

1 Trophodynamics in novel coral reef ecosystems

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19 **Keywords** Climate change · Coral bleaching · Coral reef fish · Functional group · Habitat
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Abstract Ecosystems are becoming vastly modified through disturbance. In coral reef ecosystems, the differential susceptibility of coral taxa to climate-driven bleaching is predicted to shift coral assemblages towards reefs with an increased relative abundance of taxa with high thermal tolerance. Many thermally tolerant coral species are characterised by low structural complexity, with reduced habitat niche space for the small-bodied coral reef fishes on which piscivorous mesopredators feed. This study used a patch reef array to investigate the potential impacts of climate-driven shifts in coral assemblages on the trophodynamics of reef mesopredators and their prey communities. The ‘tolerant’ reef treatment consisted only of coral taxa of low susceptibility to bleaching, while ‘vulnerable’ reefs included species of moderate to high thermal vulnerability. ‘Vulnerable’ reefs had higher structural complexity, and the fish assemblages that established on these reefs over 18 months had higher species diversity, abundance and biomass than those on ‘tolerant’ reefs. Fish assemblages on ‘tolerant’ reefs were also more strongly influenced by the introduction of a mesopredator (*Cephalopholis boenak*). Mesopredators on ‘tolerant’ reefs had lower lipid content in their muscle tissue by the end of the six-week experiment. Such sublethal energetic costs can compromise growth, fecundity and survivorship, resulting in unexpected population declines in long-lived mesopredators. This study provides valuable insight into the altered trophodynamics of future coral reef ecosystems, highlighting the potential increased vulnerability of reef fish assemblages to predation as reef structure declines, and the cost of changing prey availability on mesopredator condition.

43 **Introduction**

44 Climate change is increasingly recognised as a key driver of ecosystem structure and
45 trophic dynamics in marine and terrestrial ecosystems worldwide (Hoegh-Guldberg and
46 Bruno 2010; Byrnes et al. 2011; Buitenwerf et al. 2012; Brandt et al. 2013; Wernberg et al.
47 2016). Coral reefs are one of the most vulnerable ecosystems due to the high thermal
48 sensitivity of habitat-forming scleractinian corals (e.g. Hoegh-Guldberg et al. 2007). Indeed,
49 climate-driven increase in ocean temperature is emerging as the greatest driver of large scale
50 disturbance and regime-shifts in these ecosystems, with mass coral bleaching events
51 becoming more frequent, widespread and sustained (Hughes et al. 2017). The degree of
52 vulnerability to bleaching, however, varies substantially among coral taxa (Marshall and
53 Baird 2000; Loya et al. 2001; Grottoli et al. 2006; McClanahan et al. 2007). This differential
54 susceptibility to bleaching is predicted to result in large-scale changes in the composition of
55 coral assemblages, with an expected overall shift towards more thermally tolerant species
56 (Riegl et al. 2009; Van Woesik et al. 2011; Pratchett et al. 2014). As the frequency and
57 severity of bleaching increases, the composition of future coral assemblages will depend not
58 only on the thermal tolerance of coral taxa, but also how they respond to changing
59 disturbance regimes (Fabina et al. 2015), and their ability persist or to re-establish in the post-
60 disturbance environment (Darling et al. 2013; Graham et al. 2014).

61 Many of the coral taxa predicted to have high thermal tolerance, and therefore likely
62 to characterise many future coral reef assemblages, are also species with low structural
63 complexity (Loya et al. 2001; DeMartini et al. 2010; Alvarez-Filip et al. 2013). Habitat
64 structure is known to be a key determinant of coral reef fish species diversity, abundance, and
65 biomass (Graham and Nash 2013; Darling et al. 2017), with a loss of complexity resulting in
66 a decline in habitat niche space and refugia, leading to increased competition and predation
67 (Beukers and Jones 1997; Holbrook and Schmitt 2002; Kok et al. 2016). The predicted

68 changes in coral assemblages in response to ocean warming are therefore likely to lead to a
69 shift in coral reef fish assemblage composition (Graham et al. 2014).

