Thermal stress induces persistently altered coral reef fish assemblages

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Ecological communities are reorganizing in response to warming temperatures,
producing unexpected ecosystem configurations [1,2]. For continuous ocean habitats
this reorganization is characterized by large-scale species redistribution [3], but for
tropical discontinuous habitats such as coral reefs, spatial isolation coupled with strong
habitat dependence of fish species [4] imply that turnover and local extinctions are more
significant mechanisms [5,6]. In these systems, transient marine heatwaves are causing
coral bleaching and profoundly altering habitat structure [7]. Despite severe bleaching
events becoming more frequent [8] and projections indicating annual severe bleaching
by the 2050s at most reefs [9], long-term effects on the diversity and structure of fish
assemblages remain unclear. Using a 23-year time-series of fish and benthic surveys
spanning a thermal stress event in Seychelles, we describe and model structural changes
and recovery trajectories of fish communities after mass bleaching. Fish assemblages
transitioned into previously unseen compositions that persisted over 15 years, which
exceeds realized and projected intervals between thermal stress events on coral reefs.
After bleaching, fish communities homogenized in time and space, leading to
assemblages characterized by exceptional herbivore dominance. Composition changes
occurred despite recovery of coral habitat on some reefs, and were most pronounced
after macroalgal regime shifts on other reefs. Modification to reef habitats caused by
frequent marine heatwaves will lead to persistent changes in fish diversity, community
structure and function. Our results indicate that fish communities historically
associated with coral reefs will not reestablish following severe coral bleaching,
requiring substantial adaptation by managers and resource users.

RESULTS AND DISCUSSION

2,500 limit, currently at 2,344 words.

We investigated the effects of a marine heatwave and associated severe coral bleaching on the compositional turnover and persistence of fish assemblages. Because reef-associated fishes are highly dependent on complex coral-dominated habitat [4,10], bleaching-driven habitat collapse can reduce species richness [11] and homogenize compositions [12] within 1-3 years. Knowledge of long-term changes in fish communities following bleaching will help to reveal how recurring thermal stress events may lead to permanent changes in these communities. We focus on Seychelles where, in 1998, a strong El-Ninõ coincided with the Indian Ocean Dipole to cause severe coral bleaching, leading to loss of >90% coral cover and collapse of habitat structure [13]. Using data collected over 1994-2017, we examined temporal change in richness (α diversity) and composition (β diversity) of fish assemblages following bleaching. Because reefs either underwent regime shifts to macroalgal states or recovered coral cover and complexity [7] and also experienced severe bleaching in 2016 [8], our analyses examine compositional turnover on both regime-shifted and recovering reefs, and document how fish assemblages reorganized between successive mass bleaching events.

       Biodiversity losses were most severe on regime-shifted reefs, which were dominated by macroalgae (mean cover >20% from 2005-2017) and remained at low α diversity levels throughout the post-bleaching recovery period (Figure 1A,H). In contrast, recovering reefs steadily increased coral cover to reach pre-bleaching levels by 2014 (mean cover = 27%) (Fig. 1A,G), and α diversity increased from 46 species ($\pm$ 2.47 S.E.) in 2005 to exceed pre-bleaching levels by ~eight species in 2017 (58.5 $\pm$ 3.00). Although both reef states supported similar levels of richness prior to bleaching (1994 richness: recovering = 52.1 $\pm$ 1.92; regime-shifted = 55.3 $\pm$ 3.50) and followed similar temporal trajectories to stabilize richness levels by 2011, regime-shifted reefs did not recover pre-bleaching richness, reaching a maximum of

66   46 species (± 2.80) in 2008 (Figure 1A). Most strikingly, temporal trends in β diversity

67   indicated that fish communities settled into compositions which had not existed before

68   bleaching. Across all reefs, community compositions were dissimilar to their 1994 baseline

69   $(0.37 < \beta_{1994} < 0.77)$ and did not recover towards pre-bleaching compositions over 2005-2014

70   (*year* mean = -0.01, 95% CI = -0.02, 0.00) (Figure 1C,D). Collectively, these α and β

71   diversity patterns indicate that coral reef fish communities did not return to pre-bleaching

72   diversity levels over a 16-year recovery window (1998-2014). Persistence of post-bleaching

73   compositions has been observed for cryptobenthic fish assemblages [14], and we confirm that

74   such long-term bleaching impacts extend to species spanning multiple trophic levels and

75   providing important ecosystem services (e.g. fisheries).

76   Regeneration of coral-dominated habitat was somewhat effective in mitigating

77   bleaching impacts on fish communities, with reefs that recovered (i.e. structurally complex

78   habitat, dominated by branching corals with negligible macroalgal cover) having fish

79   compositions most similar to those recorded pre-bleaching (Figure 1B,D). However, coral

80   community composition is also a strong structuring influence on fish communities after

81   bleaching [12,14], and the contrasting effects of branching and massive corals on fish

82   compositions here imply that compositional shifts in coral growth forms are similarly

83   important. For example, stress-tolerant corals such as massive *Porites* were associated with

84   lower species richness (Figure 1B) and higher compositional dissimilarity through time

85   (β_{1994}) (Figure 1D), possibly because these sites failed to recover pre-bleaching compositions

86   of dominant branching coral growth forms [15] which provide shelter for abundant and

87   diverse small-bodied fishes [16,17]. Because several coral growth forms contribute to

88   seascape-level complexity [18,19], and bleaching impacts were minimized but not reversed

89   by fast growth of branching corals, our findings confirm that fish communities should not be

90   expected to fully recover when coral communities reassemble [20,21].

