Ecosystem Regime Shifts disrupt Trophic Structure

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Summary

Ecosystem regime shifts are becoming commonplace due to global climate change. The resulting alternative states are substantially different in form and function to the pre-disturbance state, disrupting ecosystem services and functions. Coral reef regime shifts are typically characterised by a shift in the benthic composition of the reef from coral- to macroalgal-dominance. Such fundamental shifts in the benthos are anticipated to impact the associated fish community, which is closely reliant on the reef for food and shelter, yet there is limited understanding of how regime shifts propagate through the fish community over time. This study addresses this knowledge gap using long term data of coral reef regime shifts and recovery on Seychelles reefs following the 1998 mass bleaching event. It shows how trophic structure of the reef fish community becomes increasingly dissimilar between reef states with time since disturbance. Regime shifted reefs developed a concave structure, with increased biomass in base trophic levels, as herbivorous species benefitted from increased algal resources; mid trophic level species including specialists such as corallivores declined with loss of coral habitat; while biomass was retained in upper trophic levels by large-bodied generalist invertivores. Recovering reefs also experienced an initial decline in mid trophic level biomass, but returned to a bottom-heavy, stable pyramid shape, with broad

29   trophic group representation in mid trophic levels. Given the importance of coral reef fishes

30   in maintaining the ecological resilience of coral reef ecosystems, and in supporting diverse

31   fisheries, understanding the effects of regime shifts on these communities is essential to

32   inform decisions that enhance ecological resilience and economic sustainability.

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34   *Key words: coral reef fish; coral bleaching; functional group; habitat degradation;*

35   *mesopredator; trophic level; trophic pyramid; coral reef ecology*

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38   INTRODUCTION

39   Regime shifts have been documented in a wide variety of ecosystems, from shallow

40   lakes to deserts, savannas and the open ocean (van de Koppel et al. 1997, Watson and Estes

41   2011, Kosten et al. 2012, Ecology et al. 2016) as a result of gradual change over time, or a

42   shock to the system that pushes it beyond a tipping point into an alternate state (Scheffer et al.

43   2001). Drivers often work together, whereby chronic stressors gradually erode ecosystem

44   resilience, making the system more vulnerable to a regime shift following an acute

45   disturbance event (Hughes et al. 2013). Regime shifts are characterised by dramatic changes

46   in the structure and function of the ecosystem (Scheffer et al. 2001, Folke et al. 2004), with

47   potentially broad-reaching consequent effects. Understanding the implications of these shifts

48   and identifying early warning indicators have been the primary foci of much of the research

49   into these ecological dynamics (e.g. Scheffer et al. 2009, Carpenter et al. 2011, Graham et al.

50   2015, Hicks et al. 2016).

51   In coral reef ecosystems, much of the initial research on ecosystem regime-shifts

52   focused on over-fishing of herbivores as a primary driver of change (Hughes 1994, Jackson et

53   al. 2001, Bellwood et al. 2004, Hughes et al. 2007). Subsequently, with increasing effects of

54   global climate change, mass bleaching events have become a major driver of extensive

55   habitat degradation on coral reefs (Hoegh-Guldberg et al. 2007). Following bleaching, or

56   other large scale coral mortality, reefs can either recover and move towards a pre-disturbance

57   state, or undergo benthic regime shifts from coral dominance to dominance by other benthic

58   organisms, most commonly fleshy macroalgae (Nyström et al. 2008). This macroalgal state

59   often represents an alternative stable state, with strong reinforcing feedback mechanisms,

60   from which a return to coral dominance is challenging (Mumby and Steneck 2008). Our

61   understanding of what factors contribute to driving these benthic shifts is improving (Mumby

62   et al. 2007, Graham et al. 2015), but we lack an understanding of their effects on the broader

63   ecosystem.

64   Coral reef fish communities are heavily reliant on the reef benthos for food and

65   shelter (Pratchett et al. 2008), with changes in the composition and structure of coral habitat

66   directly affecting reef fish assemblages (e.g. Friedlander and Parrish 1998, Jones et al. 2004).

67   Dramatic regime shifts in dominant benthic cover in a coral reef ecosystem are therefore

68   anticipated to have substantial effects on the composition of the associated reef fish

69   community. While we have a rudimentary understanding of how a regime shift is likely to

70   affect the functional diversity of a coral reef fish community (Graham et al. 2015), we know

71   little about the effect on community trophic structure or functional composition. Trophic

72   pyramids provide a visually intuitive means of examining and comparing the structure of

73   food webs (Lindeman 1942) and informing on the likely transfer of energy among trophic

74   levels (Trebilco et al. 2013). This simple, yet powerful tool has the potential to be used for

75   easy identification of disruption of trophic structure and function due to disturbance (Graham

76   et al. 2016). With the expectation that bleaching events will become more frequent as

77   atmospheric carbon levels increase, as demonstrated by the powerful 2016 El Nino event, it is

78   becoming increasingly important to improve our understanding of how coral reef fish

79   communities restructure following climate-driven regime shifts.

80   Coral reefs provide important resources and services for millions of people living in

81   tropical latitudes around the globe, with reef fish constituting the primary source of protein,

82   and a range of other ecosystem services, for large coastal populations (Hicks and Cinner

83   2014). With many coral reef fisheries preferentially harvesting large piscivorous and

84   herbivorous fishes, at upper and lower trophic levels, the implications of regime shifts for

85   trophic pyramids and associated biomass storage, productivity and trophic pathways, is

86   critical information. It has only recently become possible to investigate these long-term

87   ecosystem changes with sufficient time post mass bleaching.

