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3 Spatial mismatch in fish and coral loss following 2016 mass coral
4 bleaching
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8 Sharon Wismer¹, Sterling B. Tebbett¹, Robert P. Streit¹ and David R. Bellwood^{1*}
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13 ¹ARC Centre of Excellence for Coral Reef Studies and College of Science and Engineering,
14 James Cook University, Townsville, QLD 4811, Australia.
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18 *Corresponding author: david.bellwood@jcu.edu.au; +61 7 4781 4447
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1 **Abstract**

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3 Record-breaking temperatures between 2015 and 2016 led to unprecedented pan-tropical
4 bleaching of scleractinian corals. On the Great Barrier Reef (GBR), the effects were most
5 pronounced in the remote, northern region, where over 90 % of reefs exhibited bleaching.
6 Mass bleaching that results in widespread coral mortality represents a major disturbance
7 event for reef organisms, including reef fishes. Using 133 replicate 1 m² quadrats, we
8 quantified short-term changes in coral communities and spatially associated reef fish
9 assemblages, at Lizard Island, Australia, in response to the 2016 mass bleaching event.
10 Quadrats were spatially matched, permitting repeated sampling of fish and corals in the same
11 areas: before, during and 6 months after mass bleaching. As expected, we documented a
12 significant decrease in live coral cover. Subsequent decreases in fish abundance were
13 primarily driven by coral-associated damselfishes. However, these losses, were relatively
14 minor (37% decrease) and compared to the magnitude of *Acropora* loss (> 95% relative
15 decrease). Furthermore, at a local, 1 m² scale, we documented a strong spatial mismatch
16 between fish and coral loss. Post-bleaching fish losses were not highest in quadrats that
17 experienced the greatest loss of live coral. Nor were fish losses associated with a proliferation
18 of cyanobacteria. Several sites did, however, exhibit increases in fish abundance suggesting
19 substantial spatial movements. These results challenge common assumptions and emphasize
20 the need for caution when ascribing causality to observed patterns of fish loss at larger spatial
21 scales. Our results highlight the potential for short-term resilience to climate change, in
22 fishes, through local migration and habitat plasticity.

23

24 **Key words**

25 Climate change; Great Barrier Reef; coral bleaching; *Acropora*; damselfish; cyanobacteria.

26

27 **1. Introduction**

28

29 Climate change is widely regarded as the greatest threat to the persistence of coral reefs
30 worldwide (Carpenter et al., 2008; Hoegh-Guldberg et al., 2007; Hughes et al., 2003, 2018a).
31 Rising ocean temperatures are associated with stronger tropical storms (Knutson et al., 2010;
32 Walsh and Ryan, 2000), infectious coral disease outbreaks (Bruno et al., 2007; Harvell et al.,
33 1999) and most importantly, devastating episodes of mass coral bleaching (Hughes et al.,
34 2017, 2018a). Bleaching occurs when the thermal limits of corals are exceeded and the
35 symbiotic relationship with photosynthetic zooxanthellae (*Symbiodinium* spp.) is disrupted,
36 causing corals to lose colour and become physiologically damaged (Glynn, 1993; Heron et
37 al., 2016; Hoegh-Guldberg, 1999). Although corals are capable of surviving such events,
38 prolonged bleaching often leads to widespread coral mortality (Hoegh-Guldberg, 1999;
39 Hughes et al., 2018b). Over the past two decades, anomalies in sea-surface temperatures have
40 led to three major global bleaching events (e.g. Heron et al., 2016; Hughes et al., 2017,
41 2018a). This includes the unprecedented mass bleaching of Australia's Great Barrier Reef
42 (GBR) in 2016, which severely impacted over 90 % of the reefs in the remote, northern
43 region (Hughes et al., 2017, 2018b).

44

45 Coral taxa often show differential responses in their vulnerability to thermal stress. While
46 *Turbinaria* and *Porites* spp. are generally more resistant, branching pocilloporids and
47 acroporids are highly susceptible to bleaching and often experience high levels of mortality
48 (Baird and Marshall, 2002; Hoogenboom et al. 2017; Hughes et al., 2018b; Loya et al., 2001;
49 Marshall and Baird, 2000). Branching species, including *Acropora* species, play a key
50 ecosystem role for many reef fishes, providing both food and shelter (Coker et al., 2013;

51 Pratchett et al., 2008a), and most importantly, increasing the complexity (e.g. rugosity) of
52 coral reefs – an essential component in structuring reef fish assemblages (Graham et al.,
53 2006; Graham and Nash, 2013; Wilson et al., 2008). Hence, widespread loss of branching
54 corals is often tightly linked to significant decreases in reef fish abundance, particularly for
55 small, coral-associated damselfishes and obligate coral-feeding butterflyfishes (Graham et al.,
56 2006; Pratchett et al., 2008a; Wilson et al., 2006). Coral mortality, in general, has also been
57 associated with a decline of non-coral dependent reef fishes (Jones et al., 2004; Pratchett et
58 al., 2011), including planktivorous damselfishes (Booth and Beretta, 2002; Wilson et al.,
59 2006) and various invertebrate-feeding fishes (Wilson et al., 2006), while herbivores and
60 piscivores may increase in abundance following coral bleaching (Garpe et al., 2006;
61 Sheppard et al., 2002; Wilson et al., 2008). These patterns, however, may vary according to
62 the geographic location, temporal scale (i.e. duration since coral bleaching) and subsequent
63 physical and biological disturbances (e.g. tropical cyclones, crown-of-thorns starfish (CoTS)
64 outbreaks), which may further erode coral skeletons and reduce structural complexity
65 (Pratchett et al., 2008a).

66

67 Although the effects of coral bleaching on reef fishes have been well documented (reviewed
68 in Hoey et al., 2016; Pratchett et al., 2008ab, 2011, 2018; Richardson et al., 2018; Wilson et
69 al., 2006), studies to-date have been constrained by the lack of direct spatial-temporal overlap
70 in their sampling design. For example, the majority of studies assess correlative declines
71 before and after a mass bleaching event in the cover of live scleractinian coral (usually along
72 10 m point intercept transects) and the abundance of various fish species at a substantially
73 larger transect level (100 to 250 m² belt transects) (for a discussion of the importance of scale
74 in coral reef fish studies see Yeager et al., [2017]). Although the general assumption is that a
75 loss of live coral, especially habitat-forming *Acropora* species, results in a proportional net

76 loss of coral-dependent reef fishes, no studies, to the best of our knowledge, have explicitly
77 tracked host corals through a mass bleaching event and quantified the changes in the
78 associated reef fish assemblage. Hence, the direct impact of individual coral bleaching, and
79 subsequent mortality, on its 'resident' or closely associated reef fish assemblages, is still
80 largely unknown.

81

82 Our study employs a new methodology to explicitly test the assumption that coral mortality
83 leads to the loss of resident fishes. Using replicate 1 m² quadrats, we quantified short-term
84 changes in the benthic communities and associated reef fish assemblages, across the ~10 km²
85 reefal system of Lizard Island, northern GBR, in response to the 2016 mass coral bleaching
86 event. Importantly, all quadrats were spatially and temporally matched, in that, for each
87 individual quadrat: 1) both benthic and fish taxa were recorded at the same time and at the
88 same spatial scale, and 2) the original quadrat location was clearly identified and was,
89 therefore, able to be reassessed over the course of the bleaching event. Hence, using this
90 sampling design, we were also able to directly test for the strength of the spatial match in
91 coral and fish loss, particularly in coral-associated fishes with small home ranges, following a
92 major bleaching event. We also examined the short-term (6-month) consequences of acute
93 post-bleach cyanobacterial outbreaks. We hypothesized that 1) host coral mortality would
94 lead to a proportional (if non-linear) decrease in the abundance of coral-dependent reef
95 fishes, with a lesser effect on other species, and 2) that fish mortality would be exacerbated
96 by outbreaks of cyanobacteria.

97

98 **2. Materials and methods**

99

100 **2.1. Study site and timeline of the bleaching event**

101

102 Our study was conducted at Lizard Island, on the mid-continental shelf, in the northern
103 region of the GBR, Queensland, Australia (14°40'S, 145°28'E) (Figure S1 in the Electronic
104 Supplementary Material, ESM). Lizard Island is situated within a marine park and
105 experiences limited fishing pressure; yet surrounding reefs have recently suffered significant
106 environmental damage as a result of ongoing CoTS outbreaks and consecutive tropical
107 cyclones (i.e. 2014, 2015). Between February and April of 2016, Lizard Island and the
108 northern reefs of the GBR experienced prolonged elevated sea-surface temperatures (mean
109 range: 27.1 - 29.1°C; Australian Government Bureau of Meteorology, 2016), leading to a
110 devastating mass coral bleaching event across the northern 1000 km of the GBR (Hughes et
111 al. 2017). In order to document temporal changes in both benthic communities and fish
112 assemblages, we collected a series of 'photoquadrats' in 1) January-February 2016, i.e. prior
113 to the bleaching event, 2) April 2016, i.e. during peak bleaching, and 3) October 2016, i.e. 6
114 months post-bleaching.