91   Regime-shifted reefs were most dissimilar to their coral-dominated pre-bleaching

92   baselines (mean $\beta_{1994} = 0.57 \pm 0.01$ on regime-shifted reefs; 0.50 ± 0.01 on recovering reefs),

93   and β_{1994} was maximized on reefs with high macroalgal cover and low structural complexity

94   (Figure 1C,D). Declines in coral cover and flattening of habitat structure likely prevented

95   coral-associated species from relocating or recruiting to macroalgal reefs, despite these fish

96   being present on nearby recovering reefs. These patterns build upon previous observations

97   from Seychelles which have demonstrated that macroalgal overgrowth has resulted in

98   bottom-heavy fish biomass pyramids and reduced functional diversity [7,21].

99   Fish communities also homogenized in time and space. β_{seq}, a measure of

100   compositional similarity between sequential survey years, declined from 2005-2017 (*year*

101   mean = -0.05, 95% CI = -0.066, -0.026) at similar rates for recovering and regime-shifted

102   reefs (*regime state * year* mean = -0.01, 95% CI = -0.042, 0.023) (Fig. 1E,F). For recovering

103   reefs, declines in β_{seq} were mirrored by temporal changes in spatial dissimilarity, whereby

104     $\beta_{spatial}$ declined from 0.61 to 0.50 to fall below baseline $\beta_{spatial}$ levels by 2017 (Figure S1A). In

105   contrast, compositional dissimilarity of regime-shifted reefs remained greater than baseline

106   levels throughout 2005-2014 (mean $\beta_{spatial} = 0.57$) (Figure S1B). Such high spatial

107   heterogeneity suggests that habitat associations underlie compositional differences on

108   regime-shifted reefs, as macroalgal habitat quality can vary substantially among seasons and

109   years [22,23].

110   We examined how functional groups and species contributed to compositional

111   differences following bleaching by tracking temporal patterns in functional group richness

112   (Figure 2). Corallivore and invertivore group richness recovered non-linearly and, by 2014

113   had reached pre-bleaching levels on recovering reefs but not on regime-shifted reefs (Figure

114   2B,D). Herbivore richness increased linearly from 2005-2014 on both reef states though,

115   again, recovering sites consistently supported more species than regime-shifted reefs and

116   exceeded pre-bleaching levels by 2008, whereas regime-shifted reefs maintained pre-

117   bleaching levels of herbivore richness from 2008-2017 (Figure 2C). Changes in richness of

118   planktivore, mixed-diet feeding, and piscivore groups were also strongly differentiated by

119   reef regime, with planktivore, mixed-diet feeder, and piscivore groups consistently less

120   speciose than 1994 baselines on regime-shifted reefs, but less impacted on recovering reefs

121   where pre-bleaching richness levels were matched or exceeded throughout 2005-2017 (Fig.

122   2A,E,F). Regime shifts, therefore, led to a greater loss of functional redundancy (i.e. fewer

123   species with similar functional roles). This implies that on reefs close to human settlements,

124   such as Seychelles, the vulnerability of fish functional groups to fishing [24,25] will be

125   exacerbated by bleaching, with transitions to macroalgal states likely to produce communities

126   that are functionally depauperate relative to historic coral-dominated states [26]. In contrast,

127   the functional capacity of fish communities was restored on reefs that resisted regime shifts,

128   with richness levels of all six dietary groups returning to pre-bleaching baselines on

129   recovering reefs. For piscivores, which returned to pre-bleaching richness most slowly (by

130   2014) (Fig. 2F), it is likely that recovery was lagged because these are long-lived species that

131   depend on reef-associated fishes for food [27] and require temporally stable reef habitats

132   [28].

133   By comparing species-level biomass estimates of 1994 (pre-bleaching) and 2014

134   (post-bleaching) fish assemblages, we found that compositional dissimilarity between pre-

135   and post-bleaching communities was characterized by biomass changes within herbivore,

136   invertivore and mixed-diet functional feeding groups, and reduced biomass of planktivore,

137   corallivore and piscivore species (Figures 3, 4). For positive and negative biomass changes

138   combined, herbivores explained 23.0% and 27.1% of observed β_{BC} at recovering and regime-

139   shifted reefs, respectively (Figure 3A), and exhibited biomass changes of $\pm 0\text{-}163$ kg ha^{-1}

140   (Figure 4). For herbivore species, the mean biomass difference between 1994 to 2014 was

141   positive at both recovering (mean = 7.14, 95% CIs = 0.60, 13.84) and regime-shifted reefs

142   (mean = 5.01, 95% CIs = -1.375, 13.248) (Figure 3B), indicating that declines in commonly

143   observed species were outweighed by gains in newly abundant species (Figure 4). Although

144   our infrequent visual surveys cannot be used to describe population dynamics, the recovery

145   period spanned several generations of most species (Table S1) and thus these patterns are

146   likely due to positive population feedbacks in dominant species that benefited from bleaching

147   (e.g. herbivores) and slow or failed recovery of species dependent on return of habitat

148   structure (e.g. planktivores, corallivores). For example, increases in herbivore biomass are

149   often associated with coral declines [4, 29, 30] and, here, species responses depended on

150   habitat type, where browsing species associated with macroalgal reefs and scraping species

151   associated with recovering reefs [31].