88   In this study, a well-studied system, where climate-driven bleaching led to a series of

89   both regime-shifted and recovering reefs (Graham et al. 2015), was used to investigate the

90   effects of benthic regime shifts on the trophic structure of the associated reef fish community.

91   Specifically, we assessed (i) the dissimilarity in the composition of the reef fish community

92   between recovering and regime-shifted reefs with time since disturbance, (ii) how the trophic

93   pyramid structure of biomass distribution in fish communities changes between reef states

94   over time, and finally (iii) how the functional composition of the reef fish community is

95   altered.

96

97   METHODS

98   *Study Site*

99   Data collection for this study was carried out as part of a long-term periodic coral reef

100   monitoring programme in the Seychelles inner island group. These reefs were some of the

101   most severely impacted by the 1998 mass bleaching event, with live coral loss exceeding 90 %

102   at many sites (Goreau et al. 2000, Lindén et al. 2002). Monitoring data collected both before

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103   (1994) and after the bleaching event (2005, 2014) has identified two distinct ecosystem

104   trajectories (Graham et al. 2015). Of the 21 monitoring sites, 12 have steadily regained live

105   coral cover, and returned to an almost pre-bleaching state, while the other 9 sites have moved

106   into a regime-shifted state of algal dominance (Graham et al. 2006, 2015, Wilson et al. 2012).

107   To investigate the question of how the trophic structure of the associated reef fish community

108   differs between these contrasting reef states, the ten most extreme sites in terms of live hard

109   coral cover averaged up to 2014 were selected; the five highest from recovering sites, and the

110   five lowest from regime-shifted sites.

Fish and benthic surveys

112   Twenty-one reefs across the Inner Seychelles island group were surveyed in 1994 prior

113   to the 1998 mass bleaching event, and again after the bleaching in 2005 and 2014, as part of

114   an ongoing monitoring programme. Identical methods were used to survey the reef fish and

115   benthic community at each site in all years (Graham et al. 2015). At each reef, the fish

116   community was quantified using 8 to 16 replicate 7 m radius point counts, haphazardly

117   located along the reef slope at depths of 2.3 – 12.2 m (mean ± standard deviation; 6.34 ± 2.06

118   m), separated by a minimum of 15 m. At each point, the abundance of 134 species of diurnal,

119   non-cryptic, reef-associated fish was recorded, as well as the total length of each individual.

120   Length estimates were converted to biomass using published length-weight relationships for

121   each species (Froese and Pauly 2015). Each species was assigned to a functional group based

122   on their diet and feeding behaviour (Froese and Pauly 2015); browser, grazer/detritivore,

123   scraper/excavator, planktivore, corallivore, invertivore, invertivore/piscivore, piscivore (see

124   Appendix S1: Table S1). Using estimates published in Fish Base (Froese and Pauly 2015),

125   species were also assigned to one of five trophic pyramid positions (TP); TP1: 2 - 2.5; TP2:

126   2.5 – 3.0; TP3: 3.0 – 3.5; TP4: 3.5 – 4; TP5: 4 – 4.5 (Appendix S1: Table S1).

127   Benthic habitat composition was estimated within the area of each point count as the

128   percent cover of six cover types (simple and complex live hard coral, soft coral, macroalgae,

129   sand and rock). Simple corals were those hard coral taxa with massive or encrusting growth

130   forms, while complex corals were those with branching or digitate structure. Structural

131   complexity was visually estimated with a six point scale, shown to approximate other

132   measures of complexity well and to be useful in predicting fish abundance and biomass

133   (Wilson et al. 2007, Darling et al. 2017).

134

135   *Statistical analyses*

136   The benthic habitat composition between reef states (recovering versus regime-shifted)

137   in each year (1994, 2005, 2014) was compared using a principal coordinate analysis (PCO),

138   based on a Bray-Curtis similarity matrix. Data were square root transformed to reduce the

139   influence of the most dominant cover types. Eigenvectors of all benthic categories were

140   overlaid to examine their contribution to the separation between reef states.

141   To investigate how the fish community changed over the study period, a series of

142   Similarity Percentages (SIMPER) analyses were run in PRIMER v.6 (Clarke and Warwick

143   2001) to compare the average dissimilarity of the fish community between recovering and

144   regime-shifted reefs in 1994, 2005 and 2014, both in terms of species abundance (fish.500m^{-2})

145   and biomass (kg.ha^{-1}), and functional group composition based on abundance (fish.500m^{-2}).

146   The results of the functional group analysis were then weighted by the overall dissimilarity

147   between reef states (recovering vs regime-shifted) for each year, to allow for comparison of

148   the magnitude of difference in fish community functional structure among years.

149   Both the absolute biomass (kg. ha^{-1}) and relative biomass (%) of reef fish within each of

150   the five trophic positions was calculated for each reef state (recovering vs regime-shifted) and

151   each year (1994, 2005, 2014), and trophic pyramids constructed to explore the change in

152   trophic structure within the fish community following bleaching disturbance. Differences in

153   the trophic structure between recovering and regime-shifted reefs at each time point were

154   tested using multinomial regression of the TP categories as a response, with year and regime

155   state as fixed effects. The fish species contributing the most to dissimilarity in the fish

156   community composition within each state (recovering vs regime-shifted), and trophic level

157   (TP1 - TP5), before the bleaching (1994) and post-bleaching (2014) were identified using

158   SIMPER analyses on Bray-Curtis similarity matrices of square root transformed species data.

159

RESULTS

Benthic habitat

162   There was a distinct shift in the benthic composition of regime shifted reefs

163 following disturbance in relation to recovering reefs (Fig.1). Prior to the 1998 mass bleaching

164 event, all reefs were characterised by high structural complexity and live coral cover, falling

165 to the right of the first PCO axis, which accounts for 48.4 % of the total variation among sites.