70 Small-bodied species of fish are vulnerable to changes in the composition and
71 structure of the coral reef benthos (e.g. Alvarez-Filip et al. 2011; Nash et al. 2013),
72 particularly those species that are directly reliant on live coral for food or shelter (Munday et
73 al. 2008; Coker et al. 2014). While these changes are expected to result in long term
74 reductions in fisheries yields (Graham 2014; Rogers et al. 2014), there remains a lack of
75 understanding of how these changes in the fish assemblage will affect piscivorous reef
76 mesopredators. These larger bodied, more mobile species are less likely to be directly
77 affected by changes in coral assemblages, but may be vulnerable through alterations in the
78 fish assemblage on which they predate (Hempson et al. 2017). Due to the longevity of many
79 piscivores, relative to their small-bodied prey, the impacts of changing prey availability may
80 initially manifest at a sublethal level, resulting in a loss of condition due to reduced
81 nutritional value (Pratchett et al. 2004; Berumen et al. 2005), or higher energetic demands
82 associated with hunting alternate prey (Cohen et al. 2014). Reduced energy reserves can
83 reduce resource allocation to important life history functions such as growth (Kokita and
84 Nakazono 2001; Feary et al. 2009), fecundity (Jones and McCormick 2002), age of first
85 reproduction (Jonsson et al. 2013) and survivorship, resulting in potential population decline
86 in the long term (Graham et al. 2007).

87 Change in the benthic composition of coral reefs therefore has the potential to have a
88 substantial impact on reef mesopredator populations, yet there remains little known about
89 how mesopredator trophodynamics will respond to climate-driven shifts coral assemblages.
90 To address this knowledge gap, this study used an array of patch reefs with varying coral
91 compositions that simulated both undisturbed and predicted climate altered configurations.
92 This experimental setup was then used to investigate (1) the prey base among reefs in terms

93 of diversity, abundance, and biomass, (2) the role of mesopredators in shaping these prey
94 communities, and (3) the effect of differing reef compositions on the condition of
95 mesopredators.

96

97 **Methods**

98 **Study site and patch reefs**

99 This study was conducted at Lizard Island, a high continental island on the mid-shelf
100 of the northern Great Barrier Reef (14°41'31.5"S 145°27'39.3"E), using a patch reef array
101 positioned on the south-eastern side the island's lagoon between October 2013 and July 2015.
102 The experimental setup consisted of twenty large (1.5 m diameter) patch reefs, with two
103 distinct coral assemblages (i.e., thermally tolerant and thermally sensitive or vulnerable)
104 constructed in October 2013. The 10 x 2 array was built at a depth of 3 - 5 m on the sandy
105 lagoon flat, parallel to the surrounding reef, with a distance of at least 15 m separating the
106 patch reefs from each other and from the main reef. Each patch reef consisted of a coral
107 rubble base, stabilised with nylon line, and populated with equal numbers of colonies of six
108 local coral species collected from the reefs surrounding the lagoon. 'Vulnerable' reefs
109 included coral taxa that are currently abundant on reefs across the full range of thermal
110 tolerance, including those that are sensitive to increasing ocean temperatures and prone to
111 coral bleaching (bottlebrush *Acropora* sp., branching *Acropora* sp., *Porites cylindrica*,
112 *Porites* sp. massive, *Stylophora pistulata*, *Turbinaria reniformis*; Fig. 1a). 'Tolerant' reefs
113 consisted only of coral taxa that have high thermal tolerance and low vulnerability to
114 bleaching, to simulate predicted future coral assemblages (*Fungia* spp., *Goniastrea*
115 *retiformis*, *Goniopora* sp., *Porites* sp. massive, *Symphyllia radians*, *Turbinaria reniformis*;
116 Fig. 1b). Species were chosen based on the current best knowledge of their susceptibility to

117 bleaching recorded during previous natural mass bleaching events in the Indo-Pacific (e.g.
118 Marshall and Baird 2000, Loya et al. 2001, McClanahan et al. 2007).

119 The same number of taxa was used in each treatment to exclude species diversity as a
120 variable, the number and size of coral colonies kept as consistent as possible among reefs,
121 and the distribution of treatments randomised within the array. Once built, the live coral
122 cover, average height, and structural complexity of each patch reef was measured along three
123 haphazard 1.5 m transects across the reef, passing through the centre. Percentage live coral
124 cover was estimated by recording the benthos (live coral cover vs alternative substrate) at 12
125 random points along each transect. Reef height was measured as the distance from the sand to
126 the top of the coral at nine random points on each reef. Structural complexity was measured
127 using a standard rugosity index for each transect, calculated as the ratio of the linear straight
128 line distance across the reef, to the same diameter measured using a fine-linked (8 mm
129 diameter) chain draped across the surface of the reef (Luckhurst and Luckhurst 1978).