152   The relative infrequency of our fish surveys, focus on adult fish and use of a fixed

153   species list mean that we cannot disentangle the relative contributions of recruitment, growth

154   and relocation among habitat types and depths, nor account for potential emergence of new

155   species. However, it is likely that short-term dispersal among reef habitats [12,32], increased

156   population growth due to greater food availability [33], and high juvenile survivorship [34]

157   all contributed to the long-term persistence of these populations. Reef fish populations are

158   ecologically connected over relatively small scales, as larval dispersal distances are typically

159   <5 – 15 km and many species are territorial as adults (damselfishes, butterflyfishes) or inhabit

160   small home ranges (<3 km linear distance) [35]. Additionally, Seychelles reefs are isolated by

161   deep water dispersal barriers for reef fishes and by limited connectivity to distant continental

162   reefs (>1,000 km) (Kool & Graham *unpublished data*), meaning that species larval

163   connectivity or relocation from neighbouring reef systems are unlikely to be responsible for

164   the majority of compositional changes we observe.

165   Other functional groups made lower overall contributions to β_{BC}, and also tended to

166   have the greatest degree of species declines. For example, invertivores and mixed-diet

167   feeders had moderately high dissimilarity contributions (9.4 - 13.9%) that were mostly due to

168   species declines, particularly on regime-shifted reefs (Figures 3A, 4B). Although

169   dissimilarity contributions from planktivore and piscivore groups were relatively minor (1.62

170   – 4.99%), almost every species declined in biomass and group-level posterior means were

171   negative for both recovering and regime-shifted reefs (Figures 3B, 4). In contrast, corallivore

172   biomass changes were more closely linked to regime state, with biomass increases explaining

173   observed β_{BC} at recovering reefs (relative contribution from species with biomass increases =

174   1.23% and from biomass decreases = 0.13%) but biomass declines explaining observed β_{BC}

175   at regime-shifted reefs (0.23%, 1.43%). Positive responses of highly coral-associated species,

176   which could also be driven by recruitment as well as growth and relocation, reduced

177   compositional differences relative to regime-shifted reefs. Such strong effects may be

178   because corallivore species are highly dependent upon live branching coral for food and

179   shelter [36].

180   In each analysis, we considered how fishing protection influenced recovery and

181   change in fish assemblages after bleaching. By enhancing grazing functions [37] and

182   minimizing stressors on coral populations [38], ecosystem protection of coral reefs is

183   expected to accelerate recovery towards pre-bleaching conditions. Such effects, however,

184   depend upon the severity of bleaching, disturbance history, and local anthropogenic stressors.

185   For example, large-scale and well-enforced protection of the Great Barrier Reef has

186   shortened recovery times to minor bleaching events by up to ~2.4 years [20] whereas at

187   Indian Ocean reefs, where 1998 bleaching was severe and protected areas are small and less

188   effectively enforced, both fished and no-take areas experienced declines in fish richness and

189   abundance after bleaching [39]. In Seychelles, no-take areas were a poor predictor of

190   bleaching responses of benthic communities [7] and, here, did not improve recovery of fish

191   community composition after bleaching (Figure 1D,F). Protected reefs did support higher

192   species richness (Figure 1B) but experienced greater biomass declines (Figure 3C). Although

193   richness patterns were potentially confounded by high abundances that inflated diversity

194   estimates in no-take areas, large biomass declines highlight how reef protection, which

195   promoted pre-bleaching reef fish biomass [27], did not insure fish communities against

196   habitat collapse.

197   Irrespective of benthic recovery trajectory or ecosystem protection, post-bleaching

198   assemblages were characterized by a speciose and high biomass herbivore group and low

199   representation of planktivore, invertivore, and piscivore species. Such communities may be

200   considered hybrid states, which contain aspects of pre- and post-bleaching configurations but

201   with altered ecosystem functioning [6]. Concepts of such 'no-analog' states have typically

202   been developed to describe highly-degraded terrestrial ecosystems [6,40], but are equally

203   relevant for coral reefs where species may have unexpected, differential responses to climate

204   impacts [5]. For example, one striking effect of the 1998 bleaching event was to raise

205   herbivore productivity and diversity on both regime-shifted and recovering reefs. Herbivore

206   populations are expected to increase with algal productivity following rapid declines in coral

207   cover [41] but, in pristine systems, return to baseline levels once benthic habitat has returned

208   to a coral-dominated state [42]. However, on fished Seychelles reefs herbivores remained

209   dominant >10 years after bleaching, with both richness and biomass exceeding pre-bleaching

210   levels by 2014. Such sustained herbivore productivity may occur due to long-term

211   availability of diverse algal resources, but also in response to dampening of natural predation

212   levels when upper trophic levels are overexploited and their recovery from bleaching is slow.

213   Furthermore, high herbivore survivorship during the first few years after bleaching may have

214   helped to sustain large herbivore populations over decadal time scales, particularly for long-

215 lived acanthurid and scarid species [27]. Thus, high herbivore productivity may be

216 characteristic of bleached reefs that are adjacent to human populations, which may help

217 buffer fisheries from declining predatory fish populations by continuing to provide catches of

218 low trophic level species [31].

