  
86 2001). Recently, however, there have been localised reports of large-scale bioerosion on coral

87 communities in Hong Kong caused by the sea urchin *Diadema setosum* (Dumont et al. 2013,  
88 Qiu et al. 2014).

89 While it is well established that urchins play an integral role in maintaining coral reef  
90 systems through grazing algae and clearing substrate, few studies quantify the trade-off  
91 between herbivory and bioerosion, including coral species-specific effects, particularly in  
92 systems in which the key remaining herbivores are urchins. Previous studies have shown that  
93 herbivores (fishes and urchins) can increase both growth and survival of corals (Lirman 2001,  
94 Hughes et al. 2007, Burkepile and Hay 2008, Burkepile and Hay 2010, Knoester et al. 2019).  
95 In contrast, while many studies have estimated urchin bioerosion rates *in situ*, few have  
96 simultaneously tested the effects of urchins on both bioerosion and coral growth (Dumont et  
97 al. 2013). Therefore, understanding the net benefits and costs of urchins to coral communities  
98 could help informing decisions on future coral conservation and restoration efforts.

99 In this study, we used *in situ* exclusion cages to test the role of a benthic herbivore, the sea  
100 urchin *Diadema setosum*, in maintaining coral communities in a highly eutrophic and  
101 overfished system. We tested the hypothesis that *D. setosum* would facilitate coral growth  
102 and coral survival by removal of algae and sediment. We also assessed the rates of bioerosion  
103 at natural urchin densities to test the hypothesis that urchins would not increase bioerosion of  
104 live corals. Overall, we expect that urchins will reduce algal-sediment matrix, increase both  
105 coral growth and survival, while not increasing coral mortality through bioerosion, thus  
106 playing a pivotal role in maintaining corals in a eutrophic system.

107

## 108 **Methods**

### 109 *Study site*

110 Our urchin exclusion experiment to identify the effects of urchins on coral growth,  
111 bioerosion, and survival, and sediment accumulation and turf algal growth was completed at

112 Moon Island (N 22.480878, E 114.333817), Hong Kong SAR, China. The site is located just  
113 outside the Hoi Ha Wan Marine Park (HHWMP), a coral habitat protection zone in Hong  
114 Kong. It was chosen for the presence of *Diadema setosum* in proximity to coral communities.  
115 The site consists of coral communities attached to large rock boulders which formed ideal  
116 experimental units for attaching live coral fragments, settlement tiles and coral skeleton  
117 cores.

118

### 119 *Experimental design*

120 To test the effects of natural densities of urchins on coral growth, bioerosion,  
121 sedimentation and survival, urchins were either excluded (fully caged boulder but left open  
122 on the top) or allowed access to plots (urchins present; n = 9 per treatment). In addition, any  
123 potential effects of exclusion cages were tested with partial cages which had the bottom and  
124 sides open to allow urchins access (procedural control; n = 9; example photos of plots in Fig.  
125 S1). All plots included live coral fragments of *Pavona decussata*, *Platygyra carnosus*, and  
126 *Porites sp.*; a skeleton core of *Porites sp.* for monitoring bioerosion; and a 15 × 15 cm  
127 terracotta settlement tile (coral sources and skeleton core described below). Items were  
128 secured to rock substrate using marine epoxy (Splash Zone A-788 2-part Epoxy, Pettit Paint,  
129 Rockaway NJ, USA). These coral species were chosen for their abundance in Hong Kong  
130 coral communities (Cybulski et al. 2020). Plots were haphazardly distributed throughout the  
131 study site. Cages were rectangular and enclosed ~ 1 m<sup>2</sup> of substrate. They were built with 2 m  
132 long metal rods set ~ 1 m deep into the substrate, wrapped with a plastic-coated wire mesh  
133 (2.5 cm mesh squares) approximately 1.5 m high from the substrate. Approximately 30 cm  
134 of mesh was flared out across the substrate at the bottom of the cage to prevent urchins from  
135 accessing the cages. The tops of the cages were left open so fishes could enter. Crabs,  
136 gastropods, and sea cucumbers were also frequently observed in the cages. Urchins were

137 never observed inside any cages throughout the experiment. Cages were inspected  
138 concurrently with monthly surveys, scrubbed periodically to remove algal growth, and  
139 repaired when needed.

140

#### 141 *Coral growth and survival*

142 Coral fragments were sourced from existing coral nurseries maintained in a shaded 2000 L  
143 mesocosm with flow-through seawater at The Swire Institute for Marine Science (SWIMS),  
144 Cape D'Aguilar, Hong Kong. Additional samples of *P. carnosus* and *Porites sp.* were  
145 collected from Bluff Island (N 22.324386, E 114.353946) and brought back to the coral  
146 nursery mesocosm at SWIMS for seven days to recover after fragmentation. Live coral plugs  
147 were taken from colonies using a 55 mm diamond tipped hole saw drill bit and carefully pried  
148 out with a screwdriver. After the seven-day recovery period, all coral fragments were  
149 measured for buoyant weight and then attached to experiment plots. Dead, almost dead, and  
150 severely bioeroded fragments of *P. carnosus* were recovered from plots and replaced with  
151 new fragments at days 97 and 230 of the 393-day experiment to capture the rate of bioerosion  
152 and mortality (Fig. S1). All other coral fragments were collected at the completion of the  
153 experiment and buoyant weight re-measured. If corals died, the species, plot type and date  
154 was recorded for survival analyses.

