Ecosystem Regime Shifts disrupt Trophic Structure

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Summary

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

Key words: coral reef fish; coral bleaching; functional group; habitat degradation; mesopredator; trophic level; trophic pyramid; coral reef ecology

INTRODUCTION

Regime shifts have been documented in a wide variety of ecosystems, from shallow lakes to deserts, savannas and the open ocean (van de Koppel et al. 1997, Watson and Estes 2011, Kosten et al. 2012, Ecology et al. 2016) as a result of gradual change over time, or a shock to the system that pushes it beyond a tipping point into an alternate state (Scheffer et al. 2001). Drivers often work together, whereby chronic stressors gradually erode ecosystem resilience, making the system more vulnerable to a regime shift following an acute disturbance event (Hughes et al. 2013). Regime shifts are characterised by dramatic changes in the structure and function of the ecosystem (Scheffer et al. 2001, Folke et al. 2004), with potentially broad-reaching consequent effects. Understanding the implications of these shifts and identifying early warning indicators have been the primary foci of much of the research into these ecological dynamics (e.g. Scheffer et al. 2009, Carpenter et al. 2011, Graham et al. 2015, Hicks et al. 2016).

In coral reef ecosystems, much of the initial research on ecosystem regime-shifts focused on over-fishing of herbivores as a primary driver of change (Hughes 1994, Jackson et al. 2001, Bellwood et al. 2004, Hughes et al. 2007). Subsequently, with increasing effects of global climate change, mass bleaching events have become a major driver of extensive habitat degradation on coral reefs (Hoegh-Guldberg et al. 2007). Following bleaching, or other large scale coral mortality, reefs can either recover and move towards a pre-disturbance state, or undergo benthic regime shifts from coral dominance to dominance by other benthic organisms, most commonly fleshy macroalgae (Nyström et al. 2008). This macroalgal state often represents an alternative stable state, with strong reinforcing feedback mechanisms, from which a return to coral dominance is challenging (Mumby and Steneck 2008). Our understanding of what factors contribute to driving these benthic shifts is improving (Mumby et al. 2007, Graham et al. 2015), but we lack an understanding of their effects on the broader ecosystem.

Coral reef fish communities are heavily reliant on the reef benthos for food and shelter (Pratchett et al. 2008), with changes in the composition and structure of coral habitat directly affecting reef fish assemblages (e.g. Friedlander and Parrish 1998, Jones et al. 2004). Dramatic regime shifts in dominant benthic cover in a coral reef ecosystem are therefore anticipated to have substantial effects on the composition of the associated reef fish community. While we have a rudimentary understanding of how a regime shift is likely to affect the functional diversity of a coral reef fish community (Graham et al. 2015), we know little about the effect on community trophic structure or functional composition. Trophic pyramids provide a visually intuitive means of examining and comparing the structure of food webs (Lindeman 1942) and informing on the likely transfer of energy among trophic levels (Trebilco et al. 2013). This simple, yet powerful tool has the potential to be used for easy identification of disruption of trophic structure and function due to disturbance (Graham et al. 2016). With the expectation that bleaching events will become more frequent as atmospheric carbon levels increase, as demonstrated by the powerful 2016 El Nino event, it is becoming increasingly important to improve our understanding of how coral reef fish communities restructure following climate-driven regime shifts.

Coral reefs provide important resources and services for millions of people living in tropical latitudes around the globe, with reef fish constituting the primary source of protein, and a range of other ecosystem services, for large coastal populations (Hicks and Cinner 2014). With many coral reef fisheries preferentially harvesting large piscivorous and herbivorous fishes, at upper and lower trophic levels, the implications of regime shifts for trophic pyramids and associated biomass storage, productivity and trophic pathways, is critical information. It has only recently become possible to investigate these long-term ecosystem changes with sufficient time post mass bleaching.

In this study, a well-studied system, where climate-driven bleaching led to a series of both regime-shifted and recovering reefs (Graham et al. 2015), was used to investigate the effects of benthic regime shifts on the trophic structure of the associated reef fish community. Specifically, we assessed (i) the dissimilarity in the composition of the reef fish community between recovering and regime-shifted reefs with time since disturbance, (ii) how the trophic pyramid structure of biomass distribution in fish communities changes between reef states over time, and finally (iii) how the functional composition of the reef fish community is altered.

