Received: 18 January 2019 | Accepted: 13 May 2019

DOI: 10.1111/gcb.14704

PRIMARY RESEARCH ARTICLE

Global Change Biology WILEY

Thermal stress induces persistently altered coral reef fish assemblages

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Funding information
Royal Society, Grant/Award Number: CH160077 and UF140691

Abstract

Ecological communities are reorganizing in response to warming temperatures. For continuous ocean habitats this reorganization is characterized by large-scale species redistribution, but for tropical discontinuous habitats such as coral reefs, spatial isolation coupled with strong habitat dependence of fish species imply that turnover and local extinctions are more significant mechanisms. In these systems, transient marine heatwaves are causing coral bleaching and profoundly altering habitat structure, yet despite severe bleaching events becoming more frequent and projections indicating annual severe bleaching by the 2050s at most reefs, long-term effects on the diversity and structure of fish assemblages remain unclear. Using a 23-year time series spanning a thermal stress event, we describe and model structural changes and recovery trajectories of fish communities after mass bleaching. Communities changed fundamentally, with the new emergent communities dominated by herbivores and persisting for >15 years, a period exceeding realized and projected intervals between thermal stress events on coral reefs. Reefs which shifted to macroalgal states had the lowest species richness and highest compositional dissimilarity, whereas reefs where live coral recovered exceeded prebleaching fish richness, but remained dissimilar to prebleaching compositions. Given realized and projected frequencies of bleaching events, our results show that fish communities historically associated with coral reefs will not re-establish, requiring substantial adaptation by managers and resource users.

KEYWORDS

beta diversity, biodiversity, biotic homogenization, bleaching, community structure, coral reef ecology, regime shifts, thermal stress

1 | INTRODUCTION

Climate change is driving shifts in species composition that result in novel ecosystem configurations (Dornelas et al., 2014; Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Williams & Jackson, 2007). Characteristics of these shifts depend upon habitat connectivity and species' ecology. In ecosystems where habitats are relatively continuous and connectivity is high, such as shelf seas and pelagic oceans, compositional shifts occur progressively, when species relocate in response to long-term increases in mean temperature (Fossheim et al., 2015; Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015), or abruptly, when heatwaves force species to disperse towards tolerable environmental conditions (Wernberg et al., 2012). Examples of marine fish species redistributing to deeper depths and higher latitudes in shelf seas are widespread (Pecl et al., 2017) and further redistribution is expected with ongoing warming (García Molinos et al., 2016).

Other marine habitats, such as tropical coral reefs, are discontinuous, and their equatorial location and spatial isolation, coupled with the strong habitat dependence of associated species (Wilson, Graham, Pratchett, Jones, & Polunin, 2006), means that compositional responses to climate are likely to be driven by turnover and local extinctions rather than the appearance of novel taxa (Hobbs, Higgs, & Harris, 2009). Such limited capacity for species redistributions also means that warming effects in these systems will be realized after transient marine heatwaves, which can profoundly alter habitat structure (Graham, Jennings, MacNeil, Mouillot, & Wilson, 2015), rather than long-term temperature changes. Consequently, the influence of climate warming on species composition on coral reefs cannot be inferred from studies of continuous habitats at higher latitudes, where the predominant changes in communities are caused by mobile species tracking tolerable ocean temperatures.

On coral reefs, the indirect effects of warming on fish species composition result from thermal stress events that cause coral bleaching (Hughes et al., 2018), which can cause coral mortality, collapse of habitat structure, and regime shifts from coral- to algal-dominated states (Bellwood, Hughes, Folke, & Nyström, 2004). Because reef-associated fishes are highly dependent on complex coral-dominated habitat (Messmer et al., 2011; Wilson et al., 2006), bleaching-driven habitat collapse can reduce species richness (Halford & Caley, 2009) and homogenize compositions (Richardson, Graham, Pratchett, Eurich, & Hoey, 2018) within 1–3 years. Although thermal stress events and associated bleaching are episodic, the intervals between successive severe bleaching events have fallen from 27 years in the 1980s to 6 years in 2016 (Hughes et al., 2018), and projections suggest that ocean warming will lead to annual severe bleaching by the 2050s at most reefs, even under low emissions scenarios (Heron, Maynard, Hooidonk, & Eakin, 2016; van Hooidonk, Maynard, & Planes, 2013). Consequently, knowledge of whether novel fish communities persist after bleaching will help to reveal how increased frequency of thermal stress events may lead to permanent changes in these communities.

Here, we use a 23-year data set of fish and benthic surveys of coral reefs in Seychelles (1994–2017) to investigate the effects of a thermal stress event on the compositional turnover and persistence of fish assemblages. In 1998, a strong El-Ninõ coincided with the Indian Ocean Dipole to cause severe coral bleaching across the Western Indian Ocean (Goreau, McClanahan, Hayes, & Strong, 2000) and, in Seychelles, loss of >90% coral cover and collapse of habitat structure (Graham et al., 2006). Using Bayesian hierarchical models and multivariate diversity analyses, 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 (Graham et al., 2015), we were able to compare compositional turnover for both shifted and recovering reefs. Moreover, as these reefs also experienced severe bleaching in 2016 (Hughes et al., 2018), our analyses document how fish assemblages reorganized between successive mass bleaching events.

2 | MATERIALS AND METHODS

2.1 | Study sites

Six surveys of 21 Seychelles reef sites were conducted from 1994 to 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 (Graham et al., 2015). All 21 sites were surveyed in each year, except 2017, when 18 sites were surveyed.

2.2 | 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 in total length. Individual sizes (total length to nearest cm) were converted to biomass using published length–weight relationships (Froese & Pauly, 2018). Each species was assigned to one of six functional feeding groups (planktivore, corallivore, herbivore, invertivore, mixed-diet feeder, piscivore) based on published dietary information (Froese & Pauly, 2018) and assigned an estimated average age to first maturity based on life history information (Thorson, Munch, Cope, & Gao, 2017; Table S1). Following fish surveys, one diver (SKW 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; Polunin & Roberts, 1993). These visual cover and complexity estimates correlate closely with line transect methods and commonly used rugosity metrics (Wilson, Graham, & Polunin, 2007). For each survey year, benthic habitat observations were averaged across replicates to give site-level estimates of the percent cover of macroalgae, branching, massive, and encrusting corals, and structural complexity.

Fish and benthic point count surveys were repeated for eight (2011, 2014, 2017) or 16 (1994, 2005, 2008) replicates per site. Because species richness estimates depend on the area sampled, we ensured that temporal comparisons were valid by only analysing data from the first eight replicates in 1994, 2005 and 2008. By conducting surveys from a fixed species list, at similar depths, and repeating locations in space and time with equal effort (eight survey replicates per site), we minimize issues of sample incompleteness that might bias diversity estimates through a failure to detect rare species (Chao, Chazdon, Colwell, & Shen, 2005). Although we did not census all resident fish species, our species list incorporates taxa that are commonly observed on Seychelles' reefs (Chong-Seng, Mannering, Pratchett, Bellwood, & Graham, 2012).

2.3 | Temporal trends in diversity and community composition

Bleaching-induced shifts in community composition were assessed by examining temporal change in (a) α diversity (species richness), (b) β diversity (compositional dissimilarity) and (c) species biomass. First, we measured α diversity by tallying the total number of species observed at each site in each year, for the full community and each functional group. Temporal richness patterns among functional groups were assessed relative to prebleaching assemblages where, by estimating the difference between observed richness and 1994 richness for each site in 2005–2017, we examined how different functional groups responded to bleaching and subsequent habitat changes, and how those groups contributed to overall richness patterns. Although sampling effort was standardized across the time series, richness estimates may have been sensitive to spatial and temporal variation in abundances (Gotelli & Colwell, 2001).