166 Following the disturbance (2005, 2014), there is a strong separation between reefs that

167 recover from the bleaching and those moving into a regime-shifted state. In 2005, two of the

168 regime-shift reefs still retained a degree of structural complexity, but by 2014, all these reefs

169 were most strongly characterised by high levels of macroalgal cover and low coral cover and

170 structural complexity, falling to left of PCO1, while recovering reefs returned to the initial

171 pre-disturbance state.

172

173   *Fish community*

174   This same pattern of increasing divergence between recovering and regime-shift reefs is

175 evident in the fish community, with SIMPER analyses showing increasing average

176 dissimilarity in community composition in terms of functional group representation, fish

177 biomass, and abundance, between reef states following the bleaching disturbance (Table 1).

178 The trophic structure of the fish community also reflects this divergence between reef states

179 in terms of the distribution of relative biomass among trophic levels (Fig. 2). In 1994, prior to

180 the bleaching event, trophic structure of fishes was similar across all reefs surveyed, in terms

181 of relative or absolute biomass (Fig.2, Appendix S1: Fig.S3). In 2005, 7 years after mass

182 bleaching, regime-shift reefs showed a large increase in relative and absolute biomass within

183 the base trophic level (TP1), which includes herbivorous functional groups (Appendix S1:

184 Fig.S2; browsers, grazers and detritivores, scrapers and excavators), and a decrease in the

185   biomass of all higher trophic levels. Recovering reefs exhibited a similar pattern of an

186   increase in the relative and absolute biomass of TP1, and a reduction in higher trophic levels,

187   but the changes were less pronounced (Table 2). By 2014, the difference between the trophic

188   structure of recovering and regime-shifted reefs had become clearly apparent. Recovering

189   reefs had a triangular trophic pyramid structure, while regime-shifted reef pyramids had a

190   concave shape, with biomass dominated by herbivorous species in TP1, with low biomass in

191   mid trophic levels (TP2 - TP3) and comparatively high biomass at TP4. The increase in TP4

192   biomass on regime-shifted reefs was primarily due to more large-bodied invertivores,

193   particularly *Lethrinus nebulosus* and *Plectorhinchus schotaf* (Appendix S1: Table S2).

194   Dissimilarity (Bray-Curtis) in fish species composition within each trophic level pre-

195   (1994) versus post-bleaching (2005 and 2014), was higher overall for regime-shifted reefs

196   than recovering reefs (Table 3). After the initial shift in community composition from 1994 to

197   2005, by 2014 recovering reefs were more similar to their pre-disturbance composition than

198   regime shifted reefs, with reduced variation in dissimilarity measures in all trophic levels

199   except TP2. The increased dissimilarity in this trophic level was due to an increase in the

200   generalist species *Pomacentrus trilineatus*, and a decrease in two rabbit fish species, *Siganus*

201   *puelloides* and *Siganus stellatus* (Appendix S1: Table S1). On regime-shifted reefs, mean

202   dissimilarity and the degree of variation in community composition tends to increase for all

203   trophic levels, except for TP2, which is characterized by a consistently high abundance of the

204   excavating parrotfish species, *Chlorurus sordidus*.

205   Associated with this change within the reef fish community has been a shift in the

206   balance of functional groups in terms of abundance (Fig.4). Pre-disturbance (1994) fish

207   communities on recovering and regime shifted reefs had an overall dissimilarity (Bray-Curtis)

208   of only 13.3% between reefs that would follow recovering and regime-shifted trajectories

209   post-bleaching. In 2005, seven years post disturbance, dissimilarity in functional group

210 composition had risen to 25.61% between reef states. An increase in herbivorous groups on

211 regime shifted reefs; browsers (% dissimilarity ± standard deviation; 5.87 ± 0.29 %), and

212 grazers and detritivores (4.60 ± 0.36) accounted for the much of this separation. By 2014, the

213 dissimilarity had further increased to 34.2%, with browsers and grazer/detritivores

214 dominating on regime shifted reefs, while recovering reefs have a wide variety of functional

215 groups from higher trophic positions, including corallivores, planktivores and piscivores.

216

217   DISCUSSION

218   Regime shifts are increasingly common in a wide variety of ecosystems, often

219 resulting in extensive and dramatic ecological change. In Seychelles, the long-term

220 trajectories of decline and recovery on inner island coral reefs, following the 1998 mass

221 bleaching event, illustrate the major ecological implications of such a disturbance. Trophic

222 structure of the fish communities on recovering reefs (high coral cover and structural

223 complexity) and regime shifted reefs (algae-dominated with low complexity), became

224 increasingly dissimilar over time, with trophic pyramids of biomass regaining a stable

225 bottom-heavy structure on recovering reefs, while regime-shifted reefs transitioned to a

226 concave structure.

227   This change in trophic structure resulting from the redistribution of biomass between

228 trophic levels, can disrupt ecological processes and the flow of energy in the food web

229 (Trebilco et al. 2013, Graham et al. 2017). Prior to the bleaching event, in 1994, pyramids of

230 relative biomass on all surveyed reefs were bottom heavy, with substantial biomass in the

231 mid to upper trophic levels and the greatest amount of biomass located in the base trophic

232 level, as expected based on energetic theory (Trebilco et al. 2013, Hatton et al. 2015).