115

116 **2.2. Transects and photographs**

117

118 We surveyed a total of 19 sites across Lizard Island, which were haphazardly chosen, based
119 on the availability of a reef crest (ESM Figure S1). Within each site, we swam a transect
120 along the reef 'crest' (at 0 – 4 m below chart-datum). The reef 'crest' was chosen as it is
121 typically the most dynamic habitat in regards to relative rates of reef processes (Bellwood et
122 al., 2018) and often has the highest coral cover (Wismer et al., 2009). Photographs of a 1 m²
123 quadrat (Camera: Nikon Coolpix AW130) were taken at approximately 5 m intervals. Each
124 replicate quadrat consisted of three images: 1) a photograph of the reef and reef fishes (from
125 a distance of approximately 2 m), from a horizontal perspective, i.e. undisturbed and prior to

126 the placement of the quadrat (care was taken to ensure all fishes up to 1.5 m in the water
127 column were included in the photographs, however, in most cases fish were in close
128 proximity to the substratum), 2) a photograph with the 1 m² quadrat in place, using the
129 identical camera placement as in the first image, and 3) a planar ‘bird’s-eye’ view of the 1 m²
130 quadrat in place on the substratum (Figure 1). Transects varied in length (range: 50 – 210 m)
131 and contained between 12 and 38 quadrats. The precise ‘starting’ location of each transect
132 was identified using GPS coordinates. Subsequently, quadrat locations were relocated using a
133 second underwater camera containing all previous images for reference, repeating the three
134 photographs of the same 1 m² area, across all three sampling periods, i.e. before, during and
135 after coral bleaching. All transects were conducted on SCUBA by two divers between 09:00
136 and 16:00 hrs.

137

138 Our sampling method was specifically designed to minimise the ‘diver effect’ on fish
139 communities and maximise accuracy of counts on visually apparent small, coral-associated
140 fishes. Standard underwater visual census (UVC) techniques of quantifying fish assemblages,
141 especially point censuses or transects where the tape is laid first, can significantly
142 underestimate the abundance of larger vagile fishes by (50 to 70 %) through diver
143 disturbance (Dickens et al., 2011; Emslie et al., 2018). They also miss most small,
144 cryptobenthic, fishes (< 50 mm) and rely on estimations once large schools of fishes are
145 encountered (Ackerman and Bellwood, 2000). In contrast, our images were taken within
146 seconds of arriving at a site, thus minimising the diver effect and ongoing disturbance. This
147 approach is also relatively insensitive to low visibility or on-going disturbance and can yield
148 precise counts of small fishes rather than estimates of fish schools (it takes up to 30 minutes
149 to count all fish in one image (maximum 128 individuals)). The method is thus specifically
150 designed to yield replicate, high-resolution counts of small, visually-apparent coral-

151 associated reef fishes.

152

153 **2.3. Analysis of photographs**

154

155 A total of 133 (of 451) photoquadrats were analysed. Quadrats were only included if they had
156 a minimum live coral cover of 20% in the first sampling period, as we were explicitly
157 examining coral-fish linkages (coral is used in the broad sense to describe taxa in the orders:
158 Alcyonacea, Corallimorpharia, Helioporacea, Scleractinia; class: Hydrozoa (*Millepora* spp.);
159 (Veron 2000)). See ESM Text S1 for further details on quadrat selection.

160

161 To quantify the abundance and diversity of reef fishes, images were processed in Adobe
162 Illustrator, by drawing an outline of the quadrat on the first, undisturbed photograph, using
163 the second image in the series as a reference. All visible fishes within the delineated 1 m²
164 area on the first photograph, and the 1.5 m water column directly above the quadrat (using
165 the quadrat as a guide), were recorded to species level (see ESM Figure S2). To avoid
166 misidentification of visually similar species, *Chromis viridis* and *C. atripectoralis* were
167 grouped into one species category, '*C. viridis*'. To exclude the effects of recruitment pulses
168 during the summer months, analyses are based on adult fishes only (based on the loss of
169 juvenile colouration and/or being over approximately 25% of the maximum adult size).

170

171 The benthic community was quantified using the third, i.e. planar, image (see ESM Figure
172 S3) and processed using the software photoQuad (Trygonis and Sini, 2012), which generates
173 stratified randomized points (n = 40) over the photoquadrat. Under each point the benthic
174 covering was recorded. For corals, the genus, growth form and bleaching status were
175 recorded. Only corals and cyanobacteria cover are considered herein and relative benthic

176 cover of these categories was based on the 40 points. Only 10 of the 15960 benthic points
177 examined were categorized as ‘unidentifiable’ and were excluded from subsequent analyses.
178 For graphical purposes, the relative level of coral cover remaining during and after bleaching
179 was calculated individually in each plot by calculating cover remaining as a percentage of the
180 initial (100%) cover. To assess the effect of random sampling and variation in quadrat
181 placement, 15 randomly selected ‘after’ quadrats were examined using the 40 random points
182 vs the exact same 40 points as used in the ‘before’ quadrat. With a mean difference of just
183 1.4% our repeat quadrat method was found to provide a good indication of benthic changes
184 among temporal samples (see ESM text S2, ESM Table S1 for full details).

185

186 **2.4. Data analysis**

187

188 We used generalized linear mixed effects models (GLMMs) to test for differences in the
189 proportional cover of live coral, soft coral, *Acropora* spp. and scleractinian corals, as well as
190 fish abundance and fish species richness, among the three sampling periods, i.e. before,
191 during and after mass bleaching. Fish abundance data were examined using a GLMM with a
192 negative binomial distribution, to account for the non-normal and overdispersed nature of the
193 count data, while fish species richness data were examined using a GLMM with a Poisson
194 distribution, suitable for count data which is not overdispersed. Coral cover data were
195 examined using a GLMM with a binomial distribution in all cases. Where overdispersion was
196 present in the binomial models, an observation-level random effect was employed to account
197 for this. In all models, sampling period (before, during, after mass bleaching) was fitted as a
198 fixed effect, while quadrat ID nested within transect ID were fitted as a random effects. The
199 random effects accounted for the lack of spatial independence and the repeated measures
200 sampling design. Model fits were evaluated using residual plots. Statistical modelling was

201 performed in the software R (R Core Team, 2017), using the lme4 (Bates et al., 2015)
202 package.

203

204 Changes in the assemblages of corals (genera) and reef fishes (species) were first examined
205 using non-metric multi-dimensional scaling (nMDS) ordinations. Ordinations were based on
206 zero-adjusted Bray Curtis similarity matrices of square root transformed coral cover and fish
207 abundance data to decrease the impact of highly abundant taxa. Differences between groups
208 in the ordinations were tested using permutational multivariate analysis of variance
209 (PERMANOVAs). In the PERMANOVA design, sampling time was treated as a fixed factor,
210 while quadrat ID nested within transect ID were treated as random factors to account for the
211 repeated measures design and the lack of spatial independence. Following the
212 PERMANOVAs, pair-wise tests were performed to examine within-factor differences.
213 Assumptions of homogeneity of dispersions were tested using permutational analysis of
214 multivariate dispersions (PERMDISPs). Canonical analysis of principle coordinates (CAP)
215 was then used to explore specific differences among sampling periods (before, during, and
216 after mass bleaching) identified in the PERMANOVAs.

217

218 A non-parametric distance-based linear model (DISTLM) was used to examine the
219 relationship between changes in the fish assemblage (at a species level) with the changing
220 coral assemblage (genus level). Based on a multiple regression model, the DISTLM
221 examines the relationship between the fish assemblage data and coral assemblage data to find
222 the combination of coral genera that explains the greatest variation in the fish assemblage
223 data. The initial model fitted all coral genera and then a backwards selection routine based on
224 Akaike's Information Criterion (AIC) was employed to select the most parsimonious model
225 of coral genera that explained changes in the fish assemblage (ESM Table S2). Distance-

226 based redundancy analysis (dbRDA) was then used to visualise the most suitable model.
227 Multi-collinearity was initially assessed using draftsman plots. All multivariate analyses were
228 performed using PRIMER 7.0 PERMANOVA+.

229

230 In addition to the DISTLM, we also explicitly examined relationships between certain
231 benthic categories and fish loss. Specifically, linear regressions were used to examine the
232 relationship between changes in the cover of *Acropora*, scleractinian corals, structurally
233 complex corals, combined ‘total’ corals and soft coral, with changes in fish abundance, i.e.
234 before vs. after bleaching. Additionally, we examined the relationship between 1)
235 cyanobacteria cover during bleaching and fish loss (before vs. after bleaching), and 2) the
236 relationships between the cover of bleached *Acropora*, soft corals and scleractinian corals
237 with fish loss (before vs. during bleaching). Fits of linear regressions were assessed with
238 residual plots. All statistical analyses were conducted on absolute data. Data standardised to a
239 relative scale were only used for graphical purposes.