METHODS

Study Site

Data collection for this study was carried out as part of a long-term periodic coral reef monitoring programme in the Seychelles inner island group. These reefs were some of the most severely impacted by the 1998 mass bleaching event, with live coral loss exceeding 90 % at many sites (Goreau et al. 2000, Lindén et al. 2002). Monitoring data collected both before

(1994) and after the bleaching event (2005, 2014) has identified two distinct ecosystem trajectories (Graham et al. 2015). Of the 21 monitoring sites, 12 have steadily regained live coral cover, and returned to an almost pre-bleaching state, while the other 9 sites have moved into a regime-shifted state of algal dominance (Graham et al. 2006, 2015, Wilson et al. 2012). To investigate the question of how the trophic structure of the associated reef fish community differs between these contrasting reef states, the ten most extreme sites in terms of live hard coral cover averaged up to 2014 were selected; the five highest from recovering sites, and the five lowest from regime-shifted sites.

Fish and benthic surveys

Twenty-one reefs across the Inner Seychelles island group were surveyed in 1994 prior to the 1998 mass bleaching event, and again after the bleaching in 2005 and 2014, as part of an ongoing monitoring programme. Identical methods were used to survey the reef fish and benthic community at each site in all years (Graham et al. 2015). At each reef, the fish community was quantified using 8 to 16 replicate 7 m radius point counts, haphazardly located along the reef slope at depths of 2.3 – 12.2 m (mean ± standard deviation; 6.34 ± 2.06 m), separated by a minimum of 15 m. At each point, the abundance of 134 species of diurnal, non-cryptic, reef-associated fish was recorded, as well as the total length of each individual. Length estimates were converted to biomass using published length-weight relationships for each species (Froese and Pauly 2015). Each species was assigned to a functional group based on their diet and feeding behaviour (Froese and Pauly 2015); browser, grazer/detritivore, scraper/excavator, planktivore, corallivore, invertivore, invertivore/piscivore, piscivore (see Appendix S1: Table S1). Using estimates published in Fish Base (Froese and Pauly 2015), species were also assigned to one of five trophic pyramid positions (TP); TP1: 2 - 2.5; TP2: 2.5 – 3.0; TP3: 3.0 – 3.5; TP4: 3.5 – 4; TP5: 4 – 4.5 (Appendix S1: Table S1).

Benthic habitat composition was estimated within the area of each point count as the percent cover of six cover types (simple and complex live hard coral, soft coral, macroalgae, sand and rock). Simple corals were those hard coral taxa with massive or encrusting growth forms, while complex corals were those with branching or digitate structure. Structural complexity was visually estimated with a six point scale, shown to approximate other measures of complexity well and to be useful in predicting fish abundance and biomass (Wilson et al. 2007, Darling et al. 2017).

Statistical analyses

The benthic habitat composition between reef states (recovering versus regime-shifted) in each year (1994, 2005, 2014) was compared using a principal coordinate analysis (PCO), based on a Bray-Curtis similarity matrix. Data were square root transformed to reduce the influence of the most dominant cover types. Eigenvectors of all benthic categories were overlaid to examine their contribution to the separation between reef states.

To investigate how the fish community changed over the study period, a series of Similarity Percentages (SIMPER) analyses were run in PRIMER v.6 (Clarke and Warwick 2001) to compare the average dissimilarity of the fish community between recovering and regime-shifted reefs in 1994, 2005 and 2014, both in terms of species abundance (fish.500m^{-2}) and biomass (kg.ha^{-1}), and functional group composition based on abundance (fish.500m^{-2}). The results of the functional group analysis were then weighted by the overall dissimilarity between reef states (recovering vs regime-shifted) for each year, to allow for comparison of the magnitude of difference in fish community functional structure among years.