219   As low-latitude ecosystems that operate near their thermal limits [43], coral reefs are

220 more likely to reorganize and suffer local extinctions than receive temperature driven non-

221 native species. Thus, the diversity patterns documented here suggest that climate-driven

222 compositional changes on coral reefs will be particularly unique, and driven indirectly by

223 changes in physical habitat structure rather than directly by the effects of changes in

224 temperature on species distributions, for example in sub-tropical coastal [44] and temperate

225 shelf [45] ecosystems. The implications for future coral reef ecosystems are stark, given that

226 coral reef fish communities did not return to pre-bleaching diversity levels over a 16-year

227 recovery window (1998-2014) which was bounded by two climate-driven mass coral

228 bleaching events (1998, 2016). With over 60% of reefs projected to experience annual

229 bleaching-level thermal stress by ~2050 [9] and bleaching recovery windows only ~six years

230 by 2016 [8], we conclude that realized and projected increases in the frequency of thermal

231 stress events on coral reefs will cause persistent changes in fish diversity and community

232 structure. These changes will alter the functions and ecosystem services historically provided

233 by reef fishes, such as grazing rates [26] and the species accessible to fisheries [31]. This

234 poses a challenge for management and reef dependent communities to adapt to these alters

235 reef fish configurations.

236

237

238 **EXPERIMENTAL PROCEDURES**

239

Study sites

Six surveys of 21 Seychelles reef sites were conducted from 1994-2017 (one in each of the years 1994, 2005, 2008, 2011, 2014, 2017). Surveys were spatially stratified to encompass carbonate, patch, and granitic habitat types (n = 7 per habitat) in both fished (12) and protected (9) areas. All 21 sites were surveyed in each year, except 2017, when 18 sites were surveyed.

Fish and benthic survey data

Fish and benthic community surveys were conducted at each site in each year using point counts of 7 m radius. Within each point count area, one diver (NAJG or SJ) estimated individual body lengths for any diurnally active reef-associated fish on a list of 129 species and estimated to be ≥8 cm total length. Individual sizes (total length to nearest cm) were converted to biomass using published length ~ weight relationships [46]. Each species was assigned to one of six functional feeding groups (planktivore, corallivore, herbivore, invertivore, mixed-diet feeder, piscivore) based on published dietary information [46] and assigned an estimated average age to first maturity based on life history information [47] (Table S1). Following fish surveys, one diver (SW or SJ) performed visual assessments of benthic habitat composition within the point count area. Benthic composition was recorded as the percent cover (%) of macroalgae, sand, rubble and rock substrate, and three morphological types of hard coral (branching, massive, encrusting). Structural complexity was assessed on a 6-point scale ranging from flattened sites with no vertical relief (0) up to highly complex sites characterized by overhangs and caves (5) [48]. These visual cover and complexity estimates correlate closely with line transect methods and commonly-used rugosity metrics [49]. For each survey year, benthic habitat observations were averaged

264   across replicates to give site-level estimates of the percent cover of macroalgae, branching,

265   massive, and encrusting corals, and structural complexity.

266

267   Fish and benthic point count surveys were repeated for 8 (2011, 2014, 2017) or 16

268   (1994, 2005, 2008) replicates per site. Because species richness estimates depend on the area

269   sampled, we ensured that temporal comparisons were valid by only analyzing data from the

270   first 8 replicates in 1994, 2005 and 2008. By conducting surveys from a fixed species list, at

271   similar depths, and repeating locations in space and time with equal effort (8 survey

272   replicates per site), we minimize issues of sample incompleteness that might bias diversity

273   estimates through a failure to detect rare species [50]. Although we did not census all resident

274   fish species, our species list incorporates taxa that are commonly observed on Seychelles

275   reefs [51].

276

277   **Temporal trends in diversity and community composition**

278   Bleaching-induced shifts in community composition were assessed by examining temporal

279   change in 1) α diversity (i.e. species richness), 2) β diversity (i.e. compositional

280   dissimilarity), and 3) species biomass. First, we measured α diversity by tallying the total

281   number of species observed at each site in each year, for the full community and each

282   functional group. Temporal richness patterns among functional groups were assessed relative

283   to pre-bleaching assemblages where, by estimating the difference between observed richness

284   and 1994 richness for each site in 2005-2017, we examined how different functional groups

285   responded to bleaching and subsequent habitat changes, and how those groups contributed to

286   overall richness patterns. Although sampling effort was standardized across the time series,

287   richness estimates may have been sensitive to spatial and temporal variation in abundances

288   [52].

289   Shifts in community composition were described with β diversity metrics. We

290   generated species × site matrices with mean biomass (kg ha^{-1}) estimates, that were averaged

291   across replicates at each site in each year (n = 6 community matrices, each with dimensions

292   129 species x 21 sites). From these matrices, we calculated β diversity using the Bray-Curtis

293   index (β_{BC}) [53] for pairwise comparisons between sites across survey years (temporal) or

294   among sites in each survey year (spatial). β_{BC} is bounded by 0 (perfect similarity) and 1

295   (perfect dissimilarity), and quantifies biomass (x) differences of each species i at site k

296   between years a and b, relative to overall biomass:

297    $$\beta_{BC} = \frac{\sum_i(x_{ika} - x_{ikb})}{\sum_i(x_{ia} + x_{ib})} \hspace{3cm} (1)$$

298   We used β_{BC} to quantify temporal shifts in community composition in three ways.

299   First, we quantified compositional turnover relative to pre-bleaching compositions by

300   expressing β_{BC} as the site-level difference in species biomass between each survey year and

301   1994, thus giving estimates for each of the 21 sites (k) in each post-bleaching survey year

302   (e.g. $\beta_{k,2014}$ = pairwise comparison between k_{2014} and k_{1994}). This approach, hereafter β_{1994},

303   enabled us to measure the dissimilarity between pre and post-bleaching communities, and to

304   assess the degree of recovery to pre-bleaching community compositions. Second, we

305   quantified turnover between survey years by expressing β_{BC} as the site-level difference in

306   species biomass between successive survey years, thus giving estimates at 21 sites for five

307   temporal comparisons (e.g. $\beta_{k,2014}$ = pairwise comparison between k_{2014} and k_{2011}). This

308   approach, hereafter β_{seq}, was used to assess changes in composition between survey years.