155

#### 156 *Bioerosion of coral cores*

157 To quantify bioerosion, skeletons of *Porites sp.* from an old museum collection were cored  
158 with an 80 mm hole saw drill bit, with the cores then cut into discs approximately 10 mm  
159 thick with a rock saw. These coral cores were dried for 48 hours at 60°C and then weighed  
160 and 3D scanned for surface area using NextEngine 3D scanner (Santa Monica, CA, USA).  
161 Scans were done in 360° mode, with eight divisions, scanning every 45 degrees. Divisions

162 were fused together, producing a solid image using the volume merge function set to a 0.9  
163 resolution ratio in Scan Studio from NextEngine. Surface area was calculated directly by  
164 Scan Studio. To monitor summer bioerosion, coral cores were attached in May 2017 and  
165 retrieved in December (208-day deployment). New cores were attached in January 2018 for  
166 winter bioerosion rates and collected in May (120-day deployment). Retrieved cores were  
167 rinsed with fresh water and dried at 60°C for 48 hours then re-scanned and weighed. Mass  
168 and surface area data were combined and transformed for analytical purposes to  $\text{kg} \cdot \text{m}^{-2} \text{ year}$ .  
169

#### 170 *Settlement tiles*

171 To capture colonization patterns of benthic organisms (algal turf, encrusting algae, and  
172 invertebrates) and sediment accumulation trends, settlement tiles were deployed between  
173 April and November 2017 (208 days) for summer and November 2017 to March 2018 (92  
174 days) for winter. In addition, photos of each tile were taken *in situ* in July and November  
175 (summer) and January and February (winter) for percent cover analysis and colonization over  
176 time. At the end of deployment, each tile was gently removed from the substrate, placed into  
177 labelled, sealable plastic bags, and brought back to the laboratory and scraped of sediment  
178 and algae. The tile scrapings were put into a pre-weighed aluminium weigh boat, dried in a  
179 60°C oven for 48 hours and then re-weighed. Algal-sediment matrix weights were then  
180 converted to dry mass by area ( $\text{g} \cdot \text{m}^{-2}$ ).

181 Benthic assemblages which established on settlement tiles were quantified using the image  
182 annotation platform CoralNet Beta. A  $15 \times 15$ -point grid overlaid the settlement tiles, giving  
183 225 points per tile. Each point was evaluated to determine coverage identity. A random  
184 sampling of 45 tiles was used to establish a baseline for the automated annotator function.  
185 Remaining tiles and points were identified by the CoralNet annotator, and then each point  
186 was manually checked and corrected if mislabelled to ensure accuracy of identification. Items



187 identified on the tiles were sorted into five functional groups: bare tile; encrusting algae;  
188 fleshy algae; algal-sediment matrix; and sessile invertebrates. The last photo survey  
189 immediate before tile retrieval, for both end of summer and end of winter, were used for  
190 analyses to compare the affect of urchins on benthic community and sediment accumulation.

191

### 192 *Urchin surveys and monitoring*

193 Urchin density at the study site was quantified monthly using permanent belt transects (25  
194 m × 2 m; n = 3) which covered the area around all experimental plots. Over the length of the  
195 experiment, mean density of *Diadema setosum* was  $5.4 \pm 0.2$  urchins per m<sup>2</sup> (mean ± SE),  
196 ranging between  $4.3 \pm 0.7$  and  $6.8 \pm 1.3$  m<sup>-2</sup>, and did not differ among sampling periods ( $F_{8,}$   
197  $_{18} = 0.27, p = 0.97$ ). *D. setosum* was the only urchin species found at the site in substantial  
198 numbers, with individuals of *Heliocidaris crassispinus* and *Salmacis sphaeroides* seldomly  
199 observed.

200

### 201 *Data analyses*

202 To test for the effects of urchin presence on the community composition on settlement  
203 tiles, percentage cover of functional groups at the end of each season (summer and winter)  
204 were analyzed separately using PERMANOVA and visualized with nonparametric  
205 multidimensional scaling (NMDS) plots. All data were square root transformed and put into a  
206 Bray-Curtis distance matrix using 999 permutations. NMDS ordination plots were generated  
207 using Bray-Curtis distances on two dimensions. Both analyses were conducted in R Studio  
208 using the Vegan package (Oksanen et al. 2019). Dry biomass of communities on settlement  
209 tiles were compared among experimental treatments using one-way ANOVA. To evaluate the  
210 effect of urchin presence on coral survival, we used survival analysis, performed in R Studio  
211 with the package survival (Therneau 2020). For *Porites sp.*, we performed a next plus one

212 transformation to account for 100% survival in the urchin present treatment and added an  
213 artificial death to each treatment. Accelerated Failure Time models were also run to test the  
214 effect of urchins on coral survival but found similar results to the Survival Analyses and were  
215 thus not included here. The effect of urchins on growth or erosion of coral fragments was  
216 tested using a one-way ANOVA for each species. Data were transformed to the percent  
217 change per year of each fragment as fragment sizes varied within and among species. Only  
218 corals that were still alive at the end of the experiment were included in growth analyses. To  
219 investigate the effect of urchins on bioerosion of coral cores, we ran one-way ANOVAs, with  
220 summer and winter seasons analyzed separately. All statistical analyses were performed in R  
221 Studio (version 3.6.1).

222

## 223 **Results**

224 The presence of urchins caused different benthic communities to develop on settlement  
225 tiles in a season-specific way (Fig. 1). Communities where *D. setosum* were present, both  
226 open and partial cage plots, were centred around CCA and benthic microalgae (Table S1 for  
227 definitions) in the summer, and microalgae and bare tile in the winter, whereas communities  
228 when urchin were excluded centre around algal turf and serpulid worm sediment matrices in  
229 the summer, and serpulid worms and serpulid worm sediment matrices in the winter (Fig. 1A,  
230 B.).