Shifts in community composition were described with β diversity metrics. We generated species × site matrices with mean biomass (kg/ha) estimates, that were averaged across replicates at each site in each year (*n* = 6 community matrices, each with dimensions 129 species × 21 sites). From these matrices, we calculated β diversity using the Bray–Curtis index (β_{BC}; Bray & Curtis, 1957) for pairwise comparisons between sites across survey years (temporal) or among sites in each survey year (spatial). β_{BC} is bounded by 0 (perfect similarity) and 1 (perfect dissimilarity), and quantifies biomass (*x*) differences of each species *i* at site *k* between years *a* and *b*, relative to overall biomass:

$$\beta_{BC} = \frac{\sum_i \left(x_{ika} - x_{ikb}\right)}{\sum_i \left(x_{ia} + x_{ib}\right)} \quad (1)$$

We used β_{BC} to quantify temporal shifts in community composition in three ways. First, we quantified compositional turnover relative to prebleaching compositions by expressing β_{BC} as the site-level difference in species biomass between each survey year and 1994, thus giving estimates for each of the 21 sites (*k*) in each postbleaching survey year (e.g. $\beta_{k,2014}$ = pairwise comparison between k_{2014} and k_{1994}). This approach, hereafter β_{1994}, enabled us to measure the dissimilarity between pre- and postbleaching communities, and to assess the degree of recovery to prebleaching community compositions. Second, we quantified turnover between survey years by expressing β_{BC} as the site-level difference in species biomass between successive survey years, thus giving estimates at 21 sites for five temporal comparisons (e.g. $\beta_{k,2014}$ = pairwise comparison between k_{2014} and k_{2011}). This approach, hereafter β_{seq}, was used to assess changes in composition between survey years. We further assessed how variation in species abundances contributed to dissimilarity estimates by partitioning β_{1994} and β_{seq} estimates into two components: balanced abundance changes (i.e. species replaced in similar abundances) and abundance differences (i.e. loss or gain of individuals; Baselga, 2013). Third, we quantified temporal trends in spatial β diversity by estimating β_{BC} for pairwise site combinations among either recovering or regime-shifted reefs, separately for each survey year (e.g. $\beta_{1,2\_2014}$ = pairwise comparison between recovering sites 1 and 2 in 2014). Site-level dissimilarity values were the mean β_{BC} across all pairwise site comparisons in each year. This approach, hereafter $\beta_{spatial}$, enabled us to assess changes in spatial similarity of community compositions through time, separately for recovering and shifted reefs. Null and alternative β metrics indicated that temporal β diversity patterns were robust to potential sampling biases and richness gradients (Supplementary Methods).

To complement our assessment of temporal β diversity trends, we sought to identify which functional groups and species accounted for compositional differences between pre- and postbleaching assemblages. We defined pre- and postbleaching assemblages as those surveyed in 1994 and 2014, respectively, thereby incorporating potential reorganization of fish communities following the 1998 bleaching event while excluding any additional impacts of the 2016 bleaching event. For β_{BC} values generated by pairwise comparison of sites in 1994 and 2014, we measured each species' contribution to compositional dissimilarity with a SIMilarity PERcentage analysis (SIMPER; Clarke, 1993). The percentage contribution to β_{BC} was the absolute difference in biomass between 1994 and 2014 for each species *i* at each site *k*, $x_{ik,1994} - x_{ik,2014}$. Compositional shifts were reported by summing SIMPER percentages across functional groups, grouping species by the direction of biomass change (increased vs. decreased), for either recovering or regime-shifted reefs. Finally, we characterized species-level biomass changes by calculating the difference in biomass of each species before bleaching (1994) and after recovery (2014) in each reef regime.

2.4 | Modelling

We utilized Bayesian hierarchical models to compare temporal changes in fish community composition between recovering and regime-shifted reefs. For diversity metrics, models were fitted to predict variation in overall species richness (Model 1, M1), functional group richness (M2 fitted separately to six functional groups), β_{1994} (M3) and β_{seq} (M4; Tables S2 and S3). After identifying appropriate temporal structures, we hypothesized that site-specific benthic recovery rates and fishery access would predict temporal change in overall fish community diversity. Diversity models (α, β metrics) were fitted with management status (no-take or fished), branching coral, encrusting coral, massive coral and macroalgae (% cover) and structural complexity as explanatory covariates. For species-level biomass differences between 1994 and 2014, we modelled the same fixed effects used in diversity models, and as well as mean observed species size (cm; fixed term) and functional feeding group (random terms for recovering and regime-shifted reefs; M5). Model fitting procedures are described in full in the Supplementary Methods. Temporal trends in $\beta_{spatial}$, which were pairwise site comparisons and thus not independent samples, were visualized but not modelled.

All analyses were conducted in R (R Core Team, 2018). β metrics were estimated using *beta.temp* function in *betapart* (Baselga & Orme, 2012), SIMPER analyses were run in *vegan* (Oksanen et al., 2017), and Bayesian hierarchical models were implemented in Stan using *rethinking* (McElreath, 2017) following Freshwater et al. (2019). We archive our R code and model outputs at an open source repository (github.com/jpwrobinson/beta-bleaching).

3 | RESULTS

Over the postbleaching period, regime-shifted reefs were dominated by macroalgae (mean cover >20% from 2005 to 2017), whereas recovering reefs steadily increased coral cover to reach prebleaching levels by 2014 (mean cover = 27%; Figure 1g,h). By 2005, 7 years after bleaching, recovering and regime-shifted reefs both supported fewer species than prebleaching baselines, and proceeded to increase species richness at similar rates from 2005 to 2017 (Figure 1a). Although reefs that ultimately recovered and regime-shifted reefs both supported similar levels of richness prior to bleaching (1994 richness: recovering = 52.1 ± 1.92 *SE* and regime-shifted = 55.3 ± 3.50), initial richness loss was greatest on reefs that subsequently regime shifted with approximately six fewer species present (*regime shift* posterior mean = −5.88, 95% CI = −11.68, −0.10). Thus, despite similar temporal trends in species richness which had stabilized by 2011 (Figure 1a,b), regime-shifted reefs did not recover prebleaching richness, reaching a maximum of 46 species (±2.80) in 2008. In contrast, at recovering reefs, richness increased from 46 (±2.47) in 2005 to exceed prebleaching levels by approximately eight species in 2017 (58.5 ± 3.00). In addition to year and regime state, further site-level variability was linked to benthic condition and management status. Richness was highest at the reefs with the lowest macroalgal cover and highest structural complexity, and reefs in no-take areas supported approximately two (95% CI = −0.98, 6.33) more species than fished reefs (Figure 1b). Coral cover was generally a weak predictor of richness, with the strongest influence represented by moderate declines in species richness as massive coral cover increased (Figure 1b).