309   Third, we quantified temporal trends in spatial β diversity by estimating β_{BC} for pairwise site

310   combinations among either recovering or regime-shifted reefs, separately for each survey

311   year (e.g. $\beta_{1,2\_2014}$ = pairwise comparison between recovering sites 1 and 2 in 2014). Site-level

312   dissimilarity values were the mean β_{BC} across all pairwise site comparisons in each year. This

313   approach, hereafter β_{spatial}, enabled us to assess changes in spatial similarity of community

314   compositions through time, separately for recovering and shifted reefs. Null and alternative β

315   metrics indicated that temporal β diversity patterns were robust to potential sampling biases

316   and richness gradients (Supplementary Methods).

317   To complement our assessment of temporal β diversity trends, we sought to identify

318   which functional groups and species accounted for compositional differences between pre-

319   and post-bleaching assemblages. We defined pre- and post-bleaching assemblages as those

320   surveyed in 1994 and 2014, respectively, thereby incorporating potential reorganization of

321   fish communities following the 1998 bleaching event while excluding any additional impacts

322   of the 2016 bleaching event. For β_{BC} values generated by pairwise comparison of sites in

323   1994 and 2014, we measured each species' contribution to compositional dissimilarity with a

324   SIMilarity PERcentage analysis (SIMPER) [54]. The percentage contribution to β_{BC} was the

325   absolute difference in biomass between 1994 and 2014 for each species i at each site k, $x_{ik,1994}$

326    $- x_{ik,2014}$. Compositional shifts were reported by summing SIMPER percentages across

327   functional groups, grouping species by the direction of biomass change (increased vs.

328   decreased), for either recovering or regime-shifted reefs. Finally, we characterized species-

329   level biomass changes by calculating the difference in biomass of each species before

330   bleaching (1994) and after recovery (2014) in each reef regime.

331

332   **Statistical modelling**

333   We utilized Bayesian hierarchical models to compare temporal changes in fish community

334   composition between recovering and regime-shifted reefs. For diversity metrics, models were

335   fitted to predict variation in overall species richness (Model 1, M1), functional group richness

336   (M2 fitted separately to 6 functional groups), β_{1994} (M3), and β_{seq} (M4) (Tables S2, S3). After

337   identifying appropriate temporal structures, we hypothesized that site-specific benthic

338 recovery rates and fishery access would predict temporal change in overall fish community

339 diversity. Diversity models (α, β metrics) were fitted with management status (no-take or

340 fished), branching coral, encrusting coral, massive coral and macroalgae (% cover), and

341 structural complexity as explanatory covariates. For species-level biomass differences

342 between 1994 and 2014, we modelled the same fixed effects used in diversity models, and as

343 well as mean observed species size (cm; fixed term) and functional feeding group (random

344 terms for recovering and regime-shifted reefs) (M5). Model fitting procedures are described

345 in full in the Supplementary Methods. Temporal trends in $\beta_{spatial}$, which were pairwise site

346 comparisons and thus not independent samples, were visualized but not modelled.

347 All analyses were conducted in R [55]. β metrics were estimated using *beta.temp* function in

348 *betapart* [56], SIMPER analyses were run in *vegan* [57], and Bayesian hierarchical models

349 were implemented in Stan using *rethinking* [58] following [59]. We archive our R code and