130

131 **Fish assemblages**

132 Fish assemblages were allowed to establish on the patch reefs over the following 18
133 months, which included two periods of peak settlement (2013 - 14, 2014 – 15), which occur
134 annually between late October and late January at Lizard Island (Milicich and Doherty 1994).
135 In April 2015, the composition of the fish assemblage resident on each reef was surveyed.
136 Each reef was systematically searched and all fishes identified to species and their total
137 length estimated to the nearest 0.5 cm. Length estimates were converted to biomass using
138 published length-weight relationships for each species sourced from Fish Base (Froese and
139 Pauly 2016) according to the formula:

140

$$W = a \times L^b$$

141 where L is the visually estimated length recorded for an individual fish, W is
142 individual fish biomass (g), and a and b are published species specific constants.

143

144 **Mesopredator caging experiment**

145 To examine the effect of the different fish assemblages from the two coral treatments
146 on the trophodynamics of coral reef mesopredators, mesopredators were introduced in April
147 2014. The chocolate grouper, *Cephalopholis boenak*, was selected as the study mesopredator
148 species as it is both locally abundant on the Lizard Island reefs and predominantly
149 piscivorous (Beukers-Stewart and Jones 2004). Fourteen grouper were collected from the
150 reefs surrounding the lagoon using baited hook and line underwater, and placed in aquaria at
151 the Lizard Island Research Station. Only adult fish (17.1 – 21.3 cm TL) were collected to
152 avoid any confounding effects of ontogenetic diet shifts (Chan and Sadovy 2002), and to
153 ensure that there were minimal differences in the prey sizes available to the introduced
154 mesopredators, as grouper are known to be limited by their gape size.

155 Prior to the introduction of the *C. boenak* to the patch reefs, all mesopredators that
156 had recruited naturally to the patch reefs were removed using a net and clove oil anaesthetic,
157 and relocated to the reef habitat surrounding the lagoon. Using the same method, all members
158 of the family Apogonidae were also removed, as these species tend to recruit to reefs in large
159 clouds of hundreds of fish, that could confound measures of both fish assemblage
160 composition and predation. The reefs were then enclosed using cages constructed from 2.5
161 cm x 2.5 cm wire mesh attached to a 2 m x 2 m x 1.2 m frame of PVC piping. A skirt of 2.5
162 cm mesh nylon netting was attached to the base of the cage, and weighted with metal chain
163 that was buried in the sand to ensure that fish could not escape from the reefs, and to avoid
164 burrowing predators like lizardfishes from gaining access to the prey in the cages.

165 All mesopredators (*C. boenak*) were individually tagged with a unique subcutaneous
166 fluorescent elastomer tag in their pectoral fins. Their total length (TL) and wet weight (WW)
167 were recorded immediately before introducing them to the caged patch reefs. A single *C.*
168 *boenak* was introduced to seven randomly selected reefs within each treatment, while the
169 remaining six caged reefs (three for each coral treatment) were used as controls. The
170 experiment was then allowed to run for six weeks before the mesopredators were removed.
171 During this period, the cages were monitored daily and cleaned of algae and any other
172 fouling organisms. Immediately prior to removing the *C. boenak*, the fish assemblage on each
173 reef was again surveyed as per the start of the caging experiment.

174 Mesopredators are physically limited in the prey they are able to consume by their
175 gape size (Mumby et al. 2006). Therefore, to estimate the relative difference in prey biomass
176 available to the *C. boenak* introduced to the patch reefs, their gape height (cm) was measured
177 (mean \pm standard error; 3.68 ± 0.07 cm, max = 4.15 cm, min = 3.30 cm). A prey size cut-off
178 of 5 cm (TL) was consequently used to calculate the prey biomass available to all
179 mesopredators. This slightly longer size was based on the assumption that mesopredators will
180 not always consume their prey side-on, but rather head or tail first.

181

182 **Mesopredator sampling**

183 After six weeks of enclosure, *C. boenak* were removed from the reefs using a net and
184 clove oil anaesthetic, and then euthanised by immersion in ice water. Total wet weight
185 (WW), gutted weight (GW), total length (TL), body height (H), gape height (GH) and liver
186 weight (LW) were recorded for each fish. The livers were excised and fixed in 4% buffered
187 formaldehyde for histological analysis. Samples of white muscle tissue (~ 2.5 cm³) were
188 collected from between the lateral line and dorsal fin of each fish, and frozen for lipid
189 analysis.

