Trophodynamics in novel coral reef ecosystems

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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.

Introduction

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

Many of the coral taxa predicted to have high thermal tolerance, and therefore likely to characterise many future coral reef assemblages, are also species with low structural complexity (Loya et al. 2001; DeMartini et al. 2010; Alvarez-Filip et al. 2013). Habitat structure is known to be a key determinant of coral reef fish species diversity, abundance, and biomass (Graham and Nash 2013; Darling et al. 2017), with a loss of complexity resulting in a decline in habitat niche space and refugia, leading to increased competition and predation (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 cm^3) were

188   collected from between the lateral line and dorsal fin of each fish, and frozen for lipid

189   analysis.

190

Body condition indices

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

$$K = \frac{WW}{TL^3} \; x \; 100$$

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

$$HSI \; = \; \frac{LW}{GW} \; x \; 100$$

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

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

212

Statistical Analyses

213

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

Discussion

297

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

389

Figure Legends

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

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

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

Fig. 4 Notched boxplots of **a** hepatosomatic index (HSI), **b** hepatocyte densities from liver tissue sections, and **c.** percentage total lipid content in white muscle tissue of *Cephalopholis boenak* after removal from mesopredator caging experiment on vulnerable and tolerant patch 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.

References

Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Sci Rep 3:3486

Alvarez-Filip L, Gill JA, Dulvy NK (2011) Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. Ecosphere 2:1–17

Bagenal TB, Tesch FW (1978) Age and growth. In: T.B. Bagenal (eds) Methods for assessment of fish production in fresh water. Blackwell Scientific Publication, Oxford,

Berumen ML, Pratchett MS, McCormick MI (2005) Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). Mar Ecol Prog Ser 287:217–227

Beukers-Stewart BD, Jones GP (2004) The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. J Exp Mar Bio Ecol 299:155–184

Beukers JS, Jones GP (1997) Habitat complexity modifes the impact of piscivores on a coral reef fish population. Oecologia 114:50–59

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911–917

Brandt JS, Haynes MA, Kuemmerle T, Waller DM, Radeloff VC (2013) Regime shift on the roof of the world: Alpine meadows converting to shrublands in the southern Himalayas. Biol Conserv 158:116–127

Buitenwerf R, Bond WJ, Stevens N, Trollope WSW (2012) Increased tree densities in South African savannas: >50 years of data suggests CO_2 as a driver. Glob Chang Biol 18:675–684

Byrnes JE, Reed DC, Cardinale BJ, Cavanaugh KC, Holbrook SJ, Schmitt RJ (2011)

440   Climate-driven increases in storm frequency simplify kelp forest food webs. Glob

441   Chang Biol 17:2513–2524

442   Chan TTC, Sadovy Y (2002) Reproductive biology, age and growth in the chocolate hind,

443   Cephalopholis boenak (Bloch, 1790), in Hong Kong. Mar Freshw Res 53:791–803

444   Cinner JE, Huchery C, Darling ES, Humphries AT, Graham NAJ, Hicks CC, Marshall N,

445   McClanahan TR (2013) Evaluating social and ecological vulnerability of coral reef

446   fisheries to climate change. PLoS One 8:e74321–e74321

447   Cinner JE, McClanahan TR, Graham NAJ, Pratchett MS, Wilson SK, Raina JB (2009) Gear-

448   based fisheries management as a potential adaptive response to climate change and coral

449   mortality. J Appl Ecol 46:724–732

450   Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L, Ryan PG (2014) Changes in prey

451   availability impact the foraging behaviour and fitness of Cape gannets over a decade.

452   Mar Ecol Prog Ser 505:281–293

453   Coker DJ, Wilson SK, Pratchett MS (2014) Importance of live coral habitat for reef fishes.

454   Rev Fish Biol Fish 24:89–126

455   Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK

456   (2017) Relationships between structural complexity, coral traits, and reef fish

457   assemblages. Coral Reefs 36:561–575

458   Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community

459   disassembly under multiple stressors. Glob Chang Biol 19:1930–1940

460   Demartini EE, Anderson TW, Kenyon JC, Beets JP, Friedlander AM (2010) Management

461   implications of juvenile reef fish habitat preferences and coral susceptibility to

462   stressors[1]. Mar Freshw Res 61:532–540

463   Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity

464   enhances reef fish biomass and resistance to climate change. Proc Natl Acad Sci U S A

465   113:6230–6235

466   Fabina NS, Baskett ML, Gross K (2015) The differential effects of increasing frequency and

467   magnitude of extreme events on coral populations. Ecol Appl 25:1534–1545

468   Feary DA, McCormick MI, Jones GP (2009) Growth of reef fishes in response to live coral

469   cover. J Exp Mar Bio Ecol 373:45–49

470   Froese R, Pauly D (2016) FishBase, www.fishbase.org, version (10/2016).

471   http://www.fishbase.org.