Both the absolute biomass (kg. ha^{-1}) and relative biomass (%) of reef fish within each of the five trophic positions was calculated for each reef state (recovering vs regime-shifted) and each year (1994, 2005, 2014), and trophic pyramids constructed to explore the change in trophic structure within the fish community following bleaching disturbance. Differences in the trophic structure between recovering and regime-shifted reefs at each time point were tested using multinomial regression of the TP categories as a response, with year and regime state as fixed effects. The fish species contributing the most to dissimilarity in the fish community composition within each state (recovering vs regime-shifted), and trophic level (TP1 - TP5), before the bleaching (1994) and post-bleaching (2014) were identified using SIMPER analyses on Bray-Curtis similarity matrices of square root transformed species data.

RESULTS

Benthic habitat

There was a distinct shift in the benthic composition of regime shifted reefs following disturbance in relation to recovering reefs (Fig.1). Prior to the 1998 mass bleaching event, all reefs were characterised by high structural complexity and live coral cover, falling to the right of the first PCO axis, which accounts for 48.4 % of the total variation among sites. Following the disturbance (2005, 2014), there is a strong separation between reefs that recover from the bleaching and those moving into a regime-shifted state. In 2005, two of the regime-shift reefs still retained a degree of structural complexity, but by 2014, all these reefs were most strongly characterised by high levels of macroalgal cover and low coral cover and structural complexity, falling to left of PCO1, while recovering reefs returned to the initial pre-disturbance state.

Fish community

This same pattern of increasing divergence between recovering and regime-shift reefs is evident in the fish community, with SIMPER analyses showing increasing average dissimilarity in community composition in terms of functional group representation, fish biomass, and abundance, between reef states following the bleaching disturbance (Table 1). The trophic structure of the fish community also reflects this divergence between reef states in terms of the distribution of relative biomass among trophic levels (Fig. 2). In 1994, prior to the bleaching event, trophic structure of fishes was similar across all reefs surveyed, in terms of relative or absolute biomass (Fig.2, Appendix S1: Fig.S3). In 2005, 7 years after mass bleaching, regime-shift reefs showed a large increase in relative and absolute biomass within the base trophic level (TP1), which includes herbivorous functional groups (Appendix S1: Fig.S2; browsers, grazers and detritivores, scrapers and excavators), and a decrease in the biomass of all higher trophic levels. Recovering reefs exhibited a similar pattern of an increase in the relative and absolute biomass of TP1, and a reduction in higher trophic levels, but the changes were less pronounced (Table 2). By 2014, the difference between the trophic structure of recovering and regime-shifted reefs had become clearly apparent. Recovering reefs had a triangular trophic pyramid structure, while regime-shifted reef pyramids had a concave shape, with biomass dominated by herbivorous species in TP1, with low biomass in mid trophic levels (TP2 - TP3) and comparatively high biomass at TP4. The increase in TP4 biomass on regime-shifted reefs was primarily due to more large-bodied invertivores, particularly *Lethrinus nebulosus* and *Plectorhinchus schotaf* (Appendix S1: Table S2).

Dissimilarity (Bray-Curtis) in fish species composition within each trophic level pre- (1994) versus post-bleaching (2005 and 2014), was higher overall for regime-shifted reefs than recovering reefs (Table 3). After the initial shift in community composition from 1994 to 2005, by 2014 recovering reefs were more similar to their pre-disturbance composition than regime shifted reefs, with reduced variation in dissimilarity measures in all trophic levels except TP2. The increased dissimilarity in this trophic level was due to an increase in the generalist species *Pomacentrus trilineatus*, and a decrease in two rabbit fish species, *Siganus puelloides* and *Siganus stellatus* (Appendix S1: Table S1). On regime-shifted reefs, mean dissimilarity and the degree of variation in community composition tends to increase for all trophic levels, except for TP2, which is characterized by a consistently high abundance of the excavating parrotfish species, *Chlorurus sordidus*.

Associated with this change within the reef fish community has been a shift in the balance of functional groups in terms of abundance (Fig.4). Pre-disturbance (1994) fish communities on recovering and regime shifted reefs had an overall dissimilarity (Bray-Curtis) of only 13.3% between reefs that would follow recovering and regime-shifted trajectories post-bleaching. In 2005, seven years post disturbance, dissimilarity in functional group composition had risen to 25.61% between reef states. An increase in herbivorous groups on regime shifted reefs; browsers (% dissimilarity ± standard deviation; 5.87 ± 0.29 %), and grazers and detritivores (4.60 ± 0.36) accounted for the much of this separation. By 2014, the dissimilarity had further increased to 34.2%, with browsers and grazer/detritivores dominating on regime shifted reefs, while recovering reefs have a wide variety of functional groups from higher trophic positions, including corallivores, planktivores and piscivores.