233 Following the bleaching, relative biomass in the base trophic level (trophic position 2-2.5)

234 increased substantially in both reef states, likely due to the greater food availability for

235 herbivorous species with the initial increase in algal cover following the depletion of coral

236 cover from bleaching (Adam et al. 2011, Gilmour et al. 2013). The fact that this effect was

237 larger in terms of both relative and absolute biomass on regime-shift reefs alludes to the more

238 severe shift in trophic structure that had emerged on these reefs by 2014. That these reefs

239 have failed to recover, 16 years after the bleaching event also suggest that increased

240 abundance of herbivores alone is insufficient for recovery, which is dependent on the

241 composition of the herbivore community and a combination of other factors including

242 eutrophication, recruitment of corals, depth and structural complexity (Graham et al. 2015).

243   Sixteen years post-bleaching, recovering reefs had regained a triangular biomass

244 pyramid structure, representing an energetically stable food web (Hatton et al. 2015). This

245 structure indicates that the fish community had regained biomass in the mid-trophic levels

246 (trophic position 2.5-3 and 3-3.5), which includes various specialised species, such as

247 corallivores, which are extremely sensitive to loss of coral habitat (Wilson et al. 2006, Hoey

248 et al. 2016). In contrast, the concave shape of relative biomass pyramids on regime-shifted

249 reefs shows a decrease in biomass in these mid-trophic levels, likely due to the lack of habitat

250 available for species highly dependent on coral for food and shelter (Pratchett et al. 2008,

251 Wilson et al. 2010a). Biomass on these reefs was dominated by herbivorous species at the

252 base of the pyramid, supported by a proliferation of algal resources. There was also an

253 accumulation of biomass in the upper trophic levels, particularly trophic position 3.5 – 4,

254 largely attributable to an increase in the abundance of *Lethrinus nebulosus* and

255 *Plectorhinchus schotaf*. This increase may be related to the fact that both species are large-

256 bodied, generalist invertebrate feeders (Smith et al. 2003), and particularly in the case of *L.*

257 *nebulosus*, known to utilise a wide variety of habitat types, often scavenging over degraded,

258 rubble or sand substrates (Carpenter and Allen 1989, Farmer and Wilson 2011). Expansion of

259 macroalgal habitat also provides increased nursery area for lethrinid species, which may be a

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260   strong driver of increased local abundance (Wilson et al. *in press*). Another possibility is that

261   they may benefit from decreased competition from other mesopredators with narrower

262   dietary or habitat niches (e.g. *Lutjanus kasmira*). The contrasting decline in top consumers

263   with a more piscivorous diet (e.g. *Lutjanus bohar, Cephalopholis argus, C. miniata*) was

264   likely due to the decline in prey fish species in the mid trophic levels. This suggests a

265   different mechanism of concave trophic pyramid shape to that described for high biomass

266   reefs (Graham et al. 2017). At high reef fish biomass, biomass accumulated in upper and

267   lower trophic levels, likely enabling a more direct pathway between primary production and

268   large piscivores (Graham et al. 2017). Conversely, on regime shifted reefs in Seychelles, the

269   accumulation of upper trophic level fish is driven by an alternative energy pathway, with

270   abundant mobile invertebrate species on degraded reefs supporting populations of upper

271   trophic level invertivores.

272   While there may appear to be an abundance of available prey biomass in the base of

273   the pyramid, unlike in temperate marine ecosystems (Jennings and Mackinson 2003), on

274   coral reefs, herbivore biomass is largely made up of large bodied species, such as parrotfish,

275   surgeonfish, and rabbitfish. Many adults of these fish are too large to be suitable prey for

276   coral reef mesopredators which are limited by their gape size (Kingsford 1992, St John 1999).

277   This likely explains the observed decreases in the abundance of predators that prey on small

278   fish (e.g. *Parupeneus cyclostomus, Oxycheilinus digramma* and *Epibulus insidiator*; Froese

279   and Pauly 2015) on regime-shifted reefs.

280   Examination of the species diversity of the reef fish communities on recovering and

281   regime shift reefs confirms the trend of increasing dissimilarity between reef states over time.

282   On recovering reefs, the return to a stable, coral-dominated state in the reef benthos is

283   mirrored in the fish community, which shows an overall pattern of decreasing mean

284   dissimilarity and variation, moving towards a pre-disturbance state. The deviation of trophic

285   positions 2.5 - 3 from this trend, due to the increased abundance of the generalist,

286   *Pomacentrus trilineatus*, is likely due to its association with both coral and rocky reef habitat

287   (Allen 1991), giving it a competitive advantage over more specialised species when live coral

288   cover habitat declined following the bleaching. The contrasting trend on regime-shifted reefs,

289   whereby mean dissimilarity and variation increases with time since bleaching, indicates that

290   the associated fish community is consistently moving further from its pre-disturbance state.

291   On these reefs, it is again trophic positions 2.5 – 3 that deviate from the overall trend, with a

292   relatively stable degree of dissimilarity attributable to a consistently high abundance of

293   *Chlorurus sordidus*, a widespread excavating parrotfish species, that uses a broad range of

294   habitat types (Hoey and Bellwood 2008).

295   The fact that the fish communities on recovering reefs have not yet reverted to their

296   pre-disturbance state 16 years post-bleaching, despite the recovery of high coral cover,

297   suggests that there may be a shift in the composition of the coral assemblages (Wilson et al.