231 When benthic taxa are combined into functional groups (Table S1), the presence of  
232 urchins reduced the coverage of algal sediment matrix by 60% and increased the cover of  
233 CCA by 60% by the end of the summer (Fig. 1C, E;  $F_{2,23} = 13.01, p < 0.001$ ). There was a  
234 divergence of benthic community composition at the end of the winter, with an even stronger  
235 influence of urchins on the community (Fig. 1B). When urchins were present, CCA coverage

236 was 65% greater than without urchins by the end of the season. Meanwhile, there was a  
237 decrease in algal-sediment matrix by 75% (Fig. 1E and F;  $F_{2,24} = 45.76$ ,  $p < 0.001$ ).

238 When urchins were excluded, algae and sediment accumulation (algal-sediment matrix)  
239 was 29 times greater during the summer and 80 times greater during the winter compared to  
240 when urchins were present (Fig. 2;  $F_{2,23} = 8.59$ ,  $p < 0.002$ ;  $F_{2,24} = 124$ ,  $p < 0.001$ ). During  
241 the summer, there was  $22.3 \pm 6.9 \text{ g} \cdot \text{m}^{-2}$  of algal sediment accumulation when urchins were  
242 excluded from the plots but  $< 1 \text{ g} \cdot \text{m}^{-2}$  when urchins were present. This pattern was  
243 exacerbated during winter, with an average of  $1027.7 \pm 90.5 \text{ g} \cdot \text{m}^{-2}$  accumulated when  
244 urchins were excluded, compared to  $12.8 \pm 2.0 \text{ g} \cdot \text{m}^{-2}$  when urchins were present. There  
245 were no differences in the mass of algal-sediment matrix between the partial cage treatment  
246 and when urchins were present, for either summer or winter (Tukey HSD:  $p = 0.98$  and  $p =$   
247  $0.99$ , respectively).

248 When urchins were present, *Porites sp.* had 100% survival, but this was reduced to 66.7%  
249 when urchins were excluded (Fig. S2). While overall survival of *P. decussata* was lower than  
250 *Porites sp.*, mortality was still higher when urchins were excluded than present (55.6% and  
251 14.3%, respectively; Fig. S2). In contrast, *P. carnosus* suffered high mortality irrespective of  
252 urchin presence or absence. Consequently, new *P. carnosus* fragments were added to replace  
253 dead fragments on two separate occasions (Fig. S2).

254 Urchins increased the survival probability of *Porites sp.* coral fragments. When urchins  
255 were present, *Porites sp.* were 92% more likely to survive than when urchins were excluded  
256 (Cox test, Hazard Ratio (HR) = 0.08, 95% C.I. = 0.01 – 0.64,  $p = 0.018$ ) and 84% more likely  
257 to survive in partial cages than when urchins were excluded (Cox test HR = 0.16, 95% C.I. =  
258 0.03 – 0.80,  $p = 0.025$ ). Consequently, the probability of *Porites sp.* surviving until the end of  
259 the experiment (393 days) was reduced from 90% to 30% when urchins were excluded (Fig.  
260 3, Survival Analysis Log-Rank test,  $\chi^2 = 12.6$  on 2 degrees of freedom,  $p < 0.002$ ). By

261 contrast, the presence of urchins had no effect on the survival probability (Cox test,  $p = 0.13$ ,  
262  $p = 0.60$  for urchin presence and partial cages, respectively) or survival duration of *P.*  
263 *decussata* (Fig. 3, Log-Rank test,  $p = 0.260$ ). Conversely, *P. carnosus* had a lower survival  
264 probability when urchins were present. When accounting for the death of fragments and the  
265 addition of new fragments, *P. carnosus* were 4.82 times more likely to die with urchins  
266 present, compared to when they were absent (Cox test, Hazard Ratio (HR) = 4.82, 95% C.I. =  
267 1.49 – 15.6,  $p = 0.009$ ). *P. carnosus* were also less likely to survive throughout the entire  
268 duration of the experiment when urchins were present (Fig. 3; Survival Analysis Log-Rank  
269 test,  $\chi^2 = 20.0$  on 8 degrees of freedom,  $p < 0.01$ ). However, when reducing the Survival  
270 Analysis model from 393 days (the duration of the entire experiment) to 163 days (the  
271 duration of the experiment after the last set of *P. carnosus* fragments were added) the  
272 probability of *P. carnosus* surviving until the end of the experiment (the remaining 163 days)  
273 increases to  $71.4\% \pm 12.1\%$  SE when urchins were present.

274 *Porites sp.* and *P. decussata* had similar growth rates regardless of urchin presence or  
275 absence: in both cases they grew throughout the year (Fig. 4). There was no difference in  
276 buoyant weight of surviving fragments of both *Porites sp.* and *P. decussata* when urchins  
277 were excluded relative to when urchins were present (One-way ANOVA,  $F_{2,16} = 0.58$ ,  $p =$   
278  $0.571$  and  $F_{2,12} = 1.094$ ,  $p = 0.366$ , respectively). Though *Porites sp.* grew at similar rates  
279 when urchins were excluded, they were more likely to survive, and therefore have greater net  
280 growth when urchins are present. *P. decussata* had similar, though not significant survival  
281 and growth trends as *Porites sp.* and may contribute to overall net growth. In contrast, when  
282 urchins were present *P. carnosus* decreased in weight due to bioerosion (Fig 4.;  $F_{2,21} = 10.4$ ,  
283  $p < 0.001$ ).

284 The presence of urchins increased bioerosion of coral skeleton cores by 4.5 times in the  
285 summer and 3.1 times in the winter (Fig. 5;  $F_{2,23} = 59.83$ ,  $p < 0.001$ ,  $F_{2,24} = 9.13$ ,  $p < 0.002$ ,

286 respectively). There were no statistical differences between the partially caged and urchin  
287 present plots during the summer and winter (Tukey HSD  $p = 0.46$ ,  $p = 0.059$ , respectively).  
288 When urchins were excluded, the coral skeleton cores accumulated turf, sediment and  
289 macroalgae like the settlement tiles.