350 model outputs at an open source repository (github.com/jpwrobinson/beta-bleaching).
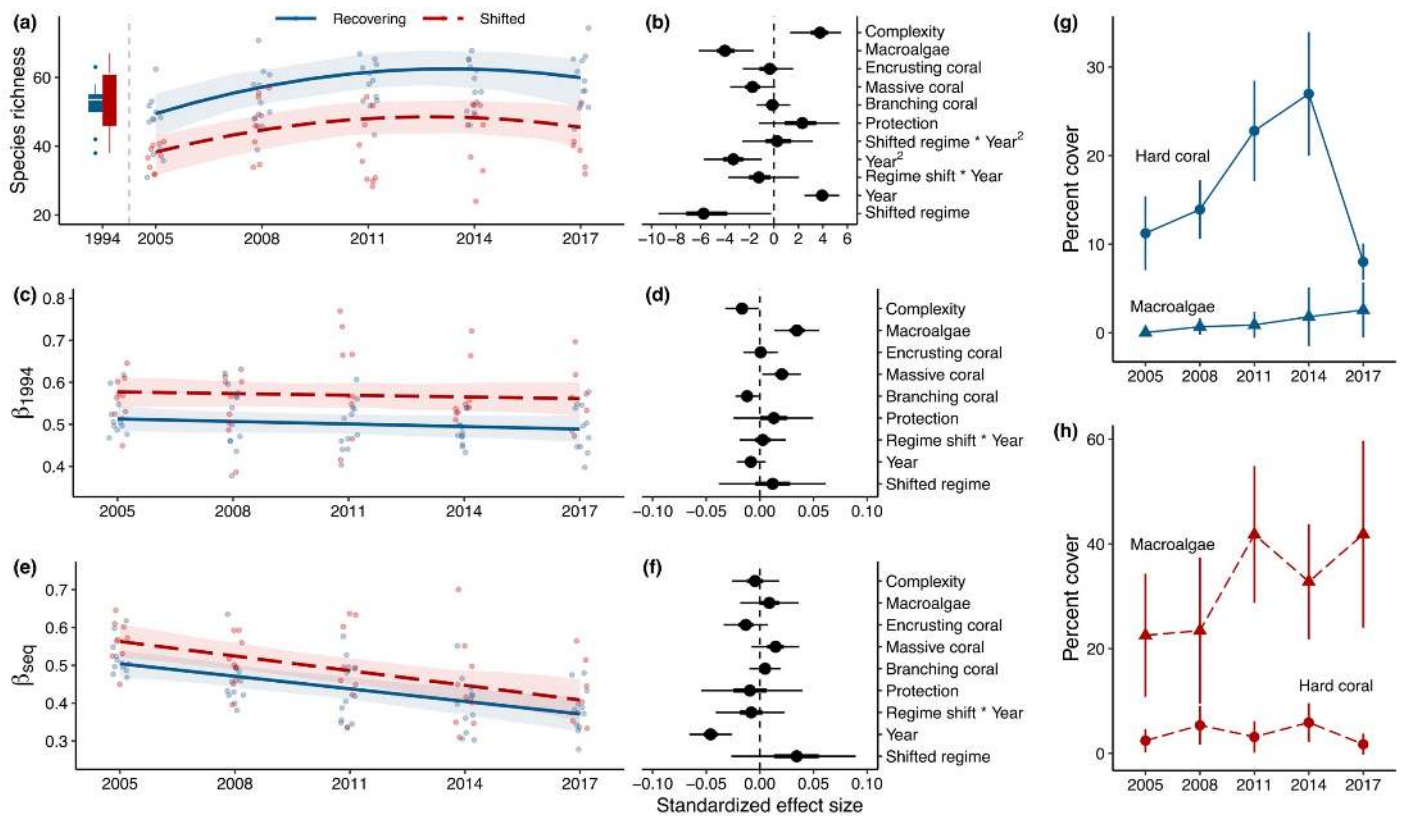
351

357 **Author contributions**
358 NAJG conceived the study. NAJG, SW and SJ conducted ecological surveys. JPWR
359 performed all statistical analyses and led the manuscript writing, with substantial input from
360 SW, SJ and NAJG.

362   **Figure 1. Temporal change in fish assemblage diversity from 2005-2017.** (A) Species

363   richness with (B) posterior parameter estimates, (C) β_{1994} with (D) posterior parameter

364   estimates, and (E) β_{seq} with (F) posterior parameter estimates. Temporal trend lines (a,c,e)

365   were generated from mean posterior predictions through time, conditioned on mean post-

366   bleaching benthic cover and complexity for recovering (blue solid line) and regime-shifted

367   (red dashed line) sites, with 95% highest posterior density intervals. Observed site-level

368   values are displayed as points jittered for each survey year, and baseline 1994 species

369   richness included as boxplots in (a). Posterior parameter estimates indicate mean (point),

370   95% (thick line) and 50% (thin line) credible intervals generated from a posterior distribution

371   of 1,000 samples for each explanatory covariate. (G-H) Temporal change in cover of hard

372   coral (blue) and macroalgae (red) on recovering (G) and regime-shifted (H) reefs, with points

373   indicating site-level mean percent cover ($\pm$ 2 standard errors). See also Figure S1 which

374   shows $\beta_{spatial}$ temporal trends, Figure S2 which shows incidence-based and null model-based

375   β estimates, and Tables S2 and S3 which show Bayesian model structures and priors.