298   2012). Changes in the coral community can lead to changes in composition of the closely

299   associated reef fish communities, which may regain pre-disturbance abundances, but have

300   altered species composition (Berumen and Pratchett 2006). Shifts in the composition of the

301   reef fish community may represent a change in the prey base available to piscivorous

302   mesopredators, requiring them to adapt their diets and alter their trophic niche (Hempson et al.

303   *in press*), with potential sublethal effects (Hempson et al. *in review*)

304   Increasing divergence in the functional composition of the reef fish communities

305   between states implies a disruption of ecological processes on regime-shifted reefs. The

306   single strongest characteristic of this change is the increase in herbivorous species on these

307   reefs, a pattern which has been observed on degraded algal reefs worldwide (e.g. Adam et al.

308   2011, Gilmour et al. 2013). While the proliferation of algal resources benefits many

309   herbivorous species, both in terms of food availability (Rasher et al. 2013), and providing

310   important nursery habitat for numerous reef species (Wilson et al. 2010b, Evans et al. 2014),

311   the loss of coral cover transforms diverse reef habitat into a comparatively uniform landscape,

312   unsuitable for the wide diversity of mid-trophic level species normally supported on a healthy

313   reef (Chong-Seng et al. 2012, Nash et al. 2013). In 2005, the dissimilarity in mid-level

314   trophic positions (2.5 – 3.5) is minimal. This may be because regime-shifted reefs still

315   retained some degree of structural complexity, providing habitat for more adaptable mid-

316   trophic level species, such as invertivores in trophic positions 3 – 3.5 (e.g. *Chaetodon*

317   *guttatissimus*, *Chaetodon kleinii*). Also, at this stage, live coral cover on recovering reefs

318   was still returning, so specialist species such as obligate corallivores in trophic position 3 –

319   3.5 (e.g. *Chaetodon trifascialis*) would still have been marginalised. By 2014, the

320   dissimilarity between reef states in the mid-trophic levels had become clearly apparent, as

321   habitat complexity declined on regime shifted reefs and recovering reefs regained increased

322   live coral cover and complexity, resulting in a divergence in the fish species supported in

323   trophic positions 2.5 - 3.5

324   Changes in the lower trophic levels carry important consequences for mesopredators

325   in the upper trophic levels of the reef fish community. In 2005, there was a higher abundance

326   of generalist mesopredators (e.g. *Parupeneus cyclostomus, Aethaloperca rogaa*) that fed on

327   both invertebrates and fish on regime-shifted than recovering reefs, while exclusively

328   piscivorous species characterised recovering reefs (e.g. *Cephalopholis argus, Cephalopholis*

329   *miniata, Epinephelus merra*). However, by 2014, even the generalist mesopredators were

330   more abundant on recovering reefs. This provides strong evidence that the high abundance of

331   herbivorous species on regime shifted reefs were not a suitable prey source for mesopredators.

332   Predation in the coral reef food web is therefore disrupted by the shift of the coral reef fish

333   community associated with a benthic regime-shift.

334   The disruption of trophic structure within the coral reef fish community has long-term

335   ecological, social and economic implications for the reefs and the people that rely on them.

336   This study provides important insight into how regime shifts are likely to affect this structure,

337   that can support better management of commercial, recreational and subsistence coral reef

338   fisheries. For example, placing greater fisheries restrictions on piscivorous species, than those

339   with more generalist invertebrate diets could help to sustain predatory guilds in post

340   disturbance systems. As climate-driven disturbance events and ecosystem regime shifts

341   become increasingly common, it is essential that we continue to improve our understanding

342   of the impacts on trophic structure to inform decisions that enhance ecological resilience,

343   food security and economic sustainability.

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356   DATA ACCESSIBILITY

357   Supporting data can be accessed in the following external repositories:

358   • Coral reef benthic and fish surveys in the Inner Seychelles

359   https://research.jcu.edu.au/researchdata/default/detail/a858bdc7a8116bff35db8558a25c2cb7/

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TABLE 1. Average dissimilarity in the fish community composition between recovering and regime-shifted reefs in 1994 (pre-bleaching), and in 2005 and 2014 (post-bleaching), calculated from SIMPER analyses of fish functional groups, biomass and abundance.

Average % Dissimilarity	1994	2005	2014
Functional Groups	13.13	25.61	34.2
Biomass (kg.Ha^{-1})	45.21	57.49	66.32
Abundance (fish.500m^{-2})	39.05	48.69	61.23

TABLE 2. Multinomial regression model coefficients and 95 % confidence intervals given relative to the baseline of TP1 for the difference between trophic pyramid structure between recovering and regime shifted reefs prior to the 1998 mass bleaching (1994) and post bleaching (2005, 2014).

Year	Trophic Position (TP)	Model Coefficient	2.5%	97.5%
1994				
	2	-0.429	-0.522	-0.336
	3	0.720	0.649	0.790
	4	-1.495	-1.617	-1.372
	5	-2.468	-2.681	-2.255
2005				
	2	0.317	0.200	0.435
	3	-0.241	-0.334	-0.148
	4	0.448	0.308	0.588
	5	-0.011	-0.287	0.266
2014				
	2	-0.161	-0.290	0.033
	3	0.007	-0.084	0.098
	4	0.419	0.274	0.564
	5	-0.587	-0.919	-0.255

539

540   TABLE 3. Mean percentage dissimilarity (± standard error; SE) in the fish community

541   composition in each trophic level on recovering and regime-shifted reefs, between 1994 (pre-

542   bleaching), and 2005 and 2014 (post-bleaching), calculated from SIMPER analyses of

543   species abundance, showing results of Welch two sample t-tests for difference in mean

544   dissimilarity between reef states.