Non-linear trends in community-level richness were reflected in differential functional group responses. In 2005, richness of corallivore and invertivore groups was lower than in 1994 on all reefs (Figure 2b,d) but, by 2014, richness had reached prebleaching levels on recovering reefs but not on regime-shifted reefs. Herbivore richness increased linearly from 2005 to 2014 in both reef states, though recovering reefs consistently supported more species than

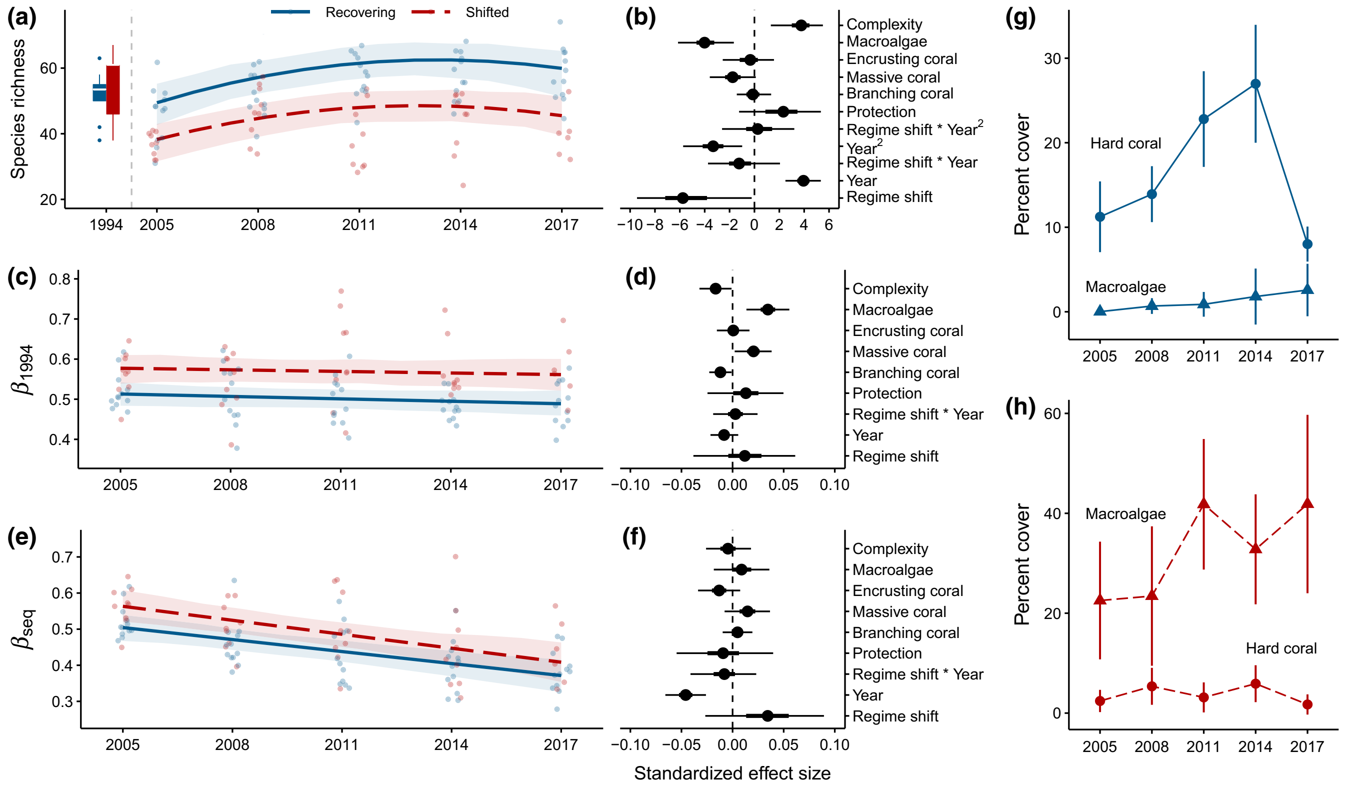

FIGURE 1 Temporal change in fish assemblage diversity from 2005 to 2017. (a) Species richness with (b) posterior parameter estimates, (c) β_{1994} with (d) posterior parameter estimates and (e) β_{seq} with (f) posterior parameter estimates. Temporal trend lines (a, c, e) were generated from mean posterior predictions through time, conditioned on mean postbleaching benthic cover and complexity for recovering (blue solid line) and regime-shifted (red dashed line) sites, with 95% highest posterior density intervals. Observed site-level values are displayed as points jittered for each survey year, and baseline 1994 species richness included as boxplots (median, 25th, 75th quantiles) in (a). Posterior parameter estimates (b, d, f) indicate mean (point), 95% (thick line), and 50% (thin line) credible intervals generated from a posterior distribution of 1,000 samples for each explanatory covariate, from models M1 (b), M3 (d) and M4 (f). Corresponding temporal change in cover of hard coral (circles) and macroalgae (triangles) on recovering (g) and regime-shifted (h) reefs, with points indicating site-level average percent cover (±2 standard errors). See Figure S7 for temporal trends in cover of major habitat-forming groups

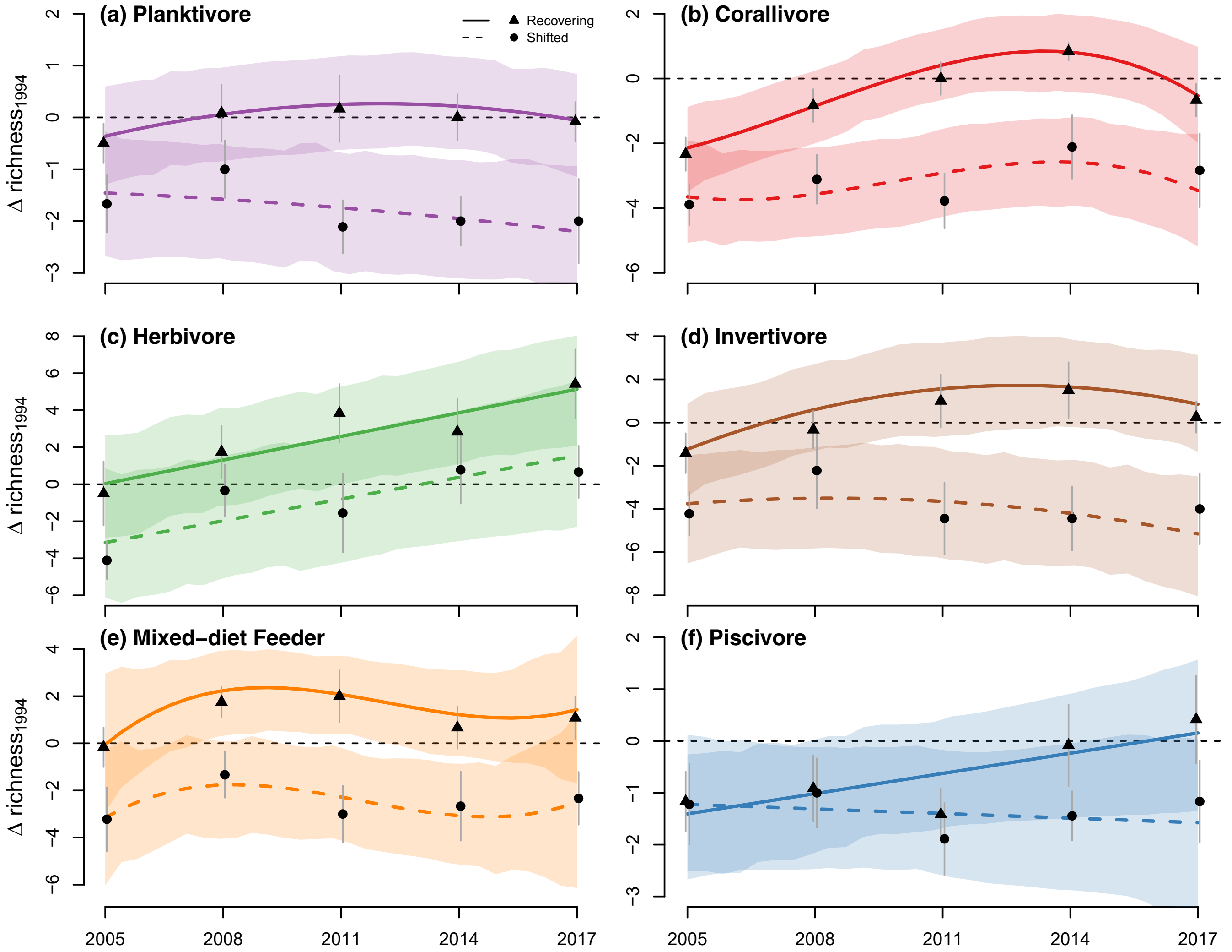

FIGURE 2 Change in species richness in each year relative to 1994. Trends for planktivores (a), corallivores (b), herbivores (c), invertivores (d), mixed-diet feeders (e) and piscivores (f). Lines are mean posterior predictions over time generated from top-ranked linear or non-linear temporal models 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)