290

## 291 **Discussion**

292 Urchins are important contributors to the health and function of coral reefs. They can  
293 prevent overgrowth of hard corals by macroalgae and maintain space bare of algae which  
294 increases coral larvae settlement (Carpenter and Edmunds 2006, Hughes et al. 2007). Yet,  
295 eutrophic conditions are generally thought to cause a shift from coral to macroalgae  
296 dominated reefs as algal growth overwhelms herbivory. Here, we show that even in a heavily  
297 developed and eutrophic system, urchins reduce algal-sediment matrix, increase CCA  
298 coverage, and subsequently can increase coral survival. When urchins were present, they  
299 reduced the benthic coverage of algae and trapped sediment by up to 14-fold, corresponding  
300 to an 80-fold decrease in algal biomass and sediment mass. This reduction in algae and  
301 sediment accumulation is crucial for coral survival as algae can overgrow coral and prevent  
302 recruitment (Samarco 1980, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006,  
303 Hughes et al. 2007, Nozawa et al. 2020), and sediment can smother coral, both causing coral  
304 death (Weber et al. 2006, Risk and Edinger 2011, Weber et al. 2012). Therefore, if  
305 herbivores, and in this case the long-spined sea urchin, *D. setosum*, are absent from large  
306 areas of coral based ecosystems for a sustained period, a phase shift from coral to algae  
307 generally occurs (Carpenter and Edmunds 2006, Hughes et al. 2007, Reverter et al. 2020).

308 While there was a substantial overall positive effect of urchins in the system, the effects on  
309 individual corals were more nuanced and species specific than generally reported. Given that  
310 urchins reduced algal growth and sediment accumulation, we expected coral growth to be

311 enhanced by the presence of urchins. Instead, we saw no difference in growth for two of the  
312 three species, *P. decussata* and *Porites sp.*, and negative growth, or bioerosion, for *P.*  
313 *carinosus*. Such nuanced outcomes are not uncommon. For example, several coral species  
314 increased in area by 20% when two herbivorous fishes were present, yet when only one fish  
315 was present or both were excluded, corals decreased in area (were bioeroded) by up to 30%  
316 (Burkepile and Hay 2008). Such species-specific responses are also commonly observed in  
317 corals with natural herbivore communities: for example, *Porites astreoides* grew four times  
318 faster when urchins and fishes were present, yet *Siderastrea siderea* was unaffected by  
319 herbivore exclusion (Lirman 2001). Therefore, not all corals respond similarly to herbivores  
320 and not all herbivores have the same affects on corals growth. Importantly, however, survival  
321 rates of corals are essential to incorporate in assessments, as the presence of herbivores tends  
322 to increase survival for most species (this study; Lirman 2001, Burkepile and Hay 2008,  
323 Knoester et al. 2019). Therefore, while herbivores may cause little difference in coral growth,  
324 they increase coral survival, which leads to net growth of coral reefs.

325 Urchins have been associated with increased health of coral reefs and the survival of coral  
326 colonies by reducing macroalgae and limiting coral overgrowth (Edmunds and Carpenter  
327 2001, Carpenter and Edmunds 2006, Hughes et al. 2007). We found that the effect of urchins  
328 on coral survival is species-dependant; survival of *Porites sp.* increased, *P. carinosus*  
329 decreased, and there was no effect on *P. decussata*. Though *Porites sp.* and *P. decussata*  
330 settled well after transplantation, *P. carinosus* seemed to immediately suffer mortality upon  
331 transplant which could be because this species is more susceptible to mortality under stressful  
332 conditions (e.g. eutrophication; Fabricius 2005, Cybulski et al. 2020). Survival in other coral  
333 species have been shown to increase when systems are healthier and have functionally  
334 redundant herbivores. For example, *Orbicella faveolata* have a two-fold increase in survival  
335 (Lirman 2001) and *Acropora verweyi* a 10% increase in survival (Knoester et al. 2019) when

336 compared to those when herbivores were excluded. Similarly, in an inclusion experiment in  
337 the Florida Keys, coral colonies had 100% survival when two herbivore species were present,  
338 but only 75% survival when both were excluded (Burkepile and Hay 2008) further  
339 emphasizing the importance of having a multiple herbivore species in an ecosystem. This is  
340 especially important in eutrophic systems where algae grow at increased rates and the  
341 compensatory feeding of herbivores is less able to reduce macroalgal dominance (Littler et al.  
342 2006, Ghedini et al. 2015).

343       Though coral growth rates were lower than we expected when urchins were present, the  
344 increase in CCA cover is an encouraging sign for the long-term health of coral communities  
345 as CCA promotes coral recruitment, increases structural integrity of reefs, and deters  
346 macroalgal settlement. CCA cover is well documented as being important as a chemical cue  
347 for coral larval settlement and recruitment (Heyward and Negri 1999, Harrington et al. 2004,  
348 Gómez-Lemos et al. 2018). In fact, several studies have found that CCA increased coral  
349 settlement and metamorphosis from 20% to 85% over other substrata (Heyward and Negri  
350 1999, Gómez-Lemos et al. 2018). As we found urchins increased CCA cover by 60% in both  
351 summer and winter, we would expect to see increased coral settlement rates over longer  
352 periods, though we did not test for this. Further, CCA also acts a binding agent, or cement,  
353 helping reinforce the strength and integrity of coral reefs (Littler and Littler 2013, Weiss and  
354 Martindale 2017). As CCA grows over dead coral skeletons and between corals, it reinforces  
355 the skeletons and increases resistance to physical disturbances (Littler and Littler 2013). Over  
356 time, the aragonite in thick CCA crust dissolves and re-precipitates as dolomite, a  
357 substantially harder mineral than the aragonite in coral skeleton (Nash et al. 2011, Nash et al.  
358 2013) and is associated with stronger reef framework (Weiss and Martindale, 2017). Further,  
359 urchin grazing activity results in grazer-resistant CCA (Davis 2009), which could reduce  
360 bioerosion and further increase coral structural integrity. Lastly, CCA has be found to deter

361 the settlement and growth of macroalgae (Vermeij et al. 2011, Gómez-Lemos and Diaz-  
362 Pulido 2017). For example, *Padina boergesenii* spore settlement was nine times lower on live  
363 CCA versus dead CCA (Gómez-Lemos and Diaz-Pulido 2017), whereas *Ulva fasciata*  
364 growth was suppressed by 55% when grown with CCA (Vermeij et al. 2011). As we found  
365 that urchin presence greatly increases CCA coverage, the secondary benefits of CCA may  
366 contribute to healthier coral communities in Hong Kong.