240

241 **3. Results**

242

243 **3.1. Changes in coral cover, reef fish abundance and reef fish species richness**

244

245 The percent cover of live coral decreased significantly over time (Figure 2a). Compared to
246 images prior to bleaching, total live coral cover was significantly lower both during (GLMM;
247 $P = < 0.001$) and after (GLMM; $P = < 0.001$) mass bleaching, with relative decreases of 36.7
248 and 44.7 % from pre-bleaching levels, respectively (Figure 2a; ESM Tables S3, S4). The
249 impact of bleaching was most pronounced for soft corals (Order Alcyonacea) and *Acropora*
250 (Order Scleractinia) (Figure 2a). Six months post-bleaching, the relative cover of soft coral

251 and *Acropora*, on average, decreased by 69.5 and 96.4 % from initial levels, respectively
252 (Figure 2a). Other scleractinian corals, excluding *Acropora* species, also decreased
253 significantly, both during (GLMM; $P < 0.001$) and after (GLMM; $P < 0.001$) bleaching, with
254 a total relative decline of 11.1% (ESM Figure S4; ESM Tables S3, S4). Absolute values
255 (mean \pm SE; range) for changes in the cover of various coral categories are provided in ESM
256 Table S5.

257

258 In general, reef fishes followed a similar pattern to corals, in that fish abundance decreased
259 significantly over time, with fewer individuals recorded during (GLMM; $P = < 0.01$) and
260 after (GLMM; $P = < 0.001$) mass bleaching, compared to initial images (Figure 2b; ESM
261 Tables S3, S4). Absolute values (mean \pm SE; range) for changes in the abundance of total
262 fishes and focal damselfishes are provided in ESM Table S6. Although species richness did
263 not decrease significantly between before and during samples (GLMM; $P = 0.096$), there
264 were fewer fish species recorded post-bleaching (GLMM; $P < 0.001$) (Figure 2c; ESM
265 Tables S3, S4).

266

267 In total, we documented changes in the abundance of 120 species of reef fishes. Of the
268 species with 5 or more individuals observed (Figure 3), the majority (76.9 %) decreased in
269 abundance in response to bleaching, with three coral-associated damselfishes (*Chromis*
270 *viridis*, *Pomacentrus moluccensis*, *Neopomacentrus azysron*) accounting for over 54 % of
271 total fish loss. These damselfishes lost most individuals (Figure 3), with relative losses
272 equating to decreases of 38.3, 32.7 and 39.1%, respectively (ESM Figure S5). Losses of
273 individuals in other species were relatively minor (Figure 3). Eight species increased in
274 abundance post-bleaching (mean = 7.5 individuals), with most additional individuals in the
275 damselfish *Acanthochromis polyacanthus* (40.4% relative increase) (Figure 3).

276

277 3.2. Community change and interrelationship

278

279 The coral community shifted significantly following the bleaching event (PERMANOVA:
280 Pseudo- $F_{2, 398} = 37.499$, $p_{[\text{perm}]} = 0.0001$), driven primarily by a near complete loss of
281 *Acropora* (Figure 4a). Pair-wise tests revealed that the coral assemblage was significantly
282 different, from pre-bleaching conditions, during ($t = 6.003$, $p_{[\text{perm}]} = 0.0001$) and after ($t =$
283 7.4394 , $p_{[\text{perm}]} = 0.0001$) mass coral bleaching as well as between peak bleaching, compared
284 to post-bleaching ($t = 3.1072$, $p_{[\text{perm}]} = 0.0001$). Based on the PERMDISP, there was no
285 significant variation in the coral community dispersion across sampling periods ($F_{2, 396} =$
286 2.2387 , $p_{[\text{perm}]} = 0.2159$).

287

288 Significant, although less pronounced, shifts in the community assemblage of reef fishes
289 were also documented (PERMANOVA: Pseudo- $F_{2, 398} = 3.5194$, $p_{[\text{perm}]} = 0.001$), largely
290 driven by a reduction in small damselfish species (Figure 4b). Pair-wise tests revealed
291 significant before vs. after bleaching ($t = 2.2597$, $p_{[\text{perm}]} = 0.0001$), before vs. during ($t =$
292 1.7029 , $p_{[\text{perm}]} = 0.004$) and during vs. after ($t = 1.5118$, $p_{[\text{perm}]} = 0.021$) effects. There was no
293 significant variation in fish assemblage dispersion among sampling periods ($F_{2, 396} = 2.9419$,
294 $p_{[\text{perm}]} = 0.0826$).

295

296 However, the DISTLM revealed that the ability of the coral assemblage to predict the change
297 in the fish assemblage at each site was minimal. The best fit model contained 13 genera of
298 coral, yet only explained 9.97% of the total variation in fish abundance ($R^2 = 0.0997$).
299 Change in *Acropora* was the single best predictor of changes in fish communities, but only
300 explained 1.28% of the total variation in fish composition (ESM Table S7).

301

302 Furthermore, based on specific linear regressions, we documented no significant relationships
303 between changes in the abundance of reef fishes and the cover of various benthic categories
304 including *Acropora*, scleractinian corals, structurally complex corals, combined ‘total’ corals,
305 soft coral, cyanobacteria, bleached *Acropora*, bleached scleractinian corals and bleached soft
306 coral (ESM Figures S6-11; ESM Tables S8, S9).

307

308

309 **3.3. Spatial responses of reef fishes to *Acropora* loss and cyanobacteria outbreaks**

310

311 Post-bleaching, live *Acropora* cover decreased in 98 % of *Acropora*-containing quadrats (i.e.
312 53 quadrats decreased in cover). *Acropora* accounted for 2.5 to 80 % of the decrease in total
313 cover, with a mean contribution of 16.8 % (Figure 5a). Total reef fish abundance both
314 decreased (n = 86 quadrats, 69.4 %) and increased (n = 38 quadrats, 30.6 %) in quadrats post-
315 bleaching, ranging from a loss of 67 individuals to an increase of 52 individuals per quadrat
316 (Figure 5b). Damselfishes likewise showed both marked decreases and increases within
317 individual quadrats (Figure 5c). However, decreases in the abundance of reef fishes,
318 including damselfishes, was evenly spread across quadrats. It was not concentrated in those
319 quadrats which exhibited the highest loss of *Acropora* (Figure 5abc). There was no
320 significant relationship between *Acropora* loss and fish loss ($R^2 = 0.0083$, $p = 0.2957$; ESM
321 Figure S6a; Table S8). This spatial mismatch of coral and fish losses was evidenced for all
322 focal coral groups (i.e. total coral, structurally complex corals, scleractinian corals, soft corals
323 and bleached categories) (ESM Figure S6-S11, ESM Table S8, S9).

324

325 A similar pattern was seen in cyanobacteria. During peak bleaching, cyanobacteria outbreaks
326 occurred in 37 quadrats, with a mean percent cover of 23.9% where present (ranging from 2.5

327 to 97.5 % of the quadrat) (Figure 6a). Again, we recorded both decreases (e.g. post-bleaching
328 n = 86 quadrats, 69.4 %) and increases (e.g. post-bleaching n = 38 quadrats, 30.6 %) in the
329 abundance of reef fishes within individual quadrats (Figure 6bc). Yet, across both sampling
330 periods, fish losses were not concentrated in quadrats containing the highest cover of
331 cyanobacteria (Figure 6abc), again with no significant relationship ($R^2 = 0.0121$, $p = 0.2076$)
332 (ESM Figure S6f; ESM Table S8).

333

334 **Discussion**

335

336 **4.1. Coral bleaching, *Acropora* loss and the effects on coral-dwelling reef fishes**

337

338 Between 2015 and 2016, record-breaking global temperatures caused widespread, pan-
339 tropical bleaching of scleractinian corals (Hughes et al., 2017, 2018a). On the GBR, the
340 effects were most pronounced in the remote, northern region (Hughes et al., 2017, 2018b).
341 Using a series of spatially and temporally matched photoquadrats, we documented the short-
342 term changes in coral and fish communities following mass coral bleaching. In general,
343 corals showed the expected changes in response to thermal stress, i.e. most corals exhibited
344 high levels of bleaching, *Acropora* species showed the highest levels of coral mortality and
345 dead corals were subsequently inundated by cyanobacteria. However, fish loss was not
346 commensurate with the magnitude of coral loss. The relative abundance of fishes decreased
347 by approximately 30%, especially planktivorous coral-dependent damselfishes. Furthermore,
348 there was no spatial match between coral loss and fish loss. Fishes responded at a reef scale,
349 but not at a local, quadrat scale.