190

191 **Body condition indices**

192 Morphometric body measurements were used to calculate Fulton's Condition Index
193 (K; Bagenal and Tesch 1978), which is a commonly used measure of robustness or 'well-
194 being' of a fish, calculated according to the formula:

195
$$K = \frac{WW}{TL^3} \times 100$$

196 Short-term changes in energy stores are often first detected in the liver (Ostaszewska
197 et al. 2005), as this is both the primary site of lipid storage in fish (Stallings et al. 2010), and
198 the tissue with the highest metabolic turnover rate (MacNeil et al. 2006). Therefore, we
199 examined the potential for a treatment effect in the livers of caged mesopredators using both
200 the hepatosomatic index and density of liver vacuoles. The hepatosomatic index (Stevenson
201 and Woods 2006) is the ratio of liver weight (LW) to gutted body weight (GW):

202
$$HSI = \frac{LW}{GW} \times 100$$

203 To examine the potential difference in glycogen stores in the livers of *C. boenak* more
204 closely, the density of hepatocyte vacuoles in transverse liver sections were examined using
205 histology. Preserved livers were embedded in paraffin wax, then cut into 5 µm sections and
206 stained with eosin and Mayer's haematoxylin. A Weibel eyepiece was then used to count
207 vacuole densities at a magnification of 400x (Pratchett et al. 2001).

208 Finally, total lipid content of white muscle tissue samples was quantified using a
209 chloroform-methanol mixture to dissolve all lipids from the tissues (Bligh and Dyer 1959).
210 The solvent was then evaporated off, and the total lipid mass weighed and expressed as a
211 percentage of the total sample.

212

213 **Statistical Analyses**

214 Differences in the structural complexity of the benthic habitat between patch reef
215 treatments (vulnerable vs tolerant) was tested using Welch's t-test, which adjusts degrees of
216 freedom to account for unequal variances between groups (Welch 1947). Similarly,
217 differences in the diversity (Shannon-Weaver Index; H), abundance (fish.reef⁻¹) and total
218 biomass (g.reef⁻¹) of the entire fish assemblage, as well as the available prey fish biomass
219 (g.reef⁻¹, based on a 5 cm body size cut off), were compared between coral treatments.

220 To examine how the fish assemblages on the patch reefs shifted in terms of their
221 composition over the duration of the 6-week mesopredator caging experiment, a principal
222 coordinates analysis (PCO) was used, based on a Bray-Curtis similarity matrix. Data were
223 square root transformed to reduce the influence of highly abundant species. Eigenvectors of
224 the species accounting for the largest separation in the fish assemblages (> 0.7 Pearson
225 correlation co-efficient) were then overlaid to show the key distinguishing taxa. The change
226 in species composition was measured in terms of the Bray-Curtis dissimilarity between the
227 fish assemblage on each reef at the end of the caging experiment compared to the start. Based
228 on the results of the PCO, the prey species, *P. chrysurus*, was identified as a potential driver
229 the differences between treatments. To test this possibility, we reran the Bray-Curtis
230 dissimilarity analysis without this species to see if there was a change in the results, or
231 whether observed effects were community driven. A linear mixed effects model was then
232 used to test for a difference in Bray-Curtis dissimilarity between reef treatments (vulnerable
233 vs tolerant), with the predator treatment (control vs *C. boenak*) included as a random effect.
234 We also tested whether there was a difference in the overall abundance (fish.reef⁻¹) and
235 biomass (g.reef⁻¹) from the beginning to the end of the caging experiment, within each
236 treatment, using a matched pair t-test (non-parametric Wilcoxon matched pair rank test)

237 Differences in the condition of mesopredators caged on vulnerable and tolerant reefs
238 in terms of Fulton's condition index (K), hepatosomatic index (HSI) and the density of
239 hepatocyte vacuoles in liver sections were all tested using notched boxplots and associated
240 95% confidence intervals. To test for a difference in body condition in *C. argus* from the
241 beginning to end of the experiment within each treatment, we used a matched pair t-test (non-
242 parametric Wilcoxon matched pair rank test).