367 The accumulation of sediment can negatively affect corals in several ways: direct  
368 smothering of corals; decreasing light availability which limits photosynthesis; an increased  
369 metabolic demand on corals to shed the sediment; and microbial processes such as  
370 respiration, fermentation and desulfurylation (Risk and Edinger 2011, Weber et al. 2012). As  
371 sediment either accumulates on corals or is suspended in the water column, the amount of  
372 light that reaches corals is reduced, decreasing the photosynthetic yield of corals and can lead  
373 to photosynthetic stress and bleaching by reducing net productivity (Weber et al. 2006, Risk  
374 and Edinger 2011). Furthermore, when sediment accumulates on corals, the colonies actively  
375 remove sediment through tentacle waving, cilia action or mucus production, all of which  
376 increase coral metabolic demand while reducing feeding and photosynthetic capabilities  
377 (Risk and Edinger 2011). Lastly, sediment-derived microbial respiration creates anoxic  
378 conditions and can kill coral tissues in as little as 15 hours (Weber et al. 2006, Weber et al.  
379 2012). In systems which have become eutrophic, where microbial communities have shifted  
380 to more pathogenic and sulphate-reducing organisms such as Hong Kong (Chen et al. 2019),  
381 it is possible that this microbial degradation could be exacerbated. Decreased photosynthetic  
382 capability, increased metabolic costs, and anoxic conditions caused by sediment buildup all  
383 have negative impacts on corals and can decrease their potential survival capabilities. As we  
384 have shown here, urchins can greatly reduce algal sediment matrices, and are an important  
385 part of coral resilience.



386 While urchins can scrape away algae which increases CCA cover and provides settlement  
387 areas for juvenile corals, overgrazing can lead to bioerosion of the coral skeleton (Glynn  
388 2015, Alvarado et al. 2017) and can be detrimental to a coral ecosystem when the erosion rate  
389 is greater than accretion (Alvarado et al. 2016). Bioerosion generally increases only after  
390 conditions lead to coral tissue death, leading to algal growth on the skeleton and favouring  
391 bioeroders over corals (Barkley et al. 2015, Glynn, 2015). In a healthy reef or coral  
392 community replete with an intact trophic web, bioerosion by urchins is minimal (Bellwood et  
393 al. 2004, Alvarado et al. 2017). When ecosystems are degraded, however, a system imbalance  
394 can drive increased bioerosion rates, but how this manifests depends on the local urchin  
395 species, population density, and size of the individuals (Glynn 2015, Alvarado et al. 2017).  
396 Urchin bioerosion rates can range from  $0.07 - 10.4 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , with urchin densities  
397 varying from less than 1 to more than 100 individuals  $\text{m}^{-2}$  (Glynn 2015). We found that when  
398 urchins were present, bioerosion ranged between  $3.3 - 4.8 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  for winter and  
399 summer, respectively.  $\text{m}^{-2} \cdot \text{yr}^{-1}$  meaning that net bioerosion by urchins was between  
400  $3.0 - 4.4 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  in this system. These rates are moderate when compared to other reef  
401 systems globally. Importantly, urchin bioerosion is often measured by extracting fecal  
402 material, separating out all calcium carbonate, and determining gut turn-over rates to estimate  
403 bioerosion (Dumont et al. 2013, Alvarado et al. 2016). In contrast, we calculated bioerosion  
404 from the loss of skeletal  $\text{CaCO}_3$  when urchins were present and absent, providing a direct  
405 (and more accurate) measure.

406 Herbivory is widely accepted as being beneficial to overall coral reef health, though the  
407 reality is much more nuanced, species-specific, and dependent on the overall state of the  
408 system. As we have shown, herbivory has positive effects on coral communities through  
409 increased CCA cover, which promotes coral settlement, strengthens reefs, and deters  
410 macroalgal settlement, and overall increased coral survival. Several studies have also

411 demonstrated faster coral growth when herbivores are present, though ours did not. Perhaps  
412 most importantly, herbivory substantially decreases algal cover and sediment accumulation,  
413 both of which kill corals and suppresses growth and recruitment if left unchecked. Yet not all  
414 corals react the same way to herbivory. *P. carnosus*, for instance, seem to be more  
415 susceptible to bioerosion when either alive or dead (Dumont et al. 2013, Qiu et al. 2014, this  
416 study). We therefore caution that herbivory has the potential to be deleterious to some corals  
417 when overfishing has led to grazer densities that are unnaturally high, but at natural densities  
418 the benefits of herbivores far outweigh any potential negatives. Importantly, degraded or  
419 highly disturbed ecosystems (i.e., overfished, eutrophic, increased terrestrial sediment run-  
420 off, bleached, etc.) can be strengthened or even restored through the positive effects of  
421 herbivores. Ultimately, it is necessary to take all aspects of herbivory into account, including  
422 coral and herbivore community diversity and composition, when evaluating the role of  
423 herbivory in coral reef ecosystems.