472   GBRMPA (2014) Great Barrier Reef Outlook Report 2014: In brief.

473   Graham NAJ (2014) Habitat complexity: Coral structural loss leads to fisheries declines. Curr

474   Biol 24:R359–R361

475   Graham NAJ, Cinner JE, Norström A V., Nyström M (2014) Coral reefs as novel

476   ecosystems: embracing new futures. Curr Opin Environ Sustain 7:9–14

477   Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef

478   ecosystems. Coral Reefs 32:315–326

479   Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007)

480   Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and

481   ecosystems. Conserv Biol 21:1291–1300

482   Gross K, Cardinale BJ, Fox JW, Gonzalez A, Loreau M, Polley HW, Reich PB, van Ruijven

483   J, Wayne Polley H, Reich PB, van Ruijven J (2014) Species Richness and the Temporal

484   Stability of Biomass Production: A New Analysis of Recent Biodiversity Experiments.

485   Am Nat 183:1–12

486   Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in

487   bleached corals. Nature 440:1186–1189

488   Hempson TN, Graham NAJ, MacNeil MA, Williamson DH, Jones GP, Almany GR (2017)

489   Coral reef mesopredators switch prey, shortening food chains, in response to habitat

490   degradation. Ecol Evol 1–10

491   Hixon MA, Beets JP (1993) Predation , prey refuges , and the structure of coral-reef fish

492   assemblages. Ecol Monogr 63:77–101

493   Hoegh-Guldberg O, Bruno JF (2010) The Impact of Climate Change on the World's Marine

494   Ecosystems. Science (80-) 328:1523–1528

495   Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell

496   CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R,

497   Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate

498   change and ocean acidification. Science (80-) 318:1737–1742

499   Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent

500   predation mortality in damselfishes. Ecology 83:2855–2868

501   Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH,

502   Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M,

503   Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin

504   CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA,

505   Hoogenboom MO, Kennedy E V., Kuo C-Y, Lough JM, Lowe RJ, Liu G, McCulloch

506   MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V,

507   Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK

508   (2017) Global Warming and Mass Bleaching of Corals. Nature 543:373–377

509   Jones G, McCormick M (2002) Numerical and energetic processes in the ecology of coral

510   reef fishes. In: Sale P.F. (eds) Coral reef fishes: dynamics and diversity in a complex

511   ecosystem. Academic Press, San Diego, pp 221–238

512   Jonsson B, Jonsson N, Finstad AG (2013) Effects of temperature and food quality on age and

513   size at maturity in ectotherms: An experimental test with Atlantic salmon. J Anim Ecol

514   82:201–210

515   Kerry JT, Bellwood DR (2012) The effect of coral morphology on shelter selection by coral

516   reef fishes. Coral Reefs 31:415–424

517   Kok JE, Graham NAJ, Hoogenboom MO (2016) Climate-driven coral reorganisation

518   influences aggressive behaviour in juvenile coral-reef fishes. Coral Reefs 35:473–483

519   Kokita T, Nakazono A (2001) Rapid response of an obligately corallivorous filefish

520   Oxymonacanthus longirostris (Monacanthidae) to a mass coral bleaching event. Coral

521   Reefs 20:155–158

522   Legović T (1989) Predation in food webs. Ecol Modell 48:267–276

523   Loya, Sakai, Yamazato, Nakano, Sambali, Van W (2001) Coral bleaching: the winners and

524   the losers. Ecol Lett 4:122–131

525   Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral

526   reef fish communities. Mar Biol 49:317–323

527   MacNeil MA, Drouillard KG, Fisk AT (2006) Variable uptake and elimination of stable

528   nitrogen isotopes between tissues in fish. Can J Fish Aquat Sci 63:345–353

529   Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: Differential

530   susceptibilities among taxa. Coral Reefs 19:155–163

531   McCann KS (2000) The diversity-stability debate. Nature 405:228–233

532   McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Ruiz Sebastiàn C, Guillaume

533   MMM, Bruggemann JH (2007) Western Indian Ocean coral communities:bleaching

534   responses and susceptibility to extinction. Mar Ecol Prog Ser 337:1–13

535   McClanahan TR, Graham N a. J, MacNeil M a., Muthiga N a., Cinner JE, Bruggemann JH,

536   Wilson SK (2011) Critical thresholds and tangible targets for ecosystem-based

537   management of coral reef fisheries. Proc Natl Acad Sci 108:17230–17233

538   Milicich MJ, Doherty PJ (1994) Larval supply of coral reef fish populations - Magnitude and

539   synchrony of replenishment to Lizard Island, Great Barrier Reef. Mar Ecol Prog Ser