243

244 **Results**

245 **Benthic habitat and fish assemblage**

246 In April 2015, immediately prior to the introduction of the mesopredator caging
247 experiment, patch reefs of the 'tolerant' treatment had significantly lower structural
248 complexity than those of the 'vulnerable' treatment (RI; Vulnerable: 2.46 ± 0.14 , Tolerant:
249 1.87 ± 0.10 , $t_{11.72} = 4.154$, $p < 0.001$, mean \pm standard error; Fig. 2a). The reef fish
250 assemblages that established over 18-month period differed significantly between treatments
251 in terms of their Shannon-Weiner Diversity (H' ; Vulnerable: 2.32 ± 0.12 , Tolerant: $1.70 \pm$
252 0.09 , $t_{17.48} = -5.01$, $p < 0.001$, Fig. 2b). Fish assemblages on vulnerable reef treatments also
253 had higher overall abundance (fish.reef⁻¹; Vulnerable: 47.45 ± 3.83 , Tolerant: 29.4 ± 2.71 ,
254 $t_{17.64} = -4.712$, $p < 0.001$), and biomass (g.reef⁻¹; Vulnerable: 340 ± 30 , Tolerant: 200 ± 50 ,
255 $t_{16.10} = -3.27$, $p < 0.005$) than those on tolerant reefs. There was more available prey biomass
256 (<5cm) on vulnerable patch reefs than on tolerant reefs (g.reef⁻¹; Vulnerable: 54 ± 3 ,
257 Tolerant: 30 ± 5 , $t_{13.03} = 4.87$, $p < 0.001$; Fig. 2c).

258 The PCO analysis showed a clear separation of fish assemblage composition between
259 vulnerable versus tolerant reefs (Fig. 3a). Fish assemblages on vulnerable reefs were
260 characterised by high abundances of *Pomacentrus moluccensis*, *Dascyllus aruanus*,
261 *Gobiodon ceramensis*, and *Halichoeres melanurus*. Tolerant reef fish assemblages were

262 distinguished by higher abundances of *Canthigaster papua* and *Balistoides viridis*, while
263 *Pomacentrus chrysurus* was equally abundant across both treatments.

264

265 **Effect of mesopredators on fish assemblages**

266 A greater shift was evident in the composition of reef fish assemblages on tolerant
267 reefs than vulnerable reefs following the introduction of the mesopredator (Fig. 3a). Bray-
268 Curtis dissimilarity of the fish assemblages between the start and end of the caging
269 experiment was somewhat greater on tolerant reefs (Vulnerable: 12.40 [6.24, 18.56],
270 Tolerant: 19.73 [13.57, 25.89]; Fig. 3b), an effect which did not change with the exclusion of
271 *P. chrysurus*, indicating that this species is not responsible for driving the response. On
272 vulnerable reefs, there was little difference in mean Bray-Curtis dissimilarity between control
273 reefs and those with *C. boenak* introduced, while on tolerant reefs, mean Bray-Curtis
274 dissimilarity in fish assemblage composition was higher for reefs with mesopredators than for
275 controls (Fig. S1). Overall abundance and biomass in the fish communities in each treatment
276 did not differ significantly from the beginning to the end of the experiment (Abundance;
277 Vulnerable: $W = -9$ $p = 0.438$, Tolerant: $W = 14$, $p = 0.281$, Biomass; Vulnerable: $W = -6$ $p =$
278 0.688 , Tolerant: $W = -4$, $p = 0.813$).

279

280 **Effect of fish assemblages on mesopredators**

281 Fulton's condition index (K) showed no difference in the robustness of *C. boenak* at
282 the start of the experiment, prior to being introduced to the patch reefs (Vulnerable: $1.516 \pm$
283 0.052 , Tolerant: 1.602 ± 0.039 , $t_{13.98} = 1.719$, $p = 0.108$). By the end of the 6-week
284 mesopredator caging experiment, fish caged on vulnerable reefs showed no decrease in their
285 Fulton's condition (K), while those on tolerant reefs showed a significant loss of body
286 condition (Vulnerable: $W = -18$, $p = 0.156$, Tolerant: $W = -24$, $p = 0.047$).

287 The hepatosomatic index (HSI) showed no difference in the liver to body mass ratio
288 in *C. boenak* between the two patch reef treatments (Fig. 4a). Similarly, the results of the
289 liver histology analyses showed no significant difference in the hepatocyte densities in *C.*
290 *boenak* caged on the two patch reef treatments (Fig. 4b). However, there was a much higher
291 variance in the density of hepatocyte vacuoles in the livers of mesopredators caged on
292 tolerant reefs than those from vulnerable reefs (Variance; Vulnerable: 0.676, Tolerant =
293 79.246). At a finer physiological scale, the results of the total lipid extraction showed a
294 higher percentage lipid composition in the white muscle tissue of *C. boenak* caged on
295 vulnerable reefs than those from tolerant reefs (Fig. 4c).