350

351 Branching corals play key functional roles on coral reefs (Bellwood et al., 2004), by
352 providing food (Coker et al., 2013) and increasing the structural complexity of reef habitats.

353 This has been identified as a key element in the survival of many species of small-bodied reef
354 fishes (Graham et al., 2006; Wilson et al., 2008). Species that live in close association with
355 branching corals, e.g. damselfishes, often exhibit pronounced decreases in abundance in
356 response to bleaching and or habitat loss, a phenomenon that has been repeatedly
357 documented across multiple spatial scales (e.g. Bellwood et al., 2006; Booth and Beretta,
358 2002; Ceccarelli et al., 2006; Halford et al., 2004; Jones et al., 2004; Pratchett et al., 2008a;
359 Spalding and Jarvis, 2002; Wilson et al., 2008). Our results support this general pattern, yet
360 they raise questions about our assumptions regarding the basis of this decline.

361

362 **4.2. Perspectives on a novel sampling methodology**

363

364 Our novel sampling methodology provides a unique, fine-scale understanding of how coral
365 bleaching, and subsequent mortality, affects reef fishes. Spatially and temporally matched
366 quadrats allowed us to track specific reef sites over the course of a mass bleaching event, and
367 for the first time, we are able to explore subsequent responses of, as well as direct
368 interactions between, corals and fishes. Our methods are particularly suited to quantifying
369 effects on reef fishes that live and feed in close proximity to corals by using quadrats that
370 generally approximate the resting home ranges of these small fishes (e.g. Nash et al., 2015).
371 Quantitative data on the home ranges and site fidelity of small coral-associated reef fishes are
372 scarce and limited to few species (but see Bellwood et al., 2016; Booth 2016; Gardiner and
373 Jones, 2016; Marnane 2000; Rueger et al., 2014; Sale, 1971). However, all evidence suggests
374 that these fishes move only centimetres to a few meters, with most exhibiting high site-
375 fidelity and/or site attachment (Streit and Bellwood, 2017, 2018). Our method is therefore
376 likely to provide a representative indication of the fishes within the local vicinity.

377 Furthermore, quadrats were extensively replicated across the ~10 km² reefal system of Lizard
378 Island, which also allowed us to examine coral – fish interactions at a broader scale.

379

380 Importantly, we were able to measure changes in fish abundance and changes in coral cover
381 simultaneously at the same fine spatial scale. This allowed us, for the first time, to assess any
382 local, small-scale correlations. By contrast, previous studies generally use estimates of fish
383 abundance and or coral cover averaged across larger areas (e.g. Booth and Beretta, 2002;
384 Sano, 2004; Shibuno et al., 1999), which provides little information in regards to where post-
385 bleaching decreases were most pronounced (i.e. bleached versus unbleached corals), as data
386 rarely provide a direct spatial overlap between fishes and corals. Moreover, by analysing
387 digital photographs, we had minimal observer-effect (scaring fishes) and were not
388 constrained by time, which ensured that all visible fishes were accounted for (i.e. counting
389 versus estimating. In some cases it took approximately 30 minutes to analyse a single m²
390 quadrat for fishes, delivering a degree of precision that is not available during typical
391 underwater visual census techniques. Fish identification could also be verified by more than
392 one observer. Finally, timing was closely tied to the bleaching event, the first series of
393 photographs were taken in January 2016, directly prior to the world’s largest bleaching event,
394 allowing us to document the short-term responses of corals and fishes in naturally occurring
395 communities within a protected reef system.

396

397 We do, however, recognize certain methodological limitations. Firstly, quantifying reef fishes
398 from digital photographs is not common practice, as it provides a single ‘snapshot’ with
399 individuals potentially hidden from view behind physical structures or photographed at an
400 angle which makes identification challenging (although this is common to all visual
401 censuses). Secondly, given the small spatial scale of individual quadrats there is the potential

402 to underestimate larger more vagile fishes. However, abundance estimates before bleaching
403 of large functionally important (e.g. Acanthuridae: 9.8 indiv. 100 m⁻²), or coral-dependent
404 (e.g. Chaetodontidae: 6.8 indiv. 100 m⁻²) species were comparable to previous estimates from
405 Lizard Island and nearby reef crests using traditional methods, 7.2 and 8.3 indiv. 100 m⁻²,
406 respectively (Bellwood et al., 2018; Pratchett and Berumen, 2008). Furthermore, our
407 sampling design was specifically designed to examine changes in small coral-associated reef
408 fishes that are documented to suffer most from the direct consequences of live coral loss
409 (Booth and Beretta, 2002; Ceccarelli et al., 2016; Graham et al., 2006). Finally, our study was
410 restricted to adult fishes and only investigates short-term (i.e. 6 months after peak bleaching)
411 responses of benthic communities and associated reef fishes. Although there are
412 methodological limitations, this novel sampling technique has the potential to reveal patterns
413 that may remain ‘hidden’ using traditional methods.

414

415 **4.3. Spatial mismatch in coral versus fish loss**

416

417 Overall, changes in fishes were far less pronounced than expected. For example, the
418 abundance of obligate live coral-dwellers (*P. moluccensis* and *C. viridis*) did not decrease in
419 proportion to *Acropora* loss. The relative cover of live *Acropora* decreased by over 95 % by
420 the third sampling period, while losses in these fishes only ranged from 32.7 in *P.*
421 *moluccensis* to 38.3 % in *C. viridis*. By contrast, in 1999, Pratchett et al. (2012) documented
422 a 30 and 40 % decrease in the abundance of *P. moluccensis* and *C. viridis* at Lizard Island,
423 respectively, in response to a CoTS outbreak that reduced total live coral cover by just 20 %
424 (primarily branching acroporids and pocilloporids). Given the staggering loss in *Acropora*
425 cover, we expected far stronger responses in these fishes. It may be that CoTS and bleaching
426 produce different chemical signatures, however, both result in similar algal-covered coral

427 skeletons after 6 months. It was particularly noteworthy that fish losses were limited even
428 when *Acropora* cover was < 5% and in many areas 0 % cover.

429

430 One of our most unexpected findings, however, was the strong spatial mismatch between fish
431 and coral loss. Quadrats depleted of live coral were expected to result in comparable
432 decreases in fish abundance, or at least, to exhibit higher fish losses compared to quadrats
433 less affected by bleaching, particularly for obligate live coral-dwellers. This was not the case.
434 At a quadrat level, the results clearly show that reef fishes, including coral-associated
435 damselfishes, increased in abundance at several sites that experienced a significant loss in the
436 cover of live coral, including *Acropora*. Hence, fishes increased in areas dominated by dead
437 corals 6 months post-bleaching, which supports the notion that fishes are capable of
438 occupying dead corals as long as the underlying skeleton, and hence, structural complexity,
439 remains intact (e.g. Lindahl et al., 2001; Sano, 2004) (see insert in Figure 5). Similarly,
440 decreases in fish abundance were not restricted to, or focused on, quadrats that exhibited a
441 loss of live coral. Although coral mortality probably played a major role in decreasing the
442 overall abundance of reef fishes post-bleaching, our results are strongly indicative of fish
443 movement. Numerous quadrats across Lizard Island exhibited increases in the abundance of
444 reef fishes post-bleaching. Fishes, therefore, may be vacating degraded habitats, possibly due
445 to increasing intra- and inter-specific competition, and moving to alternate reef locations.
446 Such post-disturbance spatial movement patterns have been inferred in several previous
447 studies. For example, in response to storm damage, fishes were thought to vacate shallow,
448 degraded reef habitats in favour of deeper waters (e.g. Letourneur, 1993; Walsh, 1983), with
449 subsequent recolonization of shallow habitats when environmental conditions were suitable
450 (Letourneur, 1993). Experimental evidence also suggests that coral-dwelling reef fishes
451 (*Dascyllus aruanus*) are able to successfully relocate to healthy coral colonies following

452 bleaching and subsequent mortality of their host coral (Coker et al., 2012). Our results
453 suggest that this behaviour may be relatively common at local scales.

454 An interesting question to consider is at what scale does this spatial mismatch dissipate?
455 However, the answer may be that no such dissipation will occur. Indeed, recent evidence
456 from the GBR, on the 2016 bleaching event, found that changes in the abundance and/or
457 richness of coral reef fishes were poorly predicted by the loss of corals at both a system level
458 (Richardson et al., 2018) and a regional level (Stuart-Smith et al., 2018). Our results, both
459 support and extend these previous findings, by revealing that this spatial mismatch between
460 fish loss and coral loss occurs down to a 1 m² scale. Evidently, the relationship between coral
461 loss and fish loss may not be as clear-cut as often assumed.