regime-shifted reefs, and exceeded prebleaching levels by 2008 (Figure 2c). In contrast, regime-shifted reefs maintained prebleaching levels of herbivore richness from 2008 to 2017 after supporting approximately three fewer species in 2005. Changes in richness of planktivore, mixed-diet feeding and piscivore groups were also strongly differentiated by reef regime. On regime-shifted reefs, planktivore, mixed-diet feeder and piscivore groups were consistently less speciose than 1994 baselines (Figure 2a,e,f). These groups were less impacted on recovering reefs, where prebleaching richness levels were matched or exceeded by planktivores and mixed-diet feeders throughout 2005–2017, and piscivores recovered by 2014 (Figure 2a,e,f).

Across all species, community compositions were dissimilar to their 1994 baseline ($0.37 < \beta_{1994} < 0.77$) and did not recover towards prebleaching compositions over 2005–2014 (*year* mean = −0.01, 95% CI = −0.02, 0.00; Figure 1c,d). Regime-shifted reefs were more dissimilar to prebleaching baselines (mean $\beta_{1994} = 0.57 \pm 0.01$) than were recovering reefs ($\beta_{1994} = 0.50 \pm 0.01$), though *regime state* was a weak predictor (mean = 0.01, 95% CI = −0.036, 0.063). As expected, β_{1994} was maximized on reefs with high macroalgal cover and low structural complexity, while no-take reefs were characterized by marginally higher dissimilarity from 1994 (Figure 1d).

Fish community compositions homogenized over time, with β_{seq} declining from 2005 to 2017 (*year* mean = −0.05, 95% CI = −0.021, −0.006) at similar rates for recovering and regime-shifted reefs (*regime shift* × *year* mean = −0.01, 95% CI = −0.019, 0.024; Figure 1e,f). Although both recovering and regime-shifted reefs slowly declined towards similarity with 1994 compositions, postbleaching fish compositions on these reefs would fail to stabilize within the next two decades (i.e. year when mean β_{seq} confidence interval spanned 0). Despite overall greater dissimilarity of regime-shifted reefs than recovering reefs (*regime shift* posterior mean = 0.04, 95% CI = −0.036, 0.63), β_{seq} was only weakly linked to site-level benthic composition, with dissimilarity maximized at reefs with high cover of massive corals or macroalgae, and minimized at reefs with high encrusting coral cover in no-take areas (Figure 1f). Dissimilarity from 1994 surveys and between postbleaching years was primarily driven by turnover among species abundances (balanced abundance dissimilarity: β_{1994} = 0.29–0.62; β_{seq} = 0.17–0.62), whereas absolute gain or loss of species was less frequent (abundance gradient dissimilarity: β_{1994} = 0.00–0.36; β_{seq} = 0.00–0.33; Figure S3).

On recovering reefs, declining β_{seq} was mirrored by temporal changes in $\beta_{spatial}$. For pairwise site comparisons of fish community compositions, $\beta_{spatial}$ declined from 0.61 to 0.50 to fall below baseline $\beta_{spatial}$ levels by 2017 (Figure S1a). In contrast, fish compositions on regime-shifted reefs did not change consistently through time, though compositional dissimilarity was greater than baseline levels throughout 2005–2014 (mean $\beta_{spatial}$ = 0.57; Figure S1b). Regime-shifted reefs also fell below baseline $\beta_{spatial}$ levels in 2017, although those estimates were based upon fewer spatial comparisons (three sites were not sampled).

Compositional dissimilarity between pre- and postbleaching communities was characterized by biomass changes within herbivore, invertivore and mixed-diet functional feeding groups, and reduced biomass of planktivore, corallivore and piscivore species. For positive and negative biomass changes combined, herbivores explained 23.0% and 27.1% of observed β_{BC} at recovering and regime-shifted reefs, respectively (Figure 3a), and exhibited biomass changes of ±0–163 kg/ha (Figure 4). For herbivore species, the mean biomass difference between 1994 and 2014 was positive at both recovering (mean = 7.14, 95% CIs = 0.60, 13.84) and regime-shifted reefs (mean = 5.01, 95% CIs = −1.375, 13.248) (Figure 3b), indicating that declines in commonly observed species were outweighed by gains in newly abundant species (Figure 4).

Other functional groups made lower overall contributions to β_{BC}, and also tended to have the greatest degree of species declines. For example, invertivores and mixed-diet feeders had moderately high dissimilarity contributions (9.4%–13.9%) that were mostly due to species declines, particularly on regime-shifted reefs (Figures 3a,b and 4b). Although dissimilarity contributions from planktivore and piscivore groups were relatively minor (1.62%–4.99%), almost every species declined in biomass and group-level posterior means were negative for both recovering and regime-shifted reefs (Figures 3b and 4). In contrast, corallivore biomass changes were more closely linked to regime state, with biomass increases explaining observed β_{BC} at recovering reefs (relative contribution from species with biomass increases = 1.23% and from biomass decreases = 0.13%) but biomass declines explaining observed β_{BC} at regime-shifted reefs (0.23%, 1.43%; Figure 3a). Corallivore biomass was low relative to other species (Figure 4), which may explain why predicted species-level biomass changes from 1994 to 2014 were uncertain and centred around zero (Figure 3b).

High variability in biomass differences across sites and species corresponded with low contributions from individual species to β dissimilarity (maximum SIMPER = 2.4%), high variance of observed biomass estimates (Figure 4; Figures S4 and S5) and group-level posterior distributions with wide confidence intervals (Figure 3b). As such, site-level explanatory covariates were uncertain predictors of species biomass change, with weak negative effects of coral cover, fishing protection and regime shifts (Figure 3c). However, size and complexity were strong predictors of biomass change, with declines more likely for large species (*body size* mean = −2.11, 95% = −4.105, −0.166) and increases more likely on reefs with high structural complexity (*complexity* mean = 4.04, 95% CIs = 0.757, 7.20; Figure 3c).