424

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434

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578 **Figure Legends**

579 **Figure 1.** Difference in the final benthic substrate community makeup under different urchin  
580 treatments at the end of (A) summer and (B) winter (NMDS plots with stress = 0.10 and 0.08,  
581 respectively); and benthic assemblages when urchins were present (C, D) and excluded (E, F)  
582 in both summer (C, E) and winter (D, F). Settlement tiles started with 100 % bare surface.  
583 Values are mean  $\pm$  SE.

584

585 **Figure 2.** Growth of turf algae and accumulation of sediment ( $\text{g} \times \text{m}^{-2}$  dry weight) when  
586 urchins are present or excluded for the (A) summer and (B) winter season. Values are the  
587 mean  $\pm$  SE.

588

589 **Figure 3.** The probability of each species of coral surviving until the end of the experiment  
590 when urchins are absent (yellow), present, (blue) absent (green), and under procedural control  
591 (blue). Kaplan-Meier plot, crosses indicated censored data points, coral fragments that did not  
592 die before the conclusion of the experiment. Letters represent significant differences amongst  
593 treatments.

594

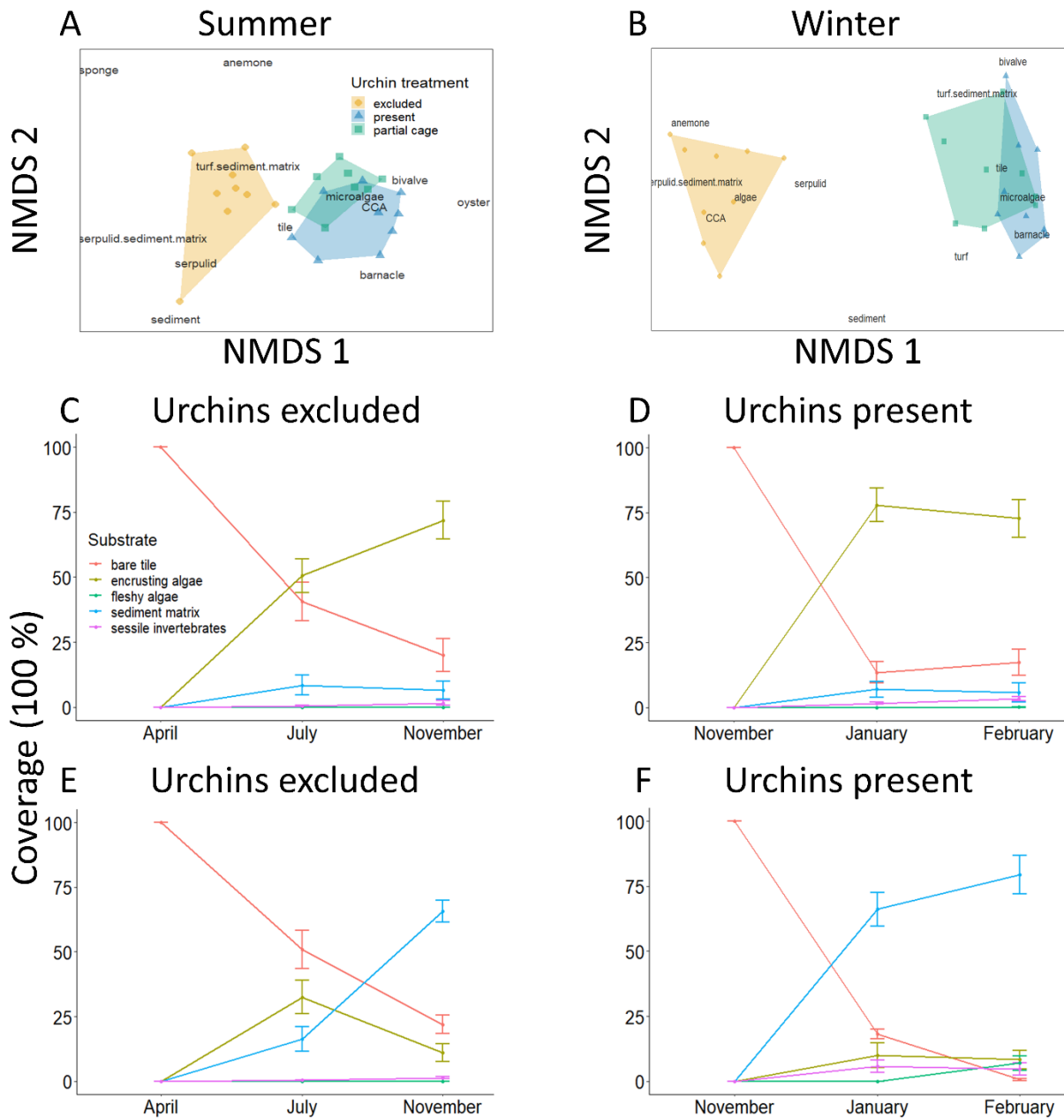
595 **Figure 4.** Percent change in the buoyant weight of corals per year when urchins were  
596 excluded, present, and present in partially caged plots. Only corals that were still alive at the  
597 end of the experiment were used for these analyses. Values are mean percent  $\pm$  SE. Asterisks  
598 represent significant differences amongst treatments.

599

600 **Figure 5.** The rates of bioerosion of coral skeleton core disks by the urchin *Diadema setosum*  
601 for (A) summer and (B) winter. Values are mean  $\pm$  SE. Letters represent significant  
602 differences between urchin treatments.