Years	Trophic Level	Recovering		Regime-Shifted		t	df	*p*
		Mean % dissimilarity	±SE	Mean % dissimilarity	±SE			
1994 vs 2005	TP 1	34.99	2.32	45.13	3.38	-2.47	7.09	0.04
	TP 2	28.59	4.46	44.50	4.20	-2.60	7.97	0.03
	TP 3	38.57	3.56	48.03	4.33	-1.69	7.71	0.13
	TP 4	52.76	4.83	45.11	7.05	0.90	7.07	0.40
	TP 5	52.33	19.53	58.68	6.73	-0.31	4.94	0.77
1994 vs 2014	TP 1	35.29	1.84	62.72	2.71	-8.36	7.05	0.00
	TP 2	44.18	5.68	37.82	4.94	0.85	7.85	0.42
	TP 3	32.45	3.72	53.10	5.60	-3.07	6.96	0.02
	TP 4	39.18	4.69	58.05	6.99	-2.24	6.99	0.06
	TP 5	41.87	9.39	71.40	12.75	-1.87	7.35	0.10

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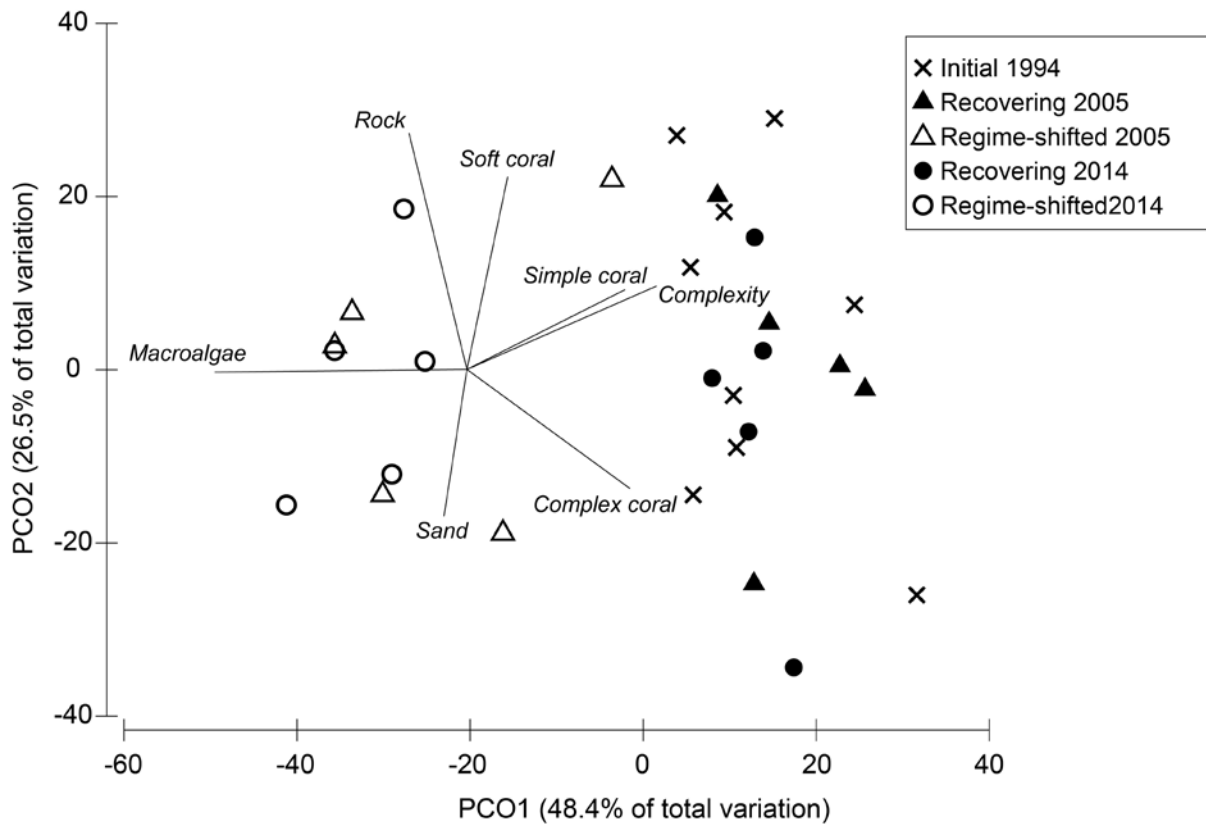
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554　Fig. 1. Principal coordinates analysis of the composition of benthic cover of ten reefs

555　surveyed in the Seychelles inner island group based on Bray-Curtis similarity (data square-

556　root transformed).　Crosses represent all reef sites surveyed in 1994, prior to the bleaching

557　1998 mass bleaching event. Black symbols represent those reefs that were surveyed in 2005

558　(triangles) and 2014 (circles) and considered to be recovering to a pre-disturbance state (n =

559　5), and open symbols represent those reefs that in 2005 (triangles) 2014 (circles) had moved