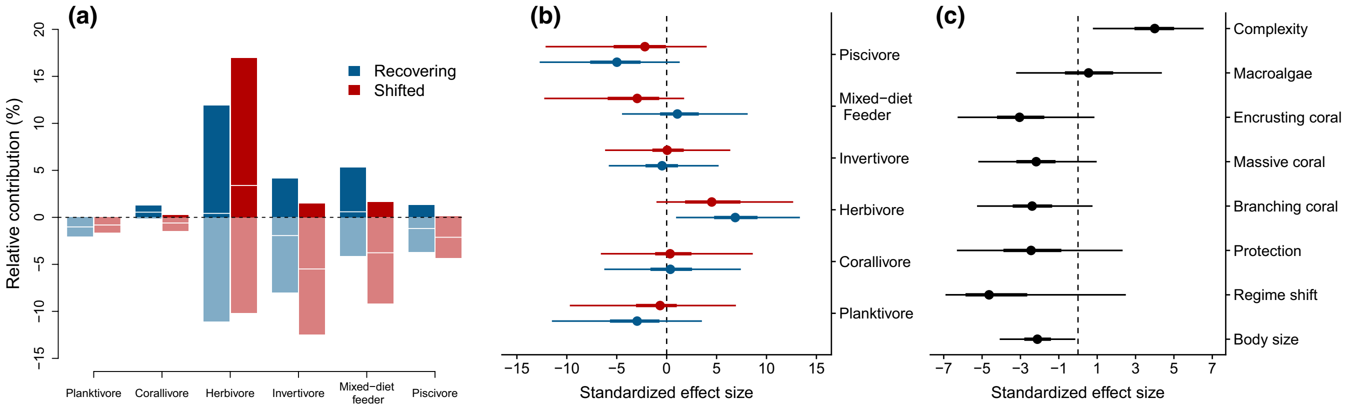

FIGURE 3 Biomass composition of fish assemblages on recovering and regime-shifted reefs. (a) SIMPER analysis of species contributions to β_{BC} dissimilarity between 1994 and 2014 for recovering (blue) and regime-shifted (red) sites. Bars are species-level contributions summed by functional feeding group for species that increased (positive *y* values, solid colour) or decreased (negative *y*, shaded colour) in biomass from 1994 to 2014, where overall β_{BC} was 0.53 at recovering reefs and 0.60 at regime-shifted reefs. White lines indicate net change in biomass. See Figure S6 for corresponding abundance-based SIMPER analysis. Right-hand panels are 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)

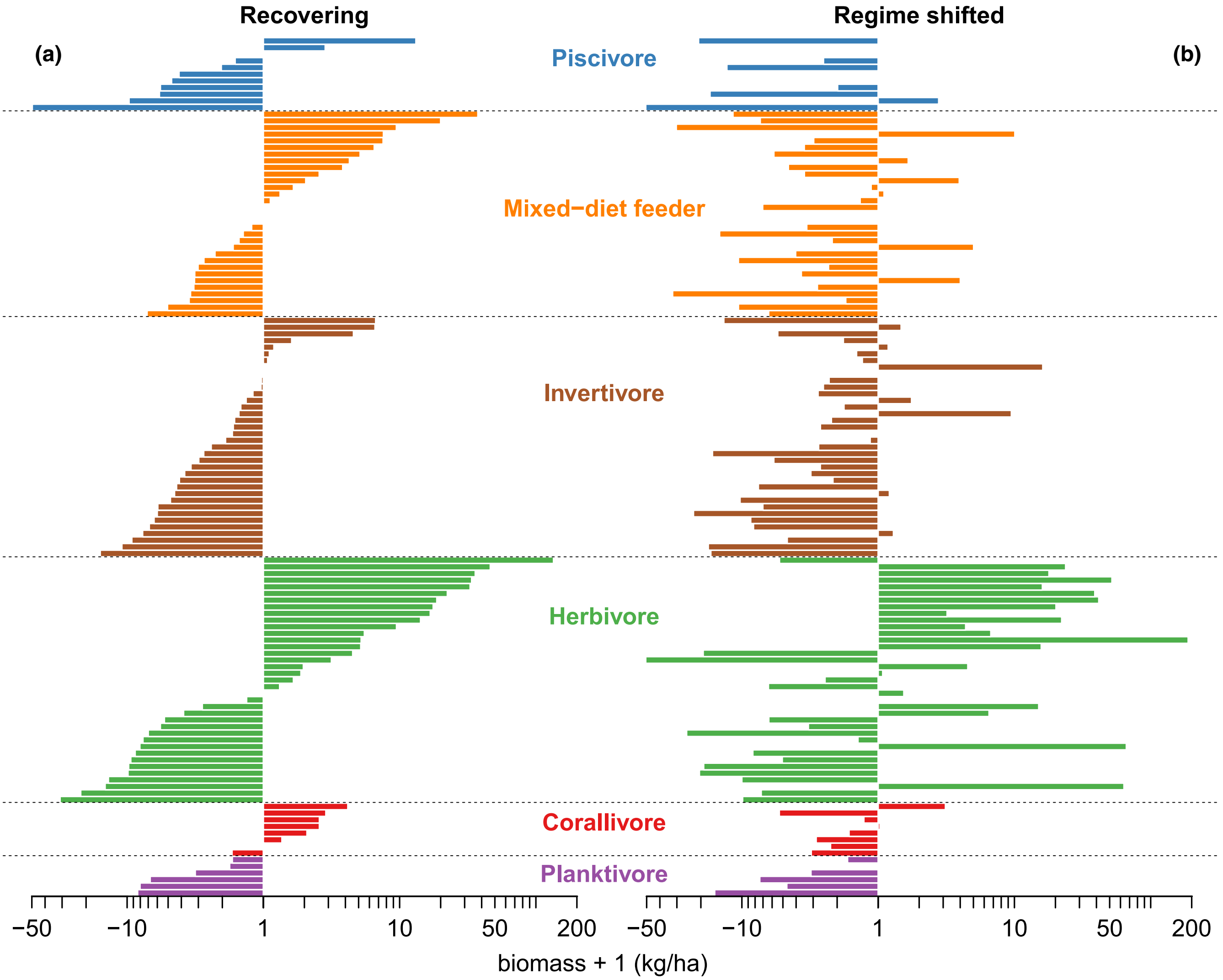

FIGURE 4 Change in species biomass between pre- and postbleaching fish assemblages on recovering and regime-shifted reefs. Bars are the mean biomass difference (kg/ha) from 1994 to 2014 for each species, on a $\log_{10}$ scale and coloured by functional feeding group. Bars directed right indicate that 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 the species order on recovering reefs. Species names and relative biomass changes are provided in Figures S4 and S5, and temporal trends in functional group biomass are provided in Figure S8. 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*)

4 | DISCUSSION

Coral reefs are already being impacted by more frequent and more intense warming events (Hughes et al., 2018) and the frequency of these events is projected to further increase as mean global temperatures continue to rise (Heron et al., 2016). Our results demonstrate that coral reef fish communities did not return to prebleaching diversity levels over a 16 year recovery window (1998–2014) which was bounded by two climate-driven mass coral bleaching events (1998, 2016). Biodiversity losses were most severe on regime-shifted reefs, which were dominated by macroalgae and where low α diversity and high β diversity (β_{1994}) levels were maintained throughout the postbleaching recovery period. Most strikingly, temporal trends in β diversity indicated that fish communities settled into novel compositions that had not existed before bleaching. Across all reefs, postbleaching assemblages were characterized by a speciose and high biomass herbivore group and low representation of planktivore, invertivore and piscivore species. Persistence of postbleaching compositions has been observed for cryptobenthic fish assemblages (Bellwood et al., 2012), and we confirm that these patterns extend to species spanning multiple trophic levels and providing important ecosystem services (e.g. fisheries).

Long-term bleaching impacts on reef fish assemblages will be dictated by how fish respond to regeneration of benthic habitat (Bellwood et al., 2012; Bonin, Almany, & Jones, 2011), with benthic resilience expected to insure against declines in fish diversity (Bellwood et al., 2004; Wilson et al., 2009). Regeneration of coral-dominated habitat mitigated some of the bleaching impacts on fish communities, with reefs that recovered (i.e. structurally complex habitat, dominated by branching corals with negligible macroalgal cover) having fish compositions most similar to those recorded prebleaching. However, coral community composition is also a strong structuring influence on fish communities after bleaching (Bellwood et al., 2012; Richardson et al., 2018), and the contrasting effects of branching and massive corals on fish compositions here imply that compositional shifts in coral growth forms are similarly important. For example, stress-tolerant corals such as massive *Porites* were associated with lower species richness and higher compositional dissimilarity through time (β_{1994} and β_{seq}), possibly because these sites failed to recover prebleaching compositions of dominant branching coral growth forms (Wilson et al., 2012) which provide shelter for abundant and diverse small-bodied fishes (Darling et al., 2017; Munday & Jones, 1998). Because several coral growth forms contribute to seascape-level complexity (Darling et al., 2017; Richardson, Graham, & Hoey, 2017), and bleaching impacts were minimized but not reversed by fast growth of branching corals, our findings confirm that fish communities should not be expected to fully recover when coral communities reassemble (Berumen & Pratchett, 2006; Mellin, MacNeil, Cheal, Emslie, & Caley, 2016).