296

297 **Discussion**

298 Novel coral reef ecosystems emerging due to climate change are expected to vary
299 substantially, in terms of both structure and function, from the structurally complex, diverse
300 assemblages we associate with current day healthy coral reefs (Graham et al. 2014). This
301 study suggests that these changes are likely to affect the trophodynamics between reef
302 mesopredators and the reef fish assemblages on which they prey. Critically, it provides
303 evidence that mesopredators could experience a loss of condition associated with decreased
304 energy reserves. It also shows that the prey fish assemblages on which they feed on tolerant
305 reefs are less diverse, and prone to greater impacts from piscivore predation. Disruption of
306 trophodynamics on future reefs is thus likely to have repercussions for both mesopredators
307 and their prey.

308 Reduced lipid energy stores and body condition (K) in the *C. boenak* caged on
309 tolerant reef treatments could be attributable to several factors, including altered prey species
310 availability or reduced available prey biomass. Like many reef mesopredators, *C. boenak* are
311 ambush predators, that rely on structure for shelter to hunt from (Shpigel and Fishelson
312 1989). They may therefore need to expend more energy in hunting and capturing prey on
313 tolerant reefs due to the decreased structural complexity. In this experiment, we excluded the
314 effects of competition, by only including a single mesopredator on each reef. On a contiguous
315 coral reef, it is possible that the depletion of lipid stores may be exacerbated as
316 mesopredators experience increased competition for shelter and prey, both factors negatively
317 affected by a loss of structural complexity (Hixon and Beets 1993; Beukers and Jones 1997;
318 Syms and Jones 2000; Kerry and Bellwood 2012). The lack of statistical evidence for an
319 effect in coarser measures of condition (HSI and hepatocyte vacuole density), is likely due to
320 the short time period of this experiment. The overall pattern of decline in body condition

321 across both treatments is likely due to the unavoidable stress of handling and caging on all *C.*
322 *boenak* during the experiment.

323 Sublethal effects, such as the loss of condition and energy reserves, in mesopredators
324 can compromise not only their ability to withstand periods of stress (Jones and McCormick
325 2002), but also the resources they are able to allocate to important life history components,
326 such as growth, age of first reproduction and fecundity (Kokita and Nakazono 2001, Pratchett
327 et al. 2006). This study was too short to empirically detect these effects, but previous field
328 studies have shown that despite mesopredators being able to adapt their diets to a changing
329 prey base, this altered trophic niche carried a cost to their condition (Berumen et al. 2005).
330 Due to the relative longevity of many reef mesopredators, sublethal costs may not be easily
331 detected in the short term, but may result in unexpected population crashes in the long term
332 (Graham et al. 2007). This has implications for fisheries management, as mesopredators are
333 often highly targeted species, and if catch rates are not managed when populations are
334 stressed and experiencing reduced recruitment rates, fisheries could face severe declines.

335 Changes in the broader fish assemblage associated with predicted shifts in coral
336 assemblages are also likely to have wide-ranging ecological and economic implications. This
337 study suggests that the abundance and diversity of reef fish assemblages will decline as coral
338 communities become dominated by taxa with higher thermal tolerance and low structural
339 complexity. This is not surprising, as a reduction in structural complexity decreases available
340 habitat niche space for fish species (Darling et al. 2017). The overall reduction in reef fish
341 biomass also supports previous findings that biodiversity and biomass are closely related,
342 with high biomass reefs supporting a high diversity of species (McClanahan et al. 2011), and
343 biomass found to scale with biodiversity (Mora et al. 2011). Reduced diversity and biomass
344 in coral reef fish assemblages would compromise the sustainability of multispecies reef

345 fisheries, with severe repercussions for the food security of some of the world's poorest
346 coastal populations (Cinner et al. 2013).