560　into a regime-shifted, algae-dominated state (n = 5).
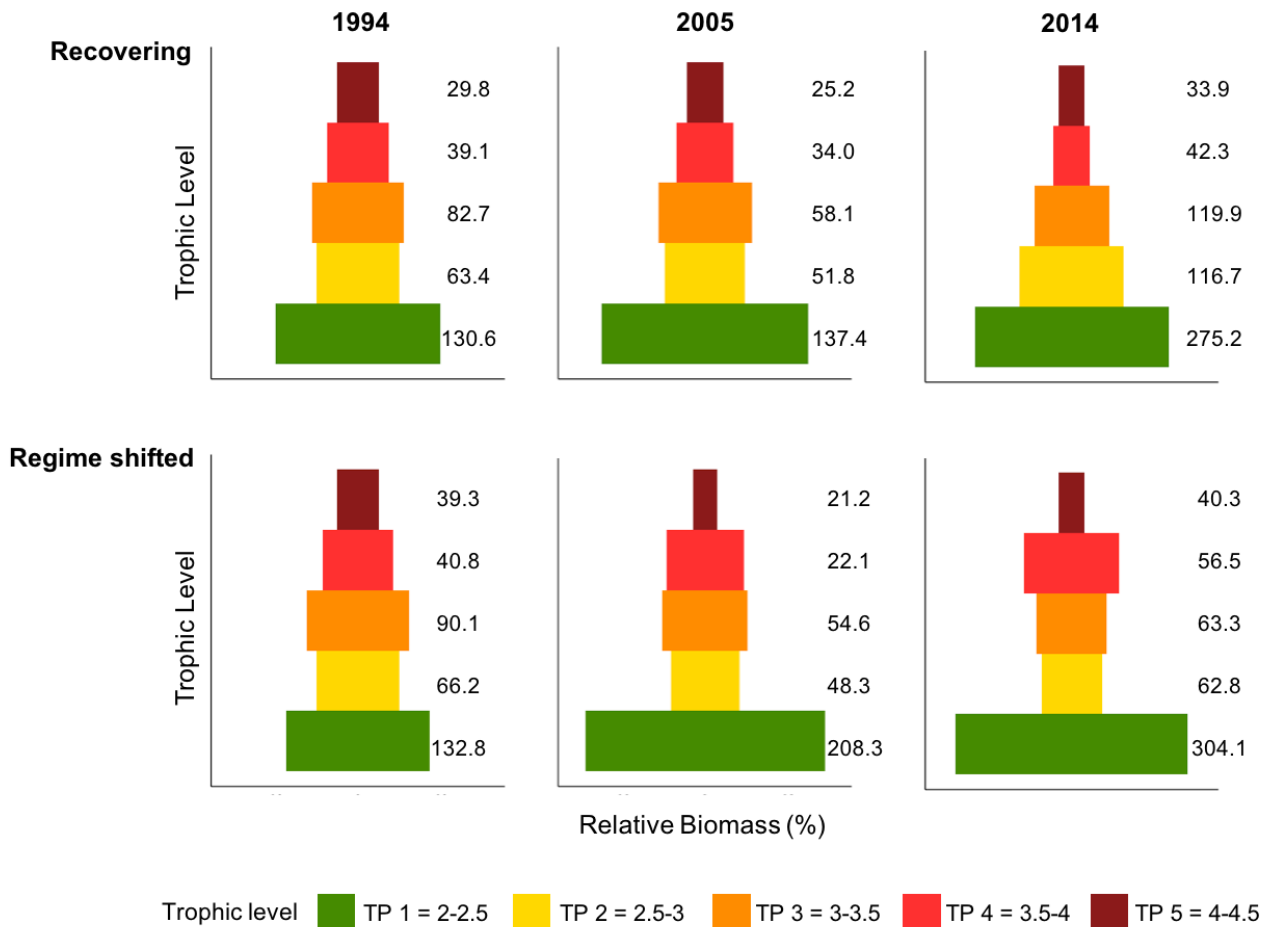
FIG. 2. Trophic pyramids showing the distribution of relative biomass (%) between five trophic positions in the reef fish communities on recovering (n = 5) and regime-shifted (n = 5) reefs in the Seychelles inner island group, both before the 1998 mass bleaching (1994) and after it (2005, 2014). Numbers in each trophic level show the absolute biomass for that trophic position (kg.Ha-1). (see Appendix S1: Fig.S3, for pyramids of absolute biomass.)
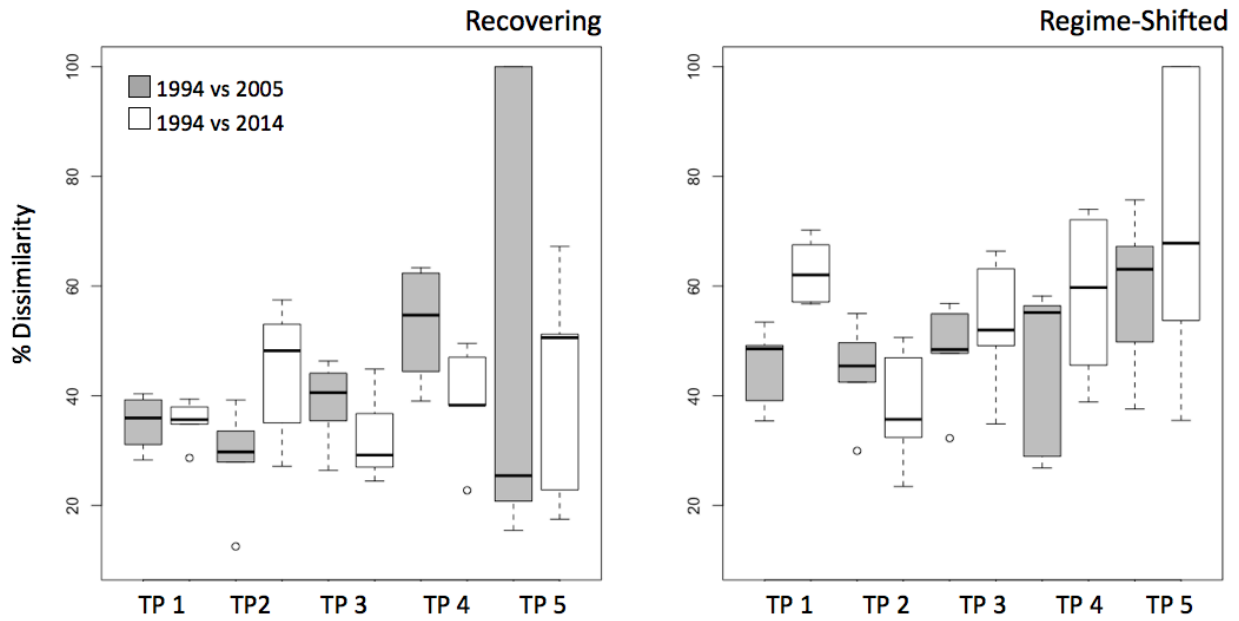
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569 FIG. 3. Percentage dissimilarity (SIMPER analysis) in fish community species composition