Regime-shifted fish communities were most distinct from their coral-dominated baselines. These patterns build on previous observations from Seychelles demonstrating that macroalgal overgrowth has resulted in bottom-heavy fish biomass pyramids and reduced functional diversity (Graham et al., 2015; Hempson, Graham, MacNeil, Hoey, & Wilson, 2018). Declines in coral cover and flattening of habitat structure likely prevented coral-associated species from relocating or recruiting to macroalgal reefs, despite these fish being present on nearby recovering reefs. Indeed, faster rates of temporal homogenization (β_{seq}) at regime-shifted sites were likely because structural collapse and macroalgal overgrowth had already occurred by 2005. High spatial heterogeneity (β_{spatial}) on regime-shifted reefs, which exceeded that of baseline or recovering reefs, also suggests that habitat associations underlie compositional differences, as macroalgal habitat quality can vary substantially among seasons and years (Fulton et al., 2014; Wilson et al., 2018).

Benthic recovery trajectory also explained differences in compositional changes among functional groups, with greater loss of functional redundancy (i.e. fewer species with similar functional roles) and capacity (i.e. decreased biomass across functional groups) after regime shifts. On reefs close to human settlements, such as Seychelles, the vulnerability of fish functional groups to fishing (D'agata et al., 2016; Mouillot et al., 2014) will be exacerbated by bleaching, with transitions to macroalgal states likely to produce communities that are functionally depauperate relative to historic coral-dominated states (Nash, Graham, Jennings, Wilson, & Bellwood, 2016). In contrast, the functional capacity of fish communities was restored on reefs that resisted regime shifts, with richness levels of all six dietary groups returning to prebleaching baselines on recovering reefs. Piscivores were slowest to return to prebleaching levels, likely because recovery lags are longest for long-lived species that depend on reef-associated fishes for food (Graham et al., 2007) and require temporally stable reef habitats (Karkarey, Kelkar, Lobo, Alcoverro, & Arthur, 2014).

Although our infrequent visual surveys cannot be used to describe population dynamics, the recovery period spanned several generations of most species (Table S1) and thus, these patterns are likely due to positive population feedbacks in dominant species that benefited from bleaching (e.g. herbivores) and slow or failed recovery of species dependent on return of habitat structure (e.g. planktivores, corallivores). For example, increases in herbivore biomass are often associated with coral declines (Cheal, Wilson, Emslie, Dolman, & Sweatman, 2008; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011; Wilson et al., 2006) and, here, species responses depended on habitat type, where browsing species associated with macroalgal reefs and scraping species associated with recovering reefs (Robinson et al., 2018). Positive responses of other coral-associated species, which could be driven by recruitment as well as growth and relocation, reduced compositional differences relative to regime-shifted reefs. These effects may be strongest when species are highly dependent upon live branching coral for food and shelter, such as corallivores (Cole, Pratchett, & Jones, 2008). However, because habitat recovery was incomplete by 2014 and habitat changed again in 2016 (Wilson, Robinson, Chong-Seng, Robinson, & Graham, 2019), recovering reefs were unable to return to their prebleaching states.

The relative infrequency of our fish surveys, focus on adult fish and use of a fixed species list mean that we cannot disentangle the relative contributions of recruitment, growth and relocation among habitat types and depths, nor account for potential appearance of new species. However, it is likely that short-term dispersal among reef habitats (Garpe, Yahya, Lindahl, & Öhman, 2006; Richardson et al., 2018), increased population growth due to greater food availability (Russ, Questel, Rizzari, & Alcala, 2015) and high juvenile survivorship (Jones, McCormick, Srinivasan, & Eagle, 2004) all contributed to the long-term persistence of these populations. Reef fish populations are ecologically connected over relatively small scales, as larval dispersal distances are typically <5–15 km and many species are territorial as adults (damselfishes, butterflyfishes) or inhabit small home ranges (<3 km linear distance; Green et al., 2015). Additionally, Seychelles' reefs are isolated by deep water dispersal barriers for reef fishes to the west and by limited connectivity to distant continental reefs (>1,000 km; Kool & Graham, unpublished data), meaning that species larval connectivity or relocation from neighbouring reef systems are unlikely to be responsible for the majority of compositional changes we observe.

In each analysis, we considered how fishing protection influenced recovery and change in fish assemblages after bleaching. By enhancing grazing functions (Williams et al., 2016) and minimizing stressors on coral populations (Selig, Casey, & Bruno, 2012), ecosystem protection of coral reefs is expected to accelerate recovery towards prebleaching conditions. In Seychelles, no-take areas were a poor predictor of bleaching responses of benthic communities

(Graham et al., 2015) and did not improve recovery of fish community composition after bleaching. Protected reefs did support higher species richness but experienced greater biomass declines. Although richness patterns were potentially confounded by high abundances that inflated diversity estimates in no-take areas, large biomass declines highlight how reef protection, which promoted prebleaching reef fish biomass (Graham et al., 2007), did not insure fish communities against habitat collapse. These results imply that the effects of protection depend upon the severity of bleaching, disturbance history and local anthropogenic stressors. For example, by conferring resistance to acute disturbances, large-scale and well-enforced protection of the Great Barrier Reef has shortened recovery times to minor bleaching events by up to ~2.4 years (Mellin et al., 2016), whereas at Indian Ocean reefs where 1998 bleaching was severe and protected areas are small and less effectively enforced, both fished and no-take areas experienced declines in fish richness and abundance after bleaching (Graham et al., 2008).

Irrespective of benthic recovery trajectory or ecosystem protection, postbleaching assemblages were characterized by a speciose and high biomass herbivore group and low representation of planktivore, invertivore and piscivore species. Furthermore, dissimilarity patterns were primarily due to balanced abundance turnover among species rather than an absolute gain or loss of dominant species. Such communities may be considered hybrid states, which contain aspects of pre- and postbleaching configurations but with altered functions (Hobbs et al., 2009). Concepts of such 'no-analog' states have typically been developed to describe highly degraded terrestrial ecosystems (Hobbs et al., 2009; Williams & Jackson, 2007), but are equally relevant for coral reefs where species may have unexpected, differential responses to climate impacts (Graham, Cinner, Norström, & Nyström, 2014). For example, one striking effect of the 1998 bleaching event was to raise herbivore productivity and diversity on both regime-shifted and recovering reefs. Herbivore populations are expected to increase with algal productivity following rapid declines in coral cover (Rogers, Blanchard, & Mumby, 2017) but, in pristine systems, to return to baseline levels once benthic habitat has returned to a coral-dominated state (Gilmour, Smith, Heyward, Baird, & Pratchett, 2013). However, on fished reefs in Seychelles, herbivores remained dominant >10 years after bleaching, with both richness and biomass exceeding prebleaching levels by 2014. Such sustained herbivore productivity may occur due to long-term availability of diverse algal resources but also due to dampening of natural predation levels when upper trophic levels are overexploited and their recovery from bleaching is slow. Furthermore, high herbivore survivorship during the first few years after bleaching may have helped to sustain large herbivore populations over decadal time scales, particularly for long-lived acanthurid and scarid species (Graham et al., 2007). Thus, high herbivore productivity may be characteristic of bleached reefs that are adjacent to human populations, which may help buffer fisheries from declining predatory fish populations by continuing to provide catches of low trophic level species (Robinson et al., 2018).