462

463 Overall, decreases in fish abundance were probably a result of predation, exacerbated by
464 coral bleaching and competition. Coker et al. (2009) demonstrated that predation on coral-
465 dwelling damselfishes (*P. moluccensis* and *Dascyllus aruanus*) was higher on bleached and
466 recently dead corals, compared to healthy colonies. This may be due to increased visibility of
467 prey in front of a white background and/or the absence of stinging nematocysts, which
468 otherwise deter predators on live corals (Coker et al., 2009), especially invertebrate predators
469 (Goatley et al., 2017). Increased predation in such suboptimal reef habitats may also drive
470 fish movement to neighbouring, healthy coral colonies (Coker et al., 2009). Competitive
471 interactions may also exacerbate fish mortality post-bleaching. Both sessile and mobile taxa
472 often compete for space within reef environments (e.g. Bonin et al., 2015; Kerry and
473 Bellwood, 2016; Lang and Chornesky, 1990; McCook et al., 2001; Webster and Hixon,
474 2000), and competition may intensify following large scale coral loss when critical resources
475 become limited. Fishes that attempt to relocate to healthy coral colonies may experience

476 increased agonistic interactions from resident fishes (Coker et al., 2012), while dominance
477 hierarchies may be altered (Bonin et al., 2015), and density-dependent mortalities increase in
478 degraded habitats (e.g. Boström-Einarsson et al., 2013; Holbrook and Schmitt, 2002).
479 However, despite these widespread reports, we only documented a 37% decline in small reef
480 fishes while recording a 96% loss of *Acropora*.

481

482 This evidence calls for care in our interpretation of the effects of reef degradation on fish
483 loss. At a local, 1 m² scale, significant coral loss does not necessarily equate to a
484 proportional, even if not linear, loss of fishes, particularly in the short-term. Our new
485 methodology revealed unprecedented variation in the responses of resident reef fishes to
486 coral loss, showing the widespread ability of fishes to use alternate reef habitats, as well as,
487 strong evidence for habitat shifts. It should be noted that some of this variation may have
488 resulted from repetitive sampling at this small scale through time. However, across individual
489 quadrats, we repeatedly documented increases in the abundance of resident reef fishes in
490 areas that exhibited significant *Acropora* loss. At other locations, we recorded the ability of
491 *C. viridis* to relocate into *Heliopora* corals (F: Helioporidae) that were previously unoccupied
492 (photographs provided in Figure 7). The ability of these fishes to switch to degraded or
493 alternate corals suggests that the ‘need’ for live *Acropora*, may be a preference, rather than an
494 obligate requirement. This pattern raises questions regarding the evolution and history of
495 coral-fish associations (Bellwood et al., 2016). In the Mediterranean, for example, *Chromis*
496 *chromis*, which is morphologically and functionally similar to *C. viridis*, has no access to, or
497 need for, live branching corals. Instead, they are commonly found over seagrass beds and
498 rocky-algal habitats (Guidetti, 2000; Guidetti et al., 2004). Our study highlights the need to

499 carefully consider the requirement and preferences of coral dwelling species, which exhibited
500 surprisingly flexible habitat associations when faced with significant coral loss.

501

502 Labile habitat associations are a key sign of potential resilience to changing reef
503 environments, particularly in species that normally express strong habitat preferences (Streit
504 and Bellwood, 2018). Invasion success of Red Sea species into the Mediterranean, for
505 example, is largely dependent on climatic affinity and ecological traits, that include home
506 range size (Belmaker et al., 2013; Parravicini et al., 2015), where shifts in such traits may
507 permit successful establishment. Success for reef fishes in modern-day, changing reefs may
508 ultimately depend on the ability of fishes to adjust and shift habitat requirements. On coral
509 reefs, obligate corallivores are often most vulnerable to coral loss, particularly species with
510 narrow dietary niche breadths (Pratchett et al., 2006). However, even highly specialized
511 coral-feeding reef fishes may be capable of feeding behaviour that is more flexible than
512 previously assumed (e.g. *Chaetodon trifascialis*) (Lawton et al., 2012), making them
513 potentially less vulnerable to climate change. Furthermore, recent experimental evidence on
514 forced movement and homing behaviour demonstrated that some damselfishes (e.g. *P.*
515 *moluccensis*) continue to migrate to other sites post-homing, even in species that exhibit
516 strong homing tendencies (Streit and Bellwood, 2017, 2018). In the current study, we show
517 that damselfishes appear to shift from host corals to alternate habitats in response to mass
518 bleaching. The association between coral-dwelling damselfishes and specific host corals or
519 reef sites may be more flexible than previously assumed.

520

521 **4.4. Cyanobacteria and the response of reef fishes**

522

523 Dense mats of cyanobacteria are often an ephemeral symptom of recent reef degradation, as
524 dying corals undergo a series of successional changes. These cyanobacterial mats are
525 associated with a range of detrimental effects including the potential to overgrow and
526 smother benthic organisms, including corals (Ford et al., 2018), inhibiting coral recruitment
527 (Kuffner et al., 2006), and increasing coral diseases (Sato et al., 2017). Cyanobacteria also
528 appear to be detrimental to fishes, increasing predation risk (McCormick, 2012; McCormick
529 et al., 2017) and producing toxins considered harmful to reef fishes (Golubic et al., 2010;
530 Leao et al., 2012). Post-bleaching colonization of cyanobacteria is therefore expected to
531 exacerbate fish loss.

532

533 At a local, 1 m² scale, however, reef fishes exhibited a response to the presence of
534 filamentous cyanobacteria that reflected their response to *Acropora* loss, with a strong spatial
535 mismatch between the cover of cyanobacteria and local declines in fish abundance. Fish
536 losses were not pronounced or concentrated in quadrats that experienced a proliferation of
537 cyanobacteria. Conversely, some of these cyanobacterial-dominated quadrats even exhibited
538 small increases in fish abundance. Again, our spatial matching methodology reveals
539 interesting patterns that question traditional assumptions and highlights the need for caution
540 when ascribing causality to observed patterns. Although, on average, our data agrees with
541 previous studies, with a significant overall decrease in the abundance of reef fishes following
542 coral loss and algal outbreaks, the patterns observed at a larger, 100 m² scale, do not translate
543 to a local, 1 m² scale. Although undoubtedly linked, care must be taken when assuming coral
544 loss and subsequent algal outbreaks have a direct causative relationship with fish decline. Our
545 data show that there is no cross-scale conformity in coral-fish interactions nor a simple linear
546 or proportional relationship between coral loss and fish declines at a quadrat level.

547

548 **4.5. Delayed effects of habitat degradation**

549

550 Although the short-term responses of adult reef fishes to mass coral bleaching were not as
551 severe as expected, we recognize the potential for lag effects due to 1) a loss of structurally
552 complex, three-dimensional habitat structure, 2) a decrease in physiological condition of
553 fishes over time, and 3) recruitment-driven population declines due to a loss of live coral
554 settlement habitat. Firstly, bleaching-induced coral mortality and the loss of structural
555 complexity have differential effects on reef fish assemblages (Pratchett et al., 2008a). Coral
556 mortality as a result of thermal stress does not compromise the underlying coral skeleton, and
557 although covered in algae, it can still be utilized by reef fishes for shelter. Hence, short-term
558 post-bleaching changes in the assemblages of reef fishes are often restricted to coral-
559 dependent species (e.g. Riegl, 2002; Shibuno et al., 1999; Spalding and Jarvis, 2002).
560 However, over time, dead coral skeletons are eroded by biological and physical agents. It is
561 this loss of structural complexity that appears to have the strongest impact on reef fishes, with
562 effects extending beyond coral-dependent species (e.g. Garpe et al., 2006; Graham et al.,
563 2006, 2007; Jones et al., 2004; Wilson et al., 2008). Most branching corals (> 80%) in our
564 study maintained their physical structure 6 months post-bleaching, although some started to
565 show signs of shortening (S.T. pers obs). Hence, structural complexity was generally
566 preserved in the timeframe of our study, and the negative impact of decreased topographic
567 complexity as a result of the recent mass bleaching event, remains to be seen.

568

569 Secondly, underlying changes in fish physiology may only manifest over time. For example,
570 Pratchett et al. (2004) found no significant short-term changes in the abundance of the
571 obligate corallivore *Chaetodon lunulatus*; however, post-bleaching fishes had a lower

572 physiological condition. A follow-up study revealed that *C. lunulatus* did indeed decrease in
573 abundance over time (Pratchett et al., 2006). Finally, habitat degradation may also negatively
574 impact fish settlement and recruitment, with population effects only evident over time. Many
575 reef fish species preferentially recruit to live coral (e.g. Coker et al., 2013; Jones et al., 2004),
576 while dead, algal-covered corals are actively avoided (e.g. Feary et al., 2007). A significant
577 decrease in suitable settlement environment may therefore prevent replenishment of coral-
578 associated species. In this context, our study must be regarded as a short-term response of
579 adult fishes. However, even across our temporal scale, the expected fish-coral association
580 was not as strong as anticipated and these data open up interesting possibilities for the long-
581 term future of these species.