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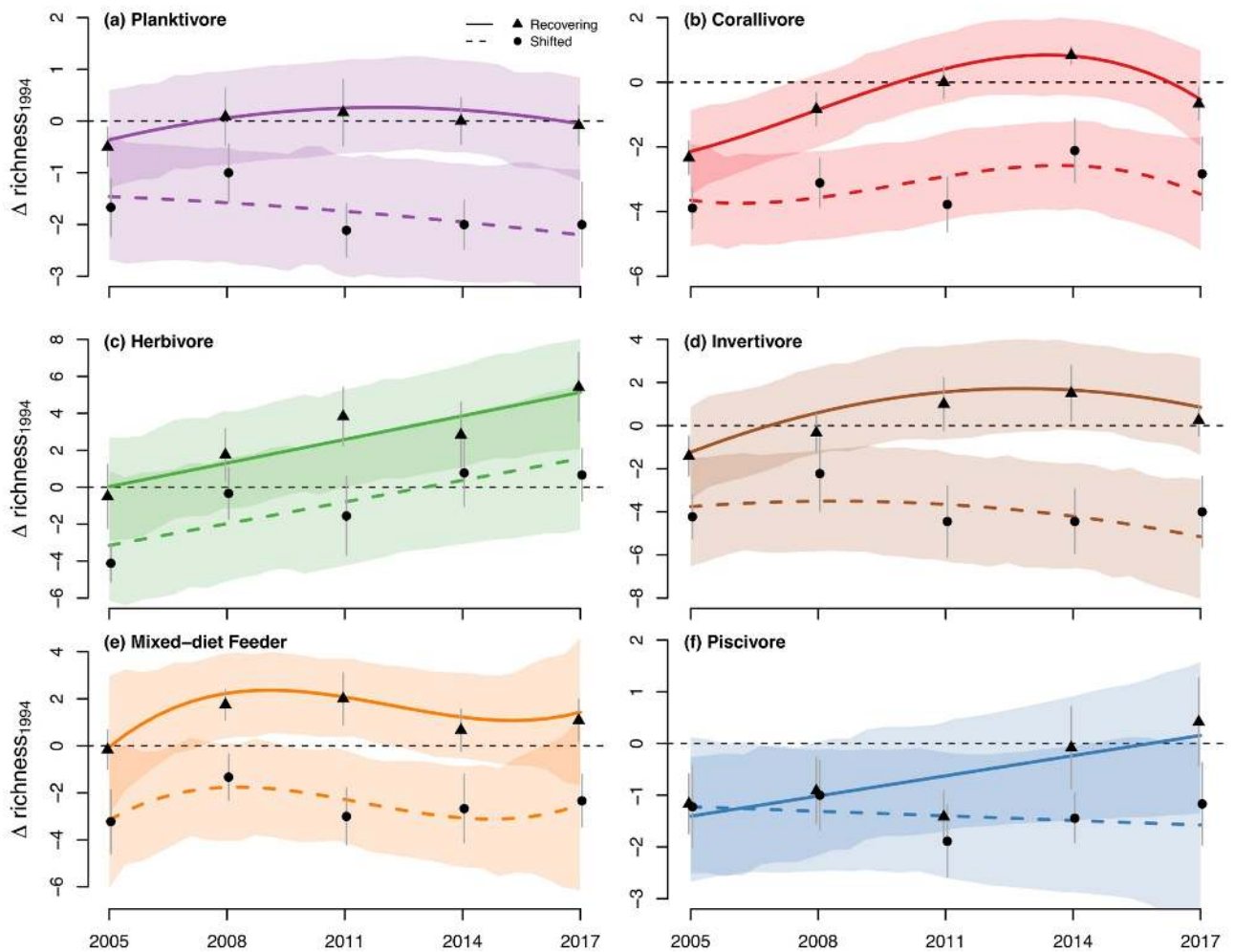
Figure 2. Change in species richness in each year relative to 1994 for functional feeding

groups. Panels show (A) planktivores, (B) corallivores, (C) herbivores, (D)

mixed-diet feeders, and (F) piscivores. Lines are mean posterior predictions over time

generated from top-ranked linear or non-linear temporal models for recovering (solid) and

regime-shifted reefs (dashed), shaded with 95% highest posterior density intervals and

overlaid with mean observed richness change (± 2 standard errors). See also Table S1 which

shows species in functional feeding groups and average age to maturity, and Tables S2-S4