540   110:121–134

541   Mora C, Aburto-Oropeza O, Ayala-Bocos A, Ayotte PM, Banks S, Bauman AG, Beger M,

542   Bessudo S, Booth DJ, Brokovich E, Brooks A, Chabanet P, Cinner JE, Cortés J, Cruz-

543   Motta JJ, Cupul-Magaña A, DeMartini EE, Edgar GJ, Feary DA, Ferse SCA,

544   Friedlander AM, Gaston KJ, Gough C, Graham NAJ, Green A, Guzman H, Hardt M,

545   Kulbicki M, Letourneur Y, Ĺpez-Pérez A, Loreau M, Loya Y, Martinez C, Mascareñas-

546   Osorio I, Morove T, Nadon MO, Nakamura Y, Paredes G, Polunin NVC, Pratchett MS,

547   Reyes Bonilla H, Rivera F, Sala E, Sandin SA, Soler G, Stuart-Smith R, Tessier E,

548   Tittensor DP, Tupper M, Usseglio P, Vigliola L, Wantiez L, Williams I, Wilson SK,

549   Zapata FA (2011) Global human footprint on the linkage between biodiversity and

550   ecosystem functioning in reef fishes. PLoS Biol 9:e1000606

551   Mumby PJ, Dahlgren CP, Harborne AR, Kappel C V., Micheli F, Brumbaugh DR, Holmes

552   KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006)

553   Fishing, trophic cascades, and the process of grazing on coral reefs. Science (80-)

554   311:98–101

555   Mumby PJ, Steneck RS, Edwards AJ, Ferrari R, Coleman R, Harborne AR, Gibson JP (2012)

556   Fishing down a Caribbean food web relaxes trophic cascades. Mar Ecol Prog Ser

557   445:13–24

558   Munday PL, Jones GP, Pratchett MS, Williams AJ (2008) Climate change and the future for

559   coral reef fishes. Fish Fish 9:261–285

560   Nash KL, Graham NAJ, Jennings S, Wilson SK, Bellwood DR, Angeler D (2016) Herbivore

561   cross-scale redundancy supports response diversity and promotes coral reef resilience. J

562   Appl Ecol 53:646–655

563   Nash KL, Graham NAJ, Wilson SK, Bellwood DR (2013) Cross-scale habitat structure drives

564   fish body size distributions on coral reefs. Ecosystems 16:478–490

565   Nyström M, Graham NAJ, Lokrantz J, Norström A V. (2008) Capturing the cornerstones of

566   coral reef resilience: Linking theory to practice. Coral Reefs 27:795–809

567   Ostaszewska T, Dabrowski K, Czumińska K, Olech W, Olejniczak M (2005) Rearing of

568   pike-perch larvae using formulated diets - First success with starter feeds. Aquac Res

569   36:1167–1176

570   Pratchett MS, Gust N, Goby G, Klanten SO (2001) Consumption of coral propagules

571   represents a significant trophic link between corals and reef fish. Coral Reefs 20:13–17

572   Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical

573   ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain

574   7:37–43

575   Pratchett MS, Wilson SK, Baird AH (2006) Declines in the abundance of Chaetodon

576   butterflyfishes following extensive coral depletion. J Fish Biol 69:1269–1280

577   Pratchett MS, Wilson SK, Berumen ML, McCormick MI (2004) Sublethal effects of coral

578   bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23:352–356

579   Riegl B, Bruckner A, Coles SL, Renaud P, Dodge RE (2009) Coral reefs: Threats and

580   conservation in an era of global change. Ann N Y Acad Sci 1162:136–186

581   Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of

582   structural complexity. Curr Biol 24:1000–1005

583   Shpigel M, Fishelson L (1989) Food habits and prey selection of three species of groupers

584   from the genus Cephalopholis (Serranidae: Teleostei). Environ Biol Fishes 24:67–73

585   Stallings CD, Coleman FC, Koenig CC, Markiewicz DA (2010) Energy allocation in

586   juveniles of a warm-temperate reef fish. Environ Biol Fishes 88:389–398

587   Stevenson RD, Woods WA (2006) Condition indices for conservation: New uses for evolving

588   tools. Integr Comp Biol 46:1169–1190

589   Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral- reef

590   fish community. Ecology 81:2714–2729

591   Welch BL (1947) The Generalization of `Student's' Problem when Several Different

592   Population Variances are Involved. Biometrika 34:28–35

593   Wernberg T, Bennett S, Babcock RC, de Bettignies T, Cure K, Depczynski M, Dufois F,

594   Fromont J, Fulton CJ, Hovey RK, Harvey ES, Holmes TH, Kendrick GA, Radford B,

595   Santana-Garcon J, Saunders BJ, Smale DA, Thomsen MS, Tuckett CA, Tuya F,

596   Vanderklift MA, Wilson S (2016) Climate-driven regime shift of a temperate marine

597   ecosystem. Science (80-) 353:169–72

598   Van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a

599   decade after coral bleaching. Mar Ecol Prog Ser 434:67–76

600