582

583 **4.6. Conclusion**

584

585 In summary, our study provides a unique perspective on the short-term effects of mass
586 bleaching on fish populations and reveals patterns that would go undetected using traditional
587 sampling methodologies. Although we documented an overall decrease in both the
588 abundance of resident reef fishes and the cover of live coral, in response to mass bleaching at
589 Lizard Island, patterns at a local, 1 m² scale, were invariably spatially mismatched. Reef
590 fishes were able to persist at degraded sites that were devoid of live coral and/or inundated
591 with cyanobacteria, while other sites exhibited considerable increases in post-bleaching fish
592 abundance that are indicative of spatial movements. Furthermore, the effects of coral loss on
593 obligate live coral-dwelling species were surprisingly limited, compared to the staggering
594 losses of live *Acropora*. These results challenge commonly held assumptions regarding the
595 tight link between live coral-dwelling damselfishes and habitat-forming *Acropora* corals. The
596 relationship between fish loss and coral loss, therefore, appears to be a rather complex one,

597 and care is needed when ascribing causality from observed patterns obtained from larger
598 spatial scales. Our results offer a degree of optimism, albeit cautious, that fishes are far more
599 behaviourally resilient than we may have previously assumed based on correlations at larger
600 spatial scales.

601

602 **Author contributions**

603 DRB conceptualized the study. RS, ST, DRB collected the data; ST processed the images and
604 analysed the data; SW wrote the first draft of the manuscript and created the figures; All
605 authors developed the manuscript.

606

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Figures



Figure 1. A photograph series of the same quadrat following our sampling methodology. Photographs a), b) and c) were taken during January-February 2016. Photograph a) was used to quantify the fish community prior to quadrat placement using b) to delineate the area for fish quantification, while c) was taken from a ‘birds-eye’ view to quantify the benthic covering. Further examples of temporal replicates are provided in the ESM (Figure S3).

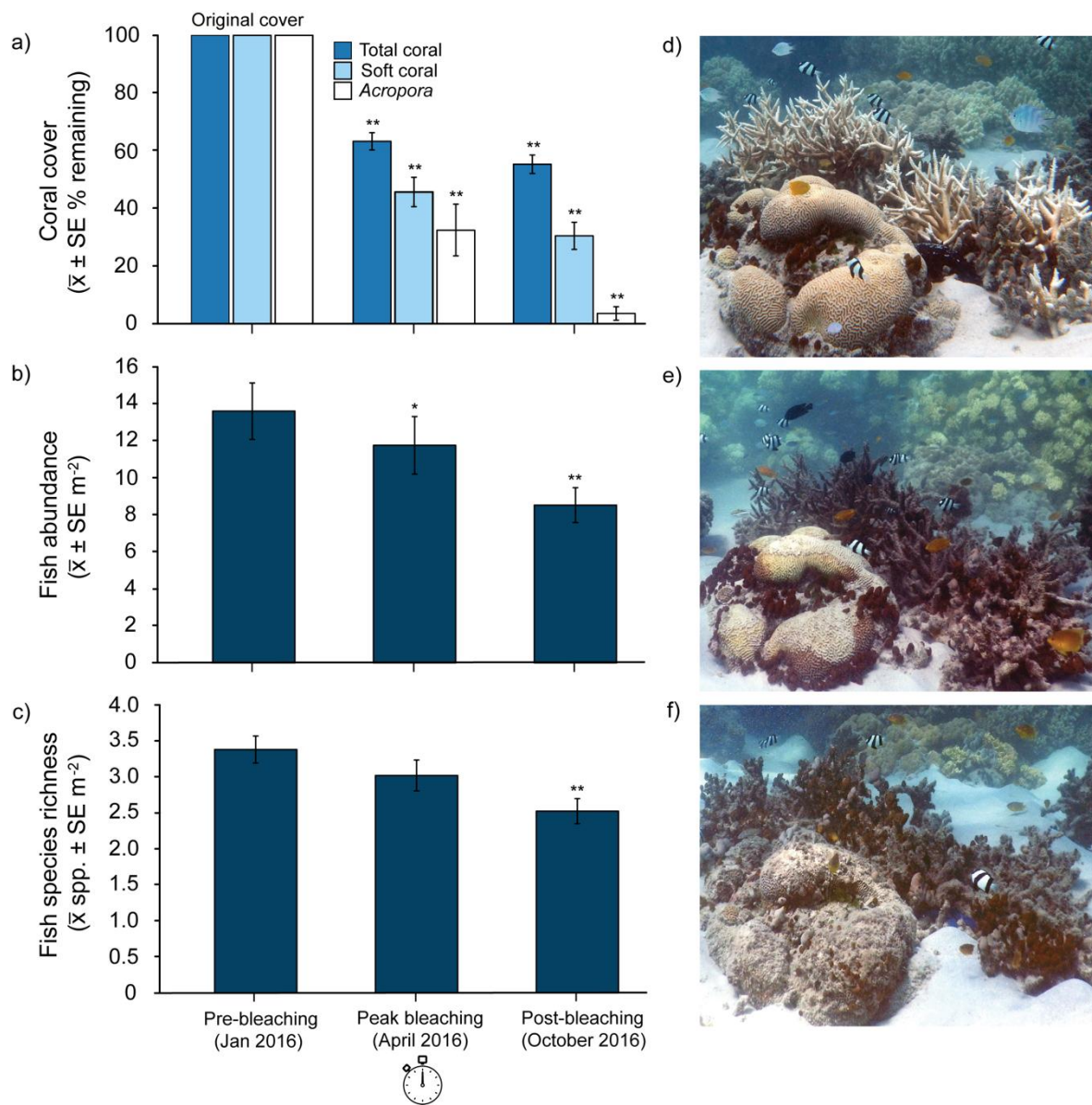


Figure 2. Temporal variation in live coral cover and reef fishes following mass coral bleaching at Lizard Island, Australia. Changes in a) coral cover, b) fish abundance and c) fish species richness, sampled before, during and after mass bleaching. Total coral includes all nominal coral-like taxa (orders: Scleractinia, Helioporacea, Alcyonacea, Corallimorpharia; class: Hydrozoa - *Millepora* spp.), presented as relative cover (i.e. percent cover remaining of the original cover). Fish values represent absolute values. Asterisks represent significant differences in comparison to the first sampling period, ** = $P < 0.001$, * = $P < 0.05$. Fish and coral changes d) before, e) during and f) after coral bleaching. Note the complete loss of *Acropora* but the coral-associated *Dascyllus aruanus* remain.

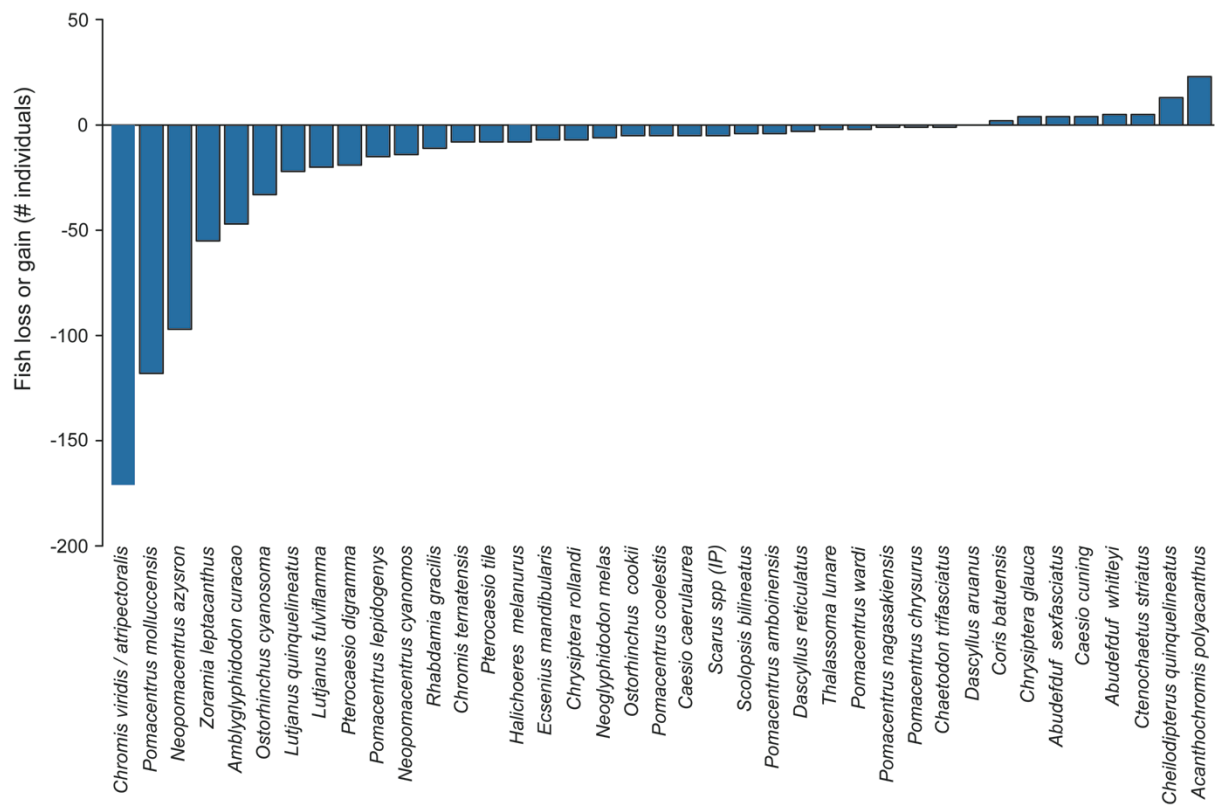


Figure 3. Response of 39 reef fish species to mass coral bleaching. Values represent total changes in the abundance of each species 6 months post-bleaching (October 2016), compared to the initial sampling period in January 2016 (values based on 133 m² of quadrats). Only species with 5 or more individuals are shown.