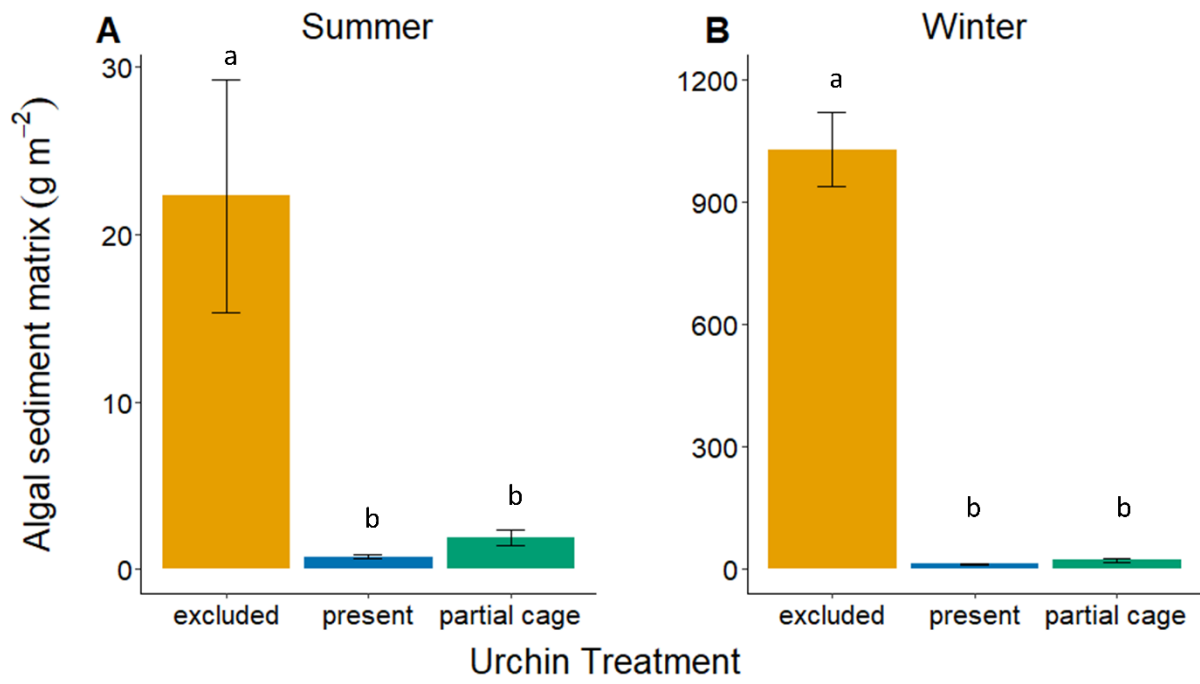
603

604 Fig 1.



605

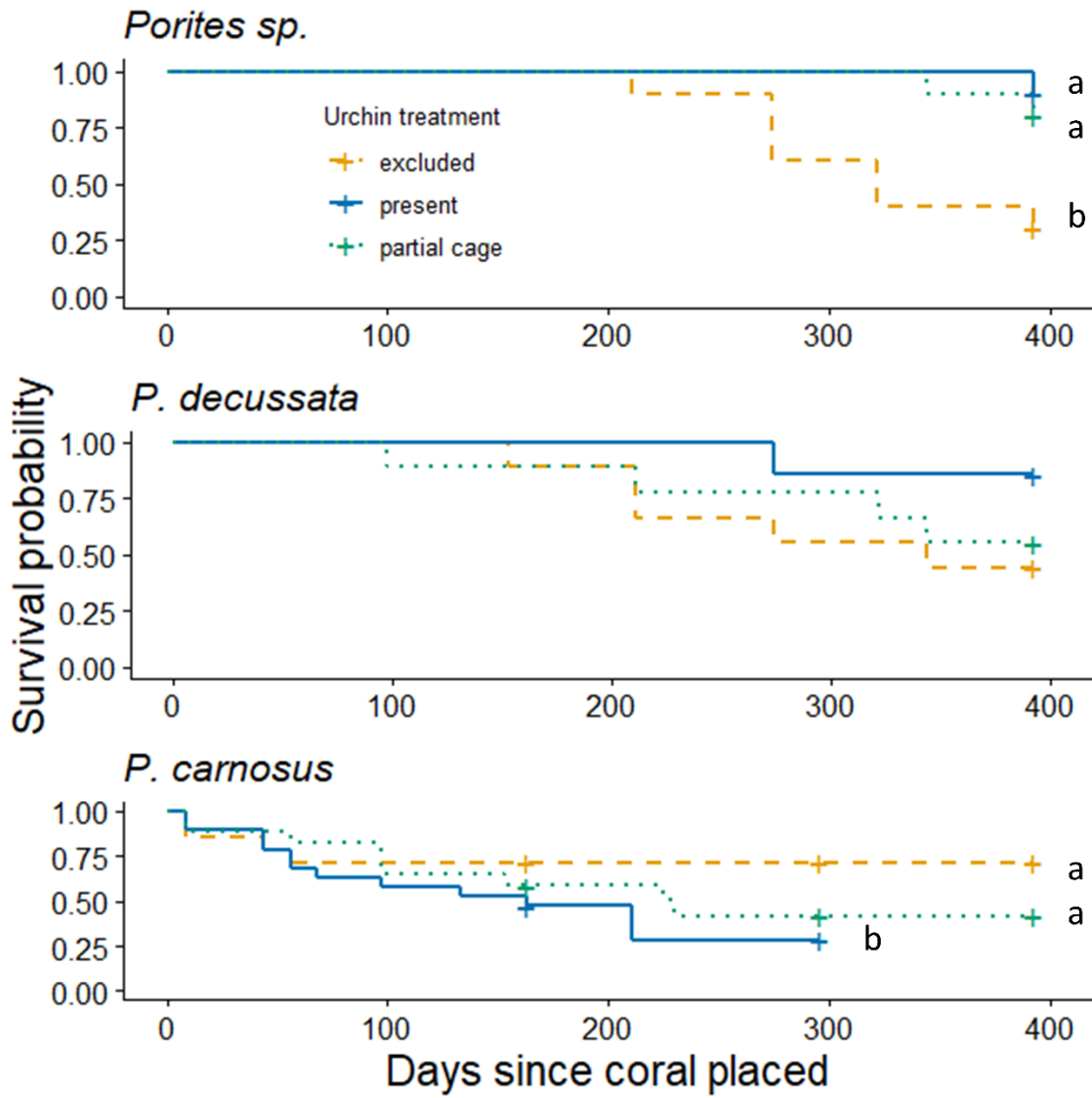
606 Fig. 2



607

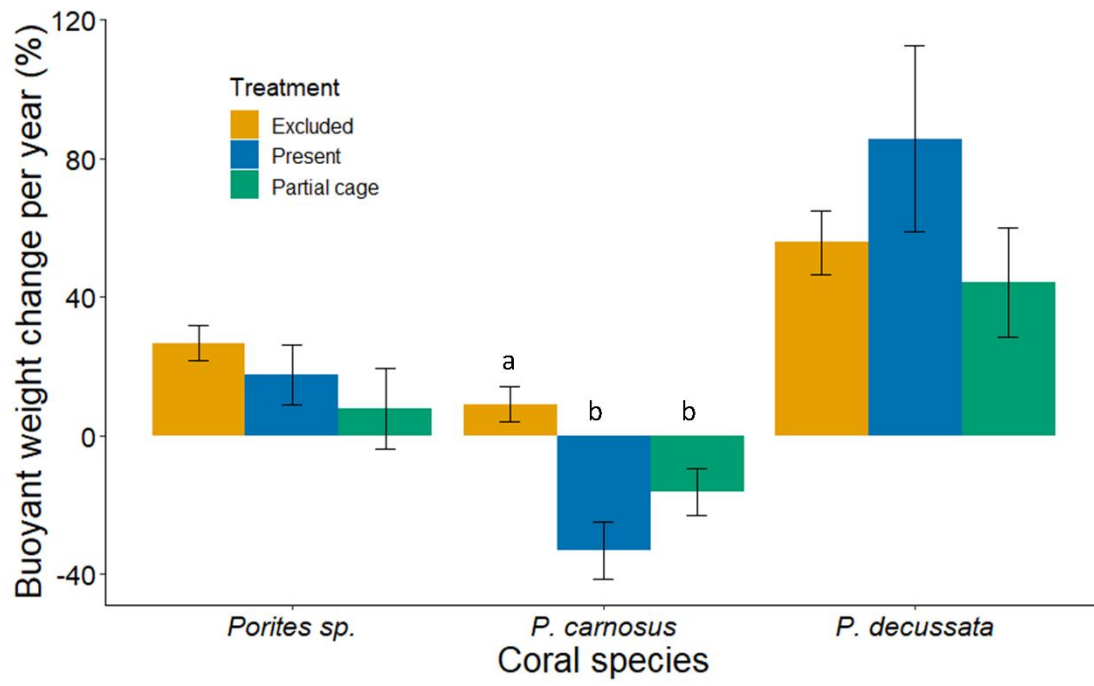