As low-latitude ecosystems that operate near their thermal limits (Rummer et al., 2014), coral reefs are more likely to reorganize and suffer local extinctions than receive non-native species which have relocated in response to temperature changes. Thus, the diversity patterns documented here suggest that climate-driven compositional changes on coral reefs will be unique, and driven indirectly by changes in physical habitat structure rather than directly by the effects of changes in temperature on species distributions, for example in subtropical coastal (Wernberg et al., 2016) and temperate shelf (Fossheim et al., 2015) ecosystems. Additional disturbances following bleaching may cause further changes to benthic habitat structure which consolidate compositional changes in fish communities. For example, increases in Seychelles' tourist and local populations likely promoted macroalgal growth and persistence by raising nutrient inputs (Graham et al., 2015), while thermal stress in 2010 caused bleaching and mortality of plating corals, though impacts on total coral cover were minimal (N. A. J. Graham, pers. obs.). Such postbleaching disturbances facilitate macroalgal dominance and depress coral recovery, and therefore contribute to the persistence of altered fish assemblages.

The implications for future coral reef ecosystems are stark, given that coral reef fish communities did not return to prebleaching diversity levels over a 16 year period (1998–2014) bounded by two climate-driven mass coral bleaching events (1998, 2016). With over 60% of reefs projected to experience annual bleaching-level thermal stress by ~2050 (van Hooidonk et al., 2013) and bleaching recovery windows only ~6 years by 2016 (Hughes et al., 2018), we conclude that realized and projected increases in the frequency of thermal stress events on coral reefs will cause persistent changes in fish diversity and community structure. Because compositional recovery was not enhanced by small-scale ecosystem protection, our study further indicates that protected areas are insufficient to mitigate global climate change impacts for many coral reefs (Graham et al., 2008; Selig et al., 2012). These changes will alter the functions and ecosystem services historically provided by reef fishes, such as grazing rates (Nash et al., 2016) and the species accessible to fisheries (Robinson et al., 2018), posing an adaptation challenge for management and reef-dependent people.

ACKNOWLEDGEMENTS

This research was supported by the Royal Society (CH160077, UF140691). We thank Seychelles Fishing Authority, Nature Seychelles and Global Vision International for field assistance, and Cameron Freshwater for statistical advice.

AUTHOR CONTRIBUTIONS

NAJG conceived the study. NAJG, SKW and SJ conducted ecological surveys. JPWR performed all statistical analyses and led the manuscript writing, with substantial input from SKW, SJ and NAJG.

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REFERENCES

Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*(2), 124–128. https://doi.org/10.1111/j.1600-0587.2012.00124.x

Baselga, A., & Orme, C. D. L. (2012). betapart : An R package for the study of beta diversity : Betapart package. *Methods in Ecology and Evolution*, *3*(5), 808–812. https://doi.org/10.1111/j.2041-210x.2012.00224.x

Bellwood, D. R., Baird, A. H., Depczynski, M., González-Cabello, A., Hoey, A. S., Lefèvre, C. D., & Tanner, J. K. (2012). Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia*, *170*(2), 567–573. https://doi.org/10.1007/s00442-012-2306-z

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833. https://doi.org/10.1038/nature02691

Berumen, M. L., & Pratchett, M. S. (2006). Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs*, *25*(4), 647–653. https://doi.org/10.1007/s00338-006-0145-2

Bonin, M. C., Almany, G. R., & Jones, G. P. (2011). Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology*, *92*(7), 1503–1512. https://doi.org/10.1890/10-0627.1

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*(4), 325–349. https://doi.org/10.2307/1942268

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T.-J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*(2), 148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Cheal, A. J., Wilson, S. K., Emslie, M. J., Dolman, A. M., & Sweatman, H. (2008). Responses of reef fish communities to coral declines on the Great Barrier Reef. *Marine Ecology Progress Series*, *372*, 211–223. https://doi.org/10.3354/meps07708

Chong-Seng, K. M., Mannering, T. D., Pratchett, M. S., Bellwood, D. R., & Graham, N. A. J. (2012). The influence of coral reef benthic condition on associated fish assemblages. *PLoS ONE*, *7*(8), e42167. https://doi.org/10.1371/journal.pone.0042167

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*, *18*(1), 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Cole, A. J., Pratchett, M. S., & Jones, G. P. (2008). Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries*, *9*(3), 286–307. https://doi.org/10.1111/j.1467-2979.2008.00290.x

D'agata, S., Mouillot, D., Wantiez, L., Friedlander, A. M., Kulbicki, M., & Vigliola, L. (2016). Marine reserves lag behind wilderness in the conservation of key functional roles. *Nature Communications*, *7*, 12000.

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*(6181), 296–299. https://doi.org/10.1126/science.1248484

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., & Dolgov, A. V. (2015). Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, *5*(7), 673–677. https://doi.org/10.1038/nclimate2647

Freshwater, C., Trudel, M., Beacham, T. D., Gauthier, S., Johnson, S. C., Neville, C.-E., & Juanes, F. (2019). Individual variation, population-specific behaviours and stochastic processes shape marine migration phenologies. *Journal of Animal Ecology*, *88*, 67–78. https://doi.org/10.1111/1365-2656.12852

Froese, R., & Pauly, D. (Eds.). (2018). *FishBase*. World Wide Web electronic publication. Retrieved from www.fishbase.org

Fulton, C. J., Depczynski, M., Holmes, T. H., Noble, M. M., Radford, B., Wernberg, T., & Wilson, S. K. (2014). Sea temperature shapes seasonal fluctuations in seaweed biomass within the Ningaloo coral reef ecosystem. *Limnology and Oceanography*, *59*(1), 156–166. https://doi.org/10.4319/lo.2014.59.1.0156

García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., ... Burrows, M. T. (2016). Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, *6*(1), 83–88. https://doi.org/10.1038/nclimate2769

Garpe, K. C., Yahya, S. A. S., Lindahl, U., & Öhman, M. C. (2006). Long-term effects of the 1998 coral bleaching event on reef fish assemblages. *Marine Ecology Progress Series*, *315*, 237–247. https://doi.org/10.3354/meps315237

Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H., & Pratchett, M. S. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science*, *340*(6128), 69–71.

Goreau, T., McClanahan, T., Hayes, R., & Strong, A. (2000). Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology*, *14*(1), 5–15. https://doi.org/10.1046/j.1523-1739.2000.00011.x

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*(4), 379–391.