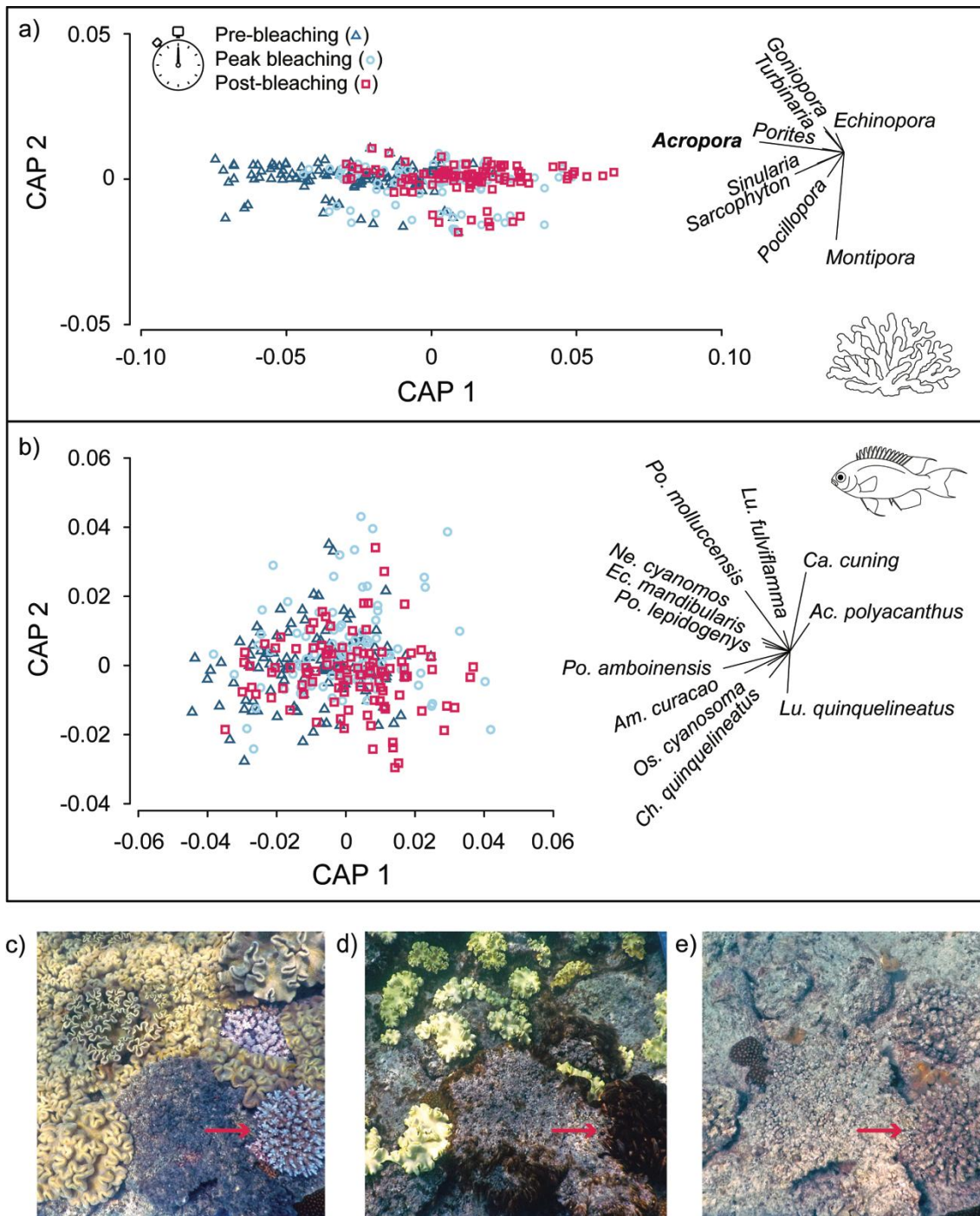


Figure 4. Coral and fish community change in response to mass bleaching. Canonical Analysis of Principal coordinates (CAP) analysis of a) coral and b) reef fishes, showing shifts in assemblages over time; Coloured symbols represent sampling periods, before (dark blue triangle), during (light blue circle) and after (red square) mass bleaching. Vectors on both CAPs were calculated following a multiple correlation model; only taxa with a correlation coefficient > 0.15 are displayed. Note the dramatic change in coral composition with the loss of *Acropora* and the absence of such a change in fish composition. Photographs show transformation of soft corals (*Sarcophyton*) and corymbose *Acropora* over time: c) pre-bleaching (intact), d) during peak bleaching (bleached; covered in cyanobacteria), and e) post-bleaching (absent; dead). Red arrows highlight changes in an *Acropora* colony over time, from live, smothered by cyanobacteria then covered in turf algae.

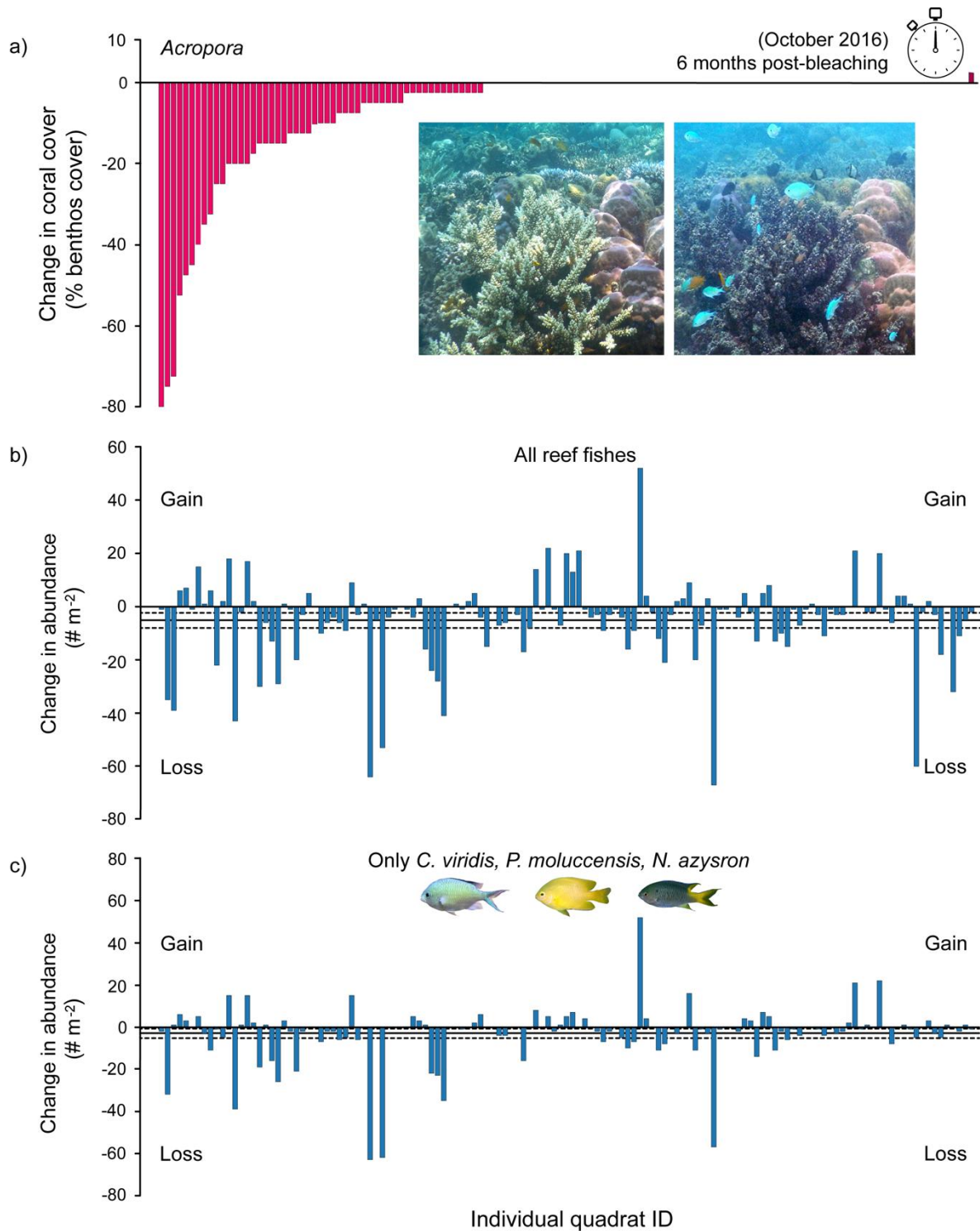


Figure 5. Spatial mismatch in fish and *Acropora* losses. Changes in a) the percent cover of *Acropora*, b) total fish abundance and c) damselfishes (*Chromis viridis*, *Pomacentrus moluccensis*, *Neopomacentrus azysron*) across individual matched quadrats before (January 2016) and after (October 2016) mass bleaching. Dashed lines: 95 % confidence interval. Insert photographs show an *Acropora* colony before and after (dead) mass bleaching. Note the fish in the insert photographs, particularly the coral associated *Chromis viridis* in the foreground and *Dascyllus reticulatus* in the background of the after photo.