which show Bayesian model structures, priors, and model selection on temporal structures.
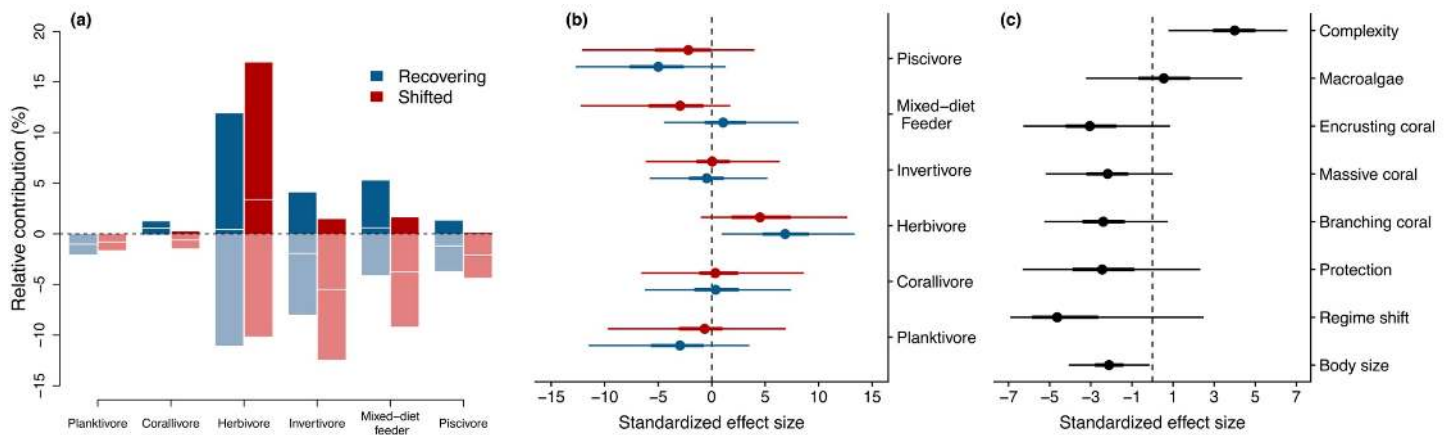
Figure 3. Biomass composition of fish assemblages on recovering and regime-shifted reefs. (A) SIMPER analysis of species contributions to β_{BC} dissimilarity between 1994 and 2014 for recovering (blue) and regime-shifted (red) sites. Bars are species-level contributions summed by functional feeding group for species that increased (positive y values, solid color) or decreased (negative y, shaded color) in biomass from 1994 to 2014, where overall β_{BC} was 0.53 at recovering sites and 0.60 at regime-shifted sites. White lines indicate net change in biomass. (B-C) Bayesian model predictions of species-level biomass change from 1994 to 2014 showing (B) the predicted change in biomass by functional group and (C) effect of fixed explanatory covariates on biomass change. Posterior parameter estimates indicate mean (point), 95% (thick line) and 50% (thin line) credible intervals, of 1,000 samples of the posterior distribution for each functional feeding group on recovering (red) and regime-shifted reefs (blue), and each fixed explanatory covariate (black). See also Tables S2 and S3 for Bayesian model structures and priors.
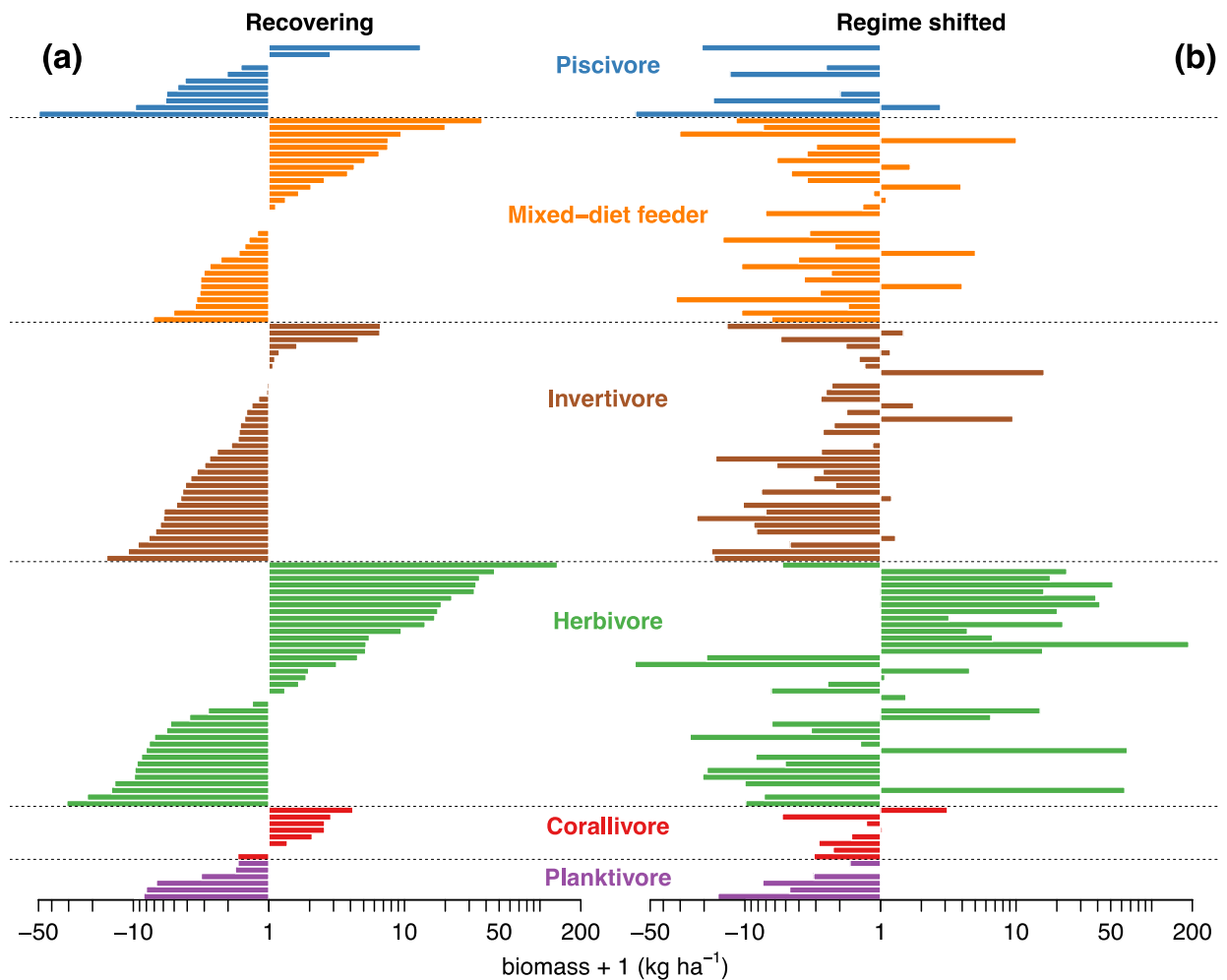
Figure 4. Change in species biomass between pre- and post-bleaching fish assemblages on recovering and regime-shifted reefs. Bars are the mean biomass difference (kg ha^{-1}) from 1994 to 2014 for each species, on a $\log_{10}$ scale and colored by functional feeding group. Bars directed right indicate that biomass increased from 1994 to 2014 and bars directed left indicate that biomass decreased from 1994 to 2014. (A) Recovering reef species are ordered by biomass change, descending from the largest increase (bars directed right) to the largest decrease (bars directed left). (B) Regime-shifted reef species, ordered to correspond with species order on recovering reefs. Missing bars indicate species that were not observed in a given year and reef state. Across all reefs, three species were not observed in either 1994 or 2014 (*Diagramma pictum*, *Epinephelus tukula*, *Lethrinus rubrioperculatus*). See also Figures S3 and S4 for species names and relative biomass changes on each reef habitat type.

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