Graham, N. A. J., Cinner, J. E., Norström, A. V., & Nyström, M. (2014). Coral reefs as novel ecosystems: embracing new futures. *Current Opinion in Environmental Sustainability*, *7*(Supplement C), 9–14. https://doi.org/10.1016/j.cosust.2013.11.023

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*(7537), 94–97. https://doi.org/10.1038/nature14140

Graham, N. A. J., McClanahan, T. R., MacNeil, M. A., Wilson, S. K., Polunin, N. V. C., Jennings, S., ... Sheppard, C. R. C. (2008). Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. *PLoS ONE*, *3*(8), e3039. https://doi.org/10.1371/journal.pone.0003039

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(22), 8425–8429. https://doi.org/10.1073/pnas.0600693103

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Robinson, J., Bijoux, J. P., & Daw, T. M. (2007). Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology*, *21*(5), 1291–1300. https://doi.org/10.1111/j.1523-1739.2007.00754.x

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., ... White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews of the Cambridge Philosophical Society*, *90*(4), 1215–1247. https://doi.org/10.1111/brv.12155

Halford, A. R., & Caley, M. J. (2009). Towards an understanding of resilience in isolated coral reefs. *Global Change Biology*, *15*(12), 3031–3045. https://doi.org/10.1111/j.1365-2486.2009.01972.x

Hempson, T. N., Graham, N. A. J., MacNeil, M. A., Hoey, A. S., & Wilson, S. K. (2018). Ecosystem regime shifts disrupt trophic structure. *Ecological Applications*, *28*(1), 191–200. https://doi.org/10.1002/eap.1639

Heron, S. F., Maynard, J. A., van Hooidonk, R., & Eakin, C. M. (2016). Warming trends and bleaching stress of the world's coral reefs 1985–2012. *Scientific Reports*, *6*, 1985–2012. https://doi.org/10.1038/srep38402

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., … Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, *359*(6371), 80–83. https://doi.org/10.1126/science.aan8048

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(21), 8251–8253. https://doi.org/10.1073/pnas.0401277101

Karkarey, R., Kelkar, N., Lobo, A. S., Alcoverro, T., & Arthur, R. (2014). Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances. *Coral Reefs*, *33*(2), 289–302. https://doi.org/10.1007/s00338-013-1117-y

Magurran, A. E., Dornelas, M., Moyes, F., Gotelli, N. J., & McGill, B. (2015). Rapid biotic homogenization of marine fish assemblages. *Nature Communications*, *6*, 8405. https://doi.org/10.1038/ncomms9405

McElreath, R. (2017). Rethinking: Statistical rethinking book package. *R Package Version*, *1*.

Mellin, C., MacNeil, M. A., Cheal, A. J., Emslie, M. J., & Caley, M. J. (2016). Marine protected areas increase resilience among coral reef communities. *Ecology Letters*, *19*(6), 629–637.

Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2011). Habitat biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, *92*(12), 2285–2298. https://doi.org/10.1890/11-0037.1

Mouillot, D., Villeger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., … Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(38), 13757–13762. https://doi.org/10.1073/pnas.1317625111

Munday, P. L., & Jones, G. P. (1998). The ecological implications of small body size among coral-reef fishes. *Ocean & Coastal Management*, *36*, 373–411.

Nash, K. L., Graham, N. A. J., Jennings, S., Wilson, S. K., & Bellwood, D. R. (2016). Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. *Journal of Applied Ecology*, *53*(3), 646–655. https://doi.org/10.1111/1365-2664.12430

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2017). vegan: Community Ecology Package. *R Package*, *Version 2.4-4*.

Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., … Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332). https://doi.org/10.1126/science.aai9214

Polunin, N. V. C., & Roberts, C. M. (1993). Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series*, *100*, 167–167. https://doi.org/10.3354/meps100167

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*, *3*(3), 424–452. https://doi.org/10.3390/d3030424

R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Richardson, L. E., Graham, N. A. J., & Hoey, A. S. (2017). Cross-scale habitat structure driven by coral species composition on tropical reefs. *Scientific Reports*, *7*(1), 7557. https://doi.org/10.1038/s41598-017-08109-4

Richardson, L. E., Graham, N. A. J., Pratchett, M. S., Eurich, J. G., & Hoey, A. S. (2018). Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology*, *24*(7), 3117–3129. https://doi.org/10.1111/gcb.14119

Robinson, J. P. W., Wilson, S. K., Robinson, J., Gerry, C., Lucas, J., Assan, C., … Graham, N. A. J. (2018). Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology & Evolution*. https://doi.org/10.1038/s41559-018-0715-z

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2017). Fisheries productivity under progressive coral reef degradation. *Journal of Applied Ecology*, *55*(3), 1041–1049. https://doi.org/10.1111/1365-2664.13051

Rummer, J. L., Couturier, C. S., Stecyk, J. A. W., Gardiner, N. M., Kinch, J. P., Nilsson, G. E., & Munday, P. L. (2014). Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Global Change Biology*, *20*(4), 1055–1066. https://doi.org/10.1111/gcb.12455

Russ, G. R., Questel, S.-L.-A., Rizzari, J. R., & Alcala, A. C. (2015). The parrotfish–coral relationship: Refuting the ubiquity of a prevailing paradigm. *Marine Biology*, *162*(10), 2029–2045. https://doi.org/10.1007/s00227-015-2728-3

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

Selig, E. R., Casey, K. S., & Bruno, J. F. (2012). Temperature-driven coral decline: The role of marine protected areas. *Global Change Biology*, *18*, 1561–1750. https://doi.org/10.1111/j.1365-2486.2012.02658.x

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. (2017). Predicting life history parameters for all fishes worldwide. *Ecological Applications*, *27*(8), 2262–2276. https://doi.org/10.1002/eap.1606

van Hooidonk, R., Maynard, J. A., & Planes, S. (2013). Temporary refugia for coral reefs in a warming world. *Nature Climate Change*, *3*, 508–511. https://doi.org/10.1038/nclimate1829

Wernberg, T., Bennett, S., Babcock, R. C., de Bettignies, T., Cure, K., Depczynski, M., … Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, *353*(6295), 169–172. https://doi.org/10.1126/science.aad8745

Wernberg, T., Smale, D. A., Tuya, F., Thomsen, M. S., Langlois, T. J., de Bettignies, T., … Rousseaux, C. S. (2012). An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change*, *3*, 78–82. https://doi.org/10.1038/nclimate1627

Williams, J. W., & Jackson, S. T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment*, *5*(9), 475–482. https://doi.org/10.1890/070037

Williams, I. D., White, D. J., Sparks, R. T., Lino, K. C., Zamzow, J. P., Kelly, E. L. A., & Ramey, H. L. (2016). Responses of herbivorous fishes and benthos to 6 years of protection at the Kahekili Herbivore fisheries management area, Maui. *PloS One*, *11*(7), e0159100.

Wilson, S. K., Depcyznski, M., Fisher, R., Holmes, T. H., Noble, M. M., Radford, B. T., … Fulton, C. J. (2018). Climatic forcing and larval dispersal capabilities shape the replenishment of fishes and their habitat-forming biota on a tropical coral reef. *Ecology and Evolution*, *8*(3), 1918–1928. https://doi.org/10.1002/ece3.3779

Wilson, S. K., Dolman, A. M., Cheal, A. J., Emslie, M. J., Pratchett, M. S., & Sweatman, H. P. A. (2009). Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs*, *28*(1), 3–14. https://doi.org/10.1007/s00338-008-0431-2

Wilson, S. K., Graham, N. A. J., Fisher, R., Robinson, J., Nash, K., Chong-Seng, K., … Quatre, R. (2012). Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. *Conservation Biology: The Journal of the Society for Conservation Biology*, *26*(6), 995–1004. https://doi.org/10.1111/j.1523-1739.2012.01926.x

Wilson, S. K., Graham, N. A. J., & Polunin, N. V. C. (2007). Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine Biology*, *151*(3), 1069–1076. https://doi.org/10.1007/s00227-006-0538-3

Wilson, S. K., Graham, N. A. J., Pratchett, M. S., Jones, G. P., & Polunin, N. V. C. (2006). Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? *Global Change Biology*, *12*(11), 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wilson, S. K., Robinson, J. P. W., Chong-Seng, K., Robinson, J., & Graham, N. A. J. (2019). Boom and bust of keystone structure on coral reefs. *Coral Reefs*. https://doi.org/10.1007/s00338-019-01818-4

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Robinson JPW, Wilson SK, Jennings S, Graham NAJ. Thermal stress induces persistently altered coral reef fish assemblages. *Glob Change Biol*. 2019;00:1–12. https://doi.org/10.1111/gcb.14704