570 within reef states and trophic positions between pre-bleaching reefs (1994), and post-

571 bleaching reefs in 2005 (grey bars), and in 2014 (white bars). Data were square root

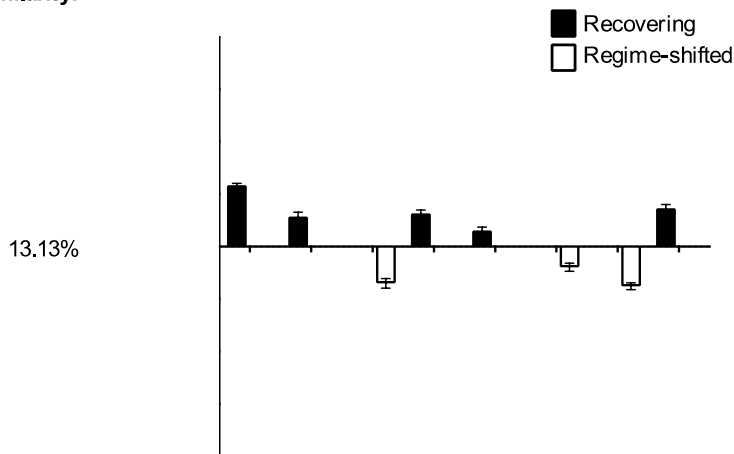572 transformed and dissimilarity measures calculated using a Bray-Curtis resemblance matrix.

573 Dark horizontal bars indicate the medians of the data, box height shows the interquartile

574 range, whiskers span minimum and maximum values, with open circles indicating outliers.
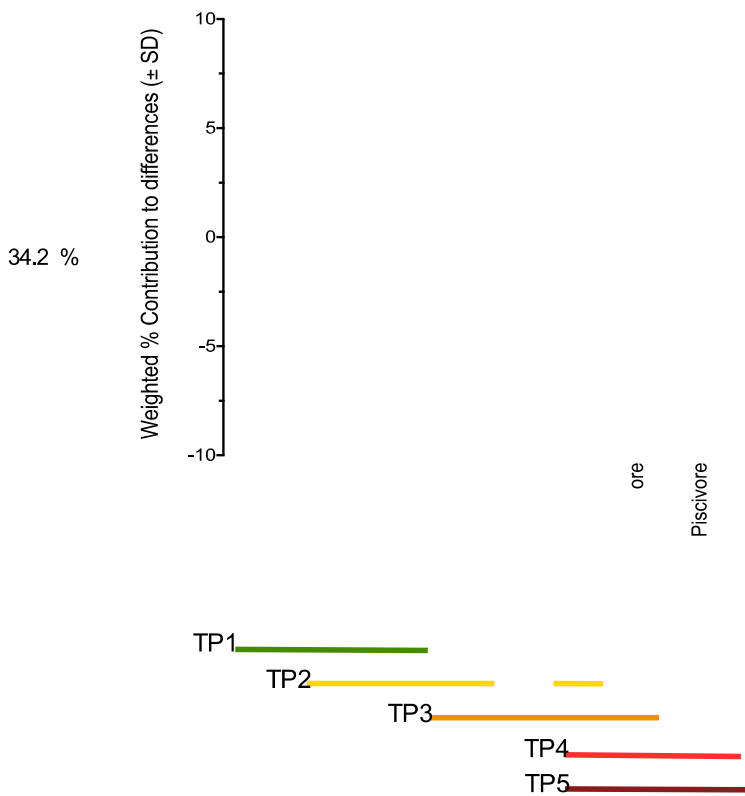
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state.

Average Dissimilarity:

Recovering
Regime-shifted

13.13%

25.61 %

2014

34.2 %

Weighted % Contribution to differences (± SD)

10

5

0

-5

-10

ore

Piscivore

TP1

TP2

TP3

TP4

TP5

FIG. 4. Differences in the fish community composition between regime-shifted (white) and recovering sites (black). The mean (± standard deviation; SD) percentage contribution of fish functional groups to the difference between reef states in Seychelles in 1994, 2005 and 2014, based on the percentage contribution of each functional group from a SIMPER analysis. Bars represent the percentage contribution for the functional group that had a higher contribution in either reef state.