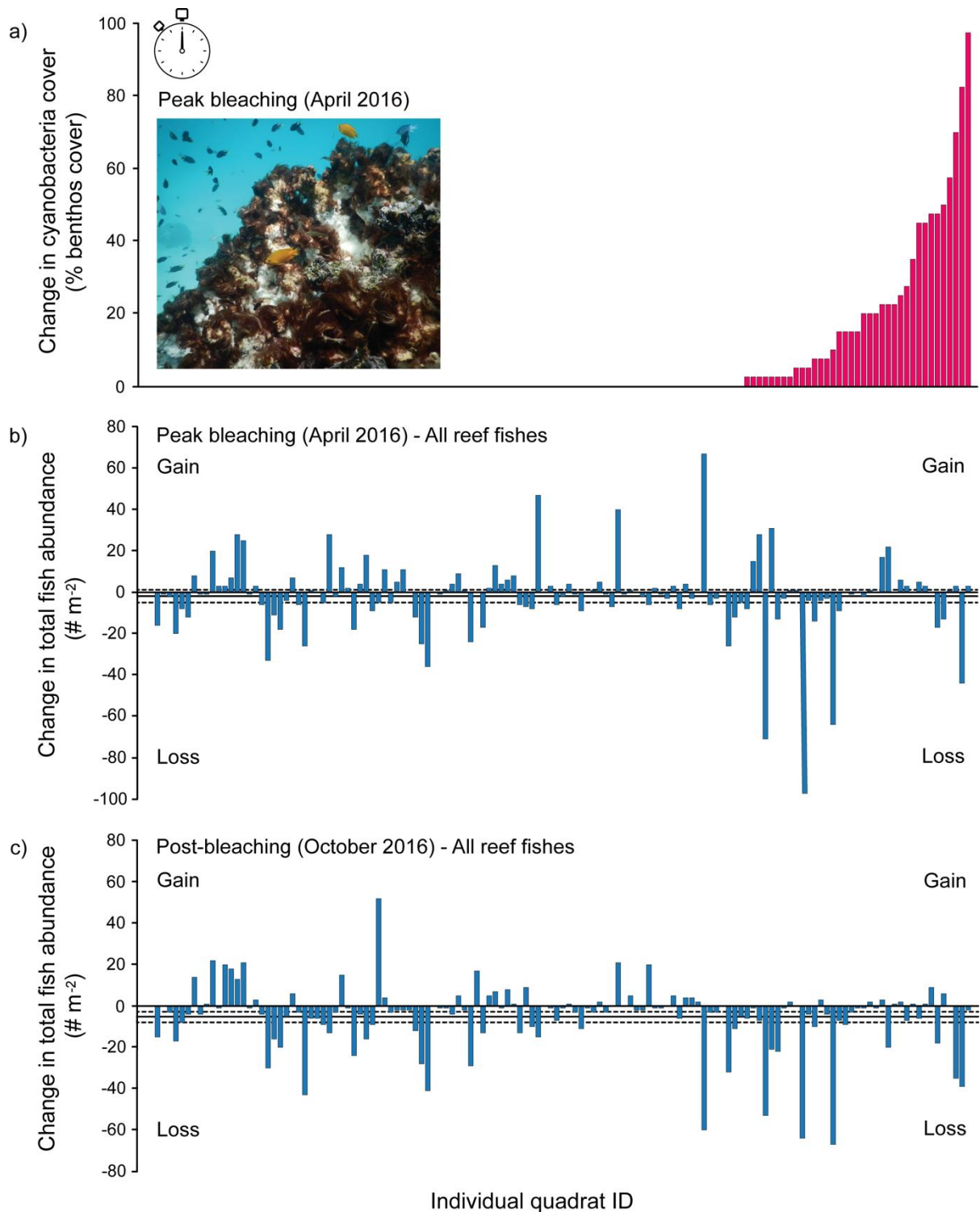


Figure 6. Spatial mismatch in cyanobacteria and fish losses. a) Percent cover of cyanobacteria across individual matched quadrats. Values represent differences between the first sampling period in January 2016 (pre-bleaching) and the second sampling period in April 2016 (peak of bleaching). b) Changes in the abundance of reef fishes within individual quadrats in April 2016 (peak bleaching) and c) in October 2016 (post-bleaching), compared to January 2016 (pre-bleaching). Dashed lines: 95 % confidence interval. Insert photograph shows invasion of cyanobacteria on bleached encrusting *Montipora*.

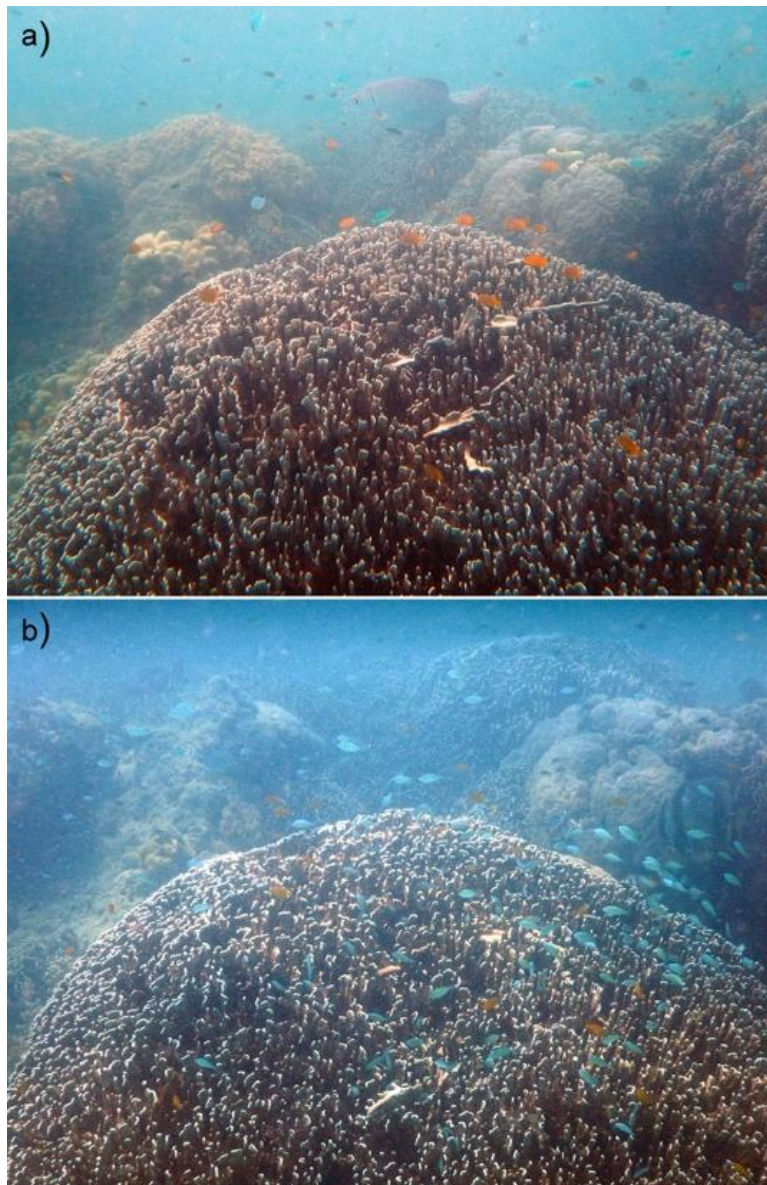


Figure 7. A *Heliopora* coral colony photographed a) before (January 2016) and b) after (October 2016) mass bleaching, showing an increase in the abundance of *Chromis viridis* between sampling periods.