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609 Fig. 3



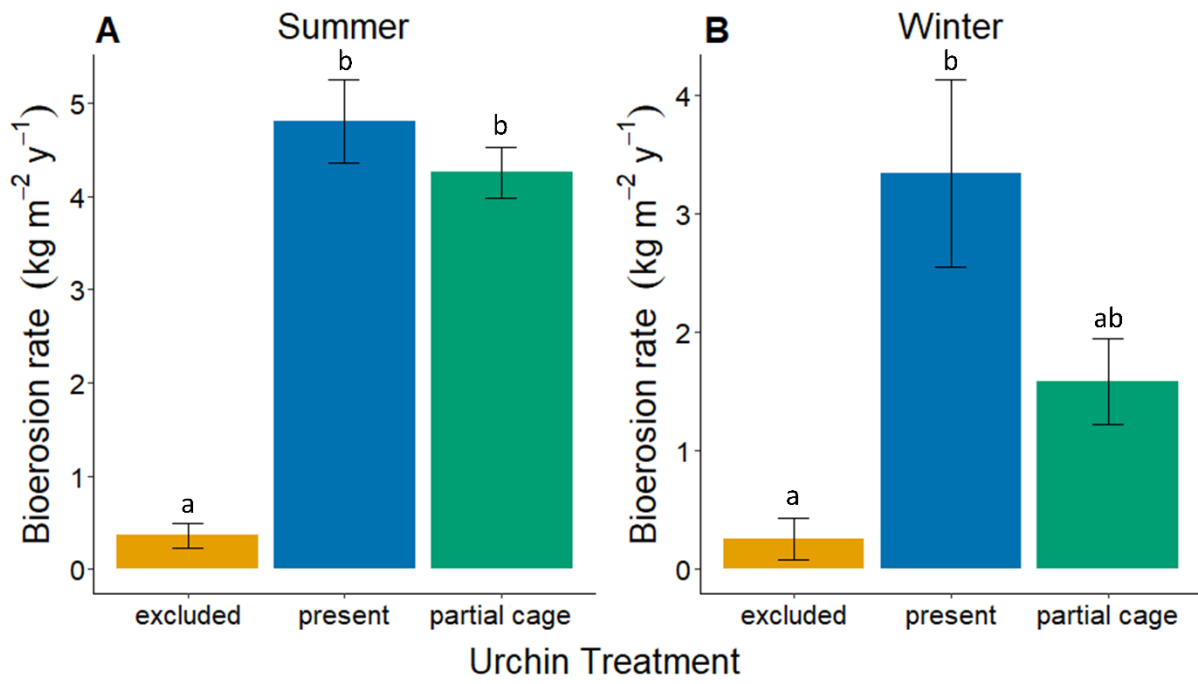
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611 Fig. 4.



612

613 Fig. 5.



614