347 High species diversity is frequently predicted to confer ecological stability to
348 communities, by increasing the functional diversity represented among species (McCann
349 2000; Gross et al. 2014; Duffy et al. 2016). Greater functional diversity can increase
350 community resilience, allowing them to better respond to perturbation (e.g. Nash et al. 2016),
351 an attribute which may become increasingly important in responding to new future
352 disturbance regimes (Nyström et al. 2008). In this study, fish assemblages on tolerant patch
353 reefs were both less diverse and more strongly affected by the introduction of a
354 mesopredator, suggesting that they may be less resilient to predation than fish assemblages
355 on vulnerable patch reefs.

356 The species that distinguished fish assemblages on vulnerable reefs from those on
357 tolerant reefs represent a variety of different functional groups (e.g. planktivores, coral
358 dwellers, mixed-feeding mid-trophic level wrasses). These species also included habitat
359 specialists that rely on complex live corals (*Dascyllus aruanus*, *Gobiodon ceramensis*)
360 (Froese and Pauly 2016). Tolerant reefs were characterised by species of the order
361 Tetraodontiformes (*Canthigaster papua*, *Balistoides viridescens*), which are known to
362 associate with rubble bottoms as juveniles, and have broad habitat use (Froese and Pauly
363 2016). Species that were ubiquitous between treatments were omnivorous habitat generalists
364 (e.g. *Pomacentrus chrysurus*). This suggests that degree of habitat specialisation likely to be
365 a strong driver of future reef fish assemblages, with generalist species potentially emerging as
366 the successful species on future novel reef assemblages due to their adaptability.

367 As atmospheric carbon concentrations continue to rise, it is improbable that coral reef
368 ecosystems will return to their pre-disturbance state. It is therefore essential that we improve
369 our understanding of how these novel configurations in future ecosystems are likely to

370 function. While the findings presented here will need to be tested on contiguous natural reefs,
371 this study provides insight into how the trophodynamics of piscivorous mesopredators and
372 their prey communities could be affected as coral assemblages shift with rising ocean
373 temperatures. Predation is one of the fundamental ecological processes in food webs
374 (Legović 1989), and therefore of key importance to understanding how ecosystem function
375 may be disrupted or maintained in future reef ecosystems. Mesopredators are also important
376 target species in many reef fisheries (Cinner et al. 2009; Mumby et al. 2012; GBRMPA
377 2014). To ensure the best possible management of these ecologically and economically
378 valuable species, is crucial that we improve our understanding of the probable effects of
379 changing prey bases and habitats on mesopredators, to maintain ecological function and
380 provision of ecosystem services.

381

382

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389

390 **Figure Legends**

391 **Fig. 1** Photos illustrating the two reef treatments in the patch reef array immediately after
392 construction in 2013, prior to recruitment of fish assemblages. All reefs were constructed on
393 a 2 m diameter base of coral rubble, with live colonies of six coral taxa each. **a.** Vulnerable
394 reefs were composed of coral taxa from the entire spectrum of predicted vulnerability to
395 increasing ocean temperatures (bottlebrush *Acropora* sp., branching *Acropora* sp., *Porites*
396 *cylindrical*, *Porites* sp. massive, *Stylophora pistulata*, *Turbinaria reniformis*). **b.** Tolerant
397 reefs consisted only of coral taxa that are expected to have high thermal tolerance (*Fungia*
398 spp., *Goniastrea retiformis*, *Goniopora* sp., *Porites* sp. massive, *Symphyllia radians*,
399 *Turbinaria reniformis*).

400

401 **Fig. 2** Comparison of mean (\pm standard error) **a** benthic structural complexity, **b** Shannon
402 Diversity (H') of fish assemblages, and **c** prey fish biomass available to *C. boenak* between
403 vulnerable and tolerant reef treatments at the start of the mesopredator caging experiment in
404 March 2015.

405

406 **Fig. 3 a** Principal Co-Ordinates Analysis of fish assemblages on patch reefs prior to
407 Mesopredator introduction and after 6 weeks. **b** Bray-Curtis similarity between fish
408 assemblages at the start and end of mesopredator caging experiment (mean \pm standard error),
409 based on square-root transformed species abundance.

410

411 **Fig. 4** Notched boxplots of **a** hepatosomatic index (HSI), **b** hepatocyte densities from liver
412 tissue sections, and **c.** percentage total lipid content in white muscle tissue of *Cephalopholis*
413 *boenak* after removal from mesopredator caging experiment on vulnerable and tolerant patch
414 reef treatments. Bold centre line indicates the median, whiskers span maximum and

415 minimum values, box height shows the interquartile range, and diagonal notches in the boxes
416 illustrate the 95% confidence interval around the median.

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