DISCUSSION

Regime shifts are increasingly common in a wide variety of ecosystems, often resulting in extensive and dramatic ecological change. In Seychelles, the long-term trajectories of decline and recovery on inner island coral reefs, following the 1998 mass bleaching event, illustrate the major ecological implications of such a disturbance. Trophic structure of the fish communities on recovering reefs (high coral cover and structural complexity) and regime shifted reefs (algae-dominated with low complexity), became increasingly dissimilar over time, with trophic pyramids of biomass regaining a stable bottom-heavy structure on recovering reefs, while regime-shifted reefs transitioned to a concave structure.

This change in trophic structure resulting from the redistribution of biomass between trophic levels, can disrupt ecological processes and the flow of energy in the food web (Trebilco et al. 2013, Graham et al. 2017). Prior to the bleaching event, in 1994, pyramids of relative biomass on all surveyed reefs were bottom heavy, with substantial biomass in the mid to upper trophic levels and the greatest amount of biomass located in the base trophic level, as expected based on energetic theory (Trebilco et al. 2013, Hatton et al. 2015). Following the bleaching, relative biomass in the base trophic level (trophic position 2-2.5) increased substantially in both reef states, likely due to the greater food availability for herbivorous species with the initial increase in algal cover following the depletion of coral cover from bleaching (Adam et al. 2011, Gilmour et al. 2013). The fact that this effect was larger in terms of both relative and absolute biomass on regime-shift reefs alludes to the more severe shift in trophic structure that had emerged on these reefs by 2014. That these reefs have failed to recover, 16 years after the bleaching event also suggest that increased abundance of herbivores alone is insufficient for recovery, which is dependent on the composition of the herbivore community and a combination of other factors including eutrophication, recruitment of corals, depth and structural complexity (Graham et al. 2015).

Sixteen years post-bleaching, recovering reefs had regained a triangular biomass pyramid structure, representing an energetically stable food web (Hatton et al. 2015). This structure indicates that the fish community had regained biomass in the mid-trophic levels (trophic position 2.5-3 and 3-3.5), which includes various specialised species, such as corallivores, which are extremely sensitive to loss of coral habitat (Wilson et al. 2006, Hoey et al. 2016). In contrast, the concave shape of relative biomass pyramids on regime-shifted reefs shows a decrease in biomass in these mid-trophic levels, likely due to the lack of habitat available for species highly dependent on coral for food and shelter (Pratchett et al. 2008, Wilson et al. 2010a). Biomass on these reefs was dominated by herbivorous species at the base of the pyramid, supported by a proliferation of algal resources. There was also an accumulation of biomass in the upper trophic levels, particularly trophic position 3.5 – 4, largely attributable to an increase in the abundance of *Lethrinus nebulosus* and *Plectorhinchus schotaf*. This increase may be related to the fact that both species are large-bodied, generalist invertebrate feeders (Smith et al. 2003), and particularly in the case of *L. nebulosus*, known to utilise a wide variety of habitat types, often scavenging over degraded, rubble or sand substrates (Carpenter and Allen 1989, Farmer and Wilson 2011). Expansion of macroalgal habitat also provides increased nursery area for lethrinid species, which may be a strong driver of increased local abundance (Wilson et al. *in press*). Another possibility is that they may benefit from decreased competition from other mesopredators with narrower dietary or habitat niches (e.g. *Lutjanus kasmira*). The contrasting decline in top consumers with a more piscivorous diet (e.g. *Lutjanus bohar, Cephalopholis argus, C. miniata*) was likely due to the decline in prey fish species in the mid trophic levels. This suggests a different mechanism of concave trophic pyramid shape to that described for high biomass reefs (Graham et al. 2017). At high reef fish biomass, biomass accumulated in upper and lower trophic levels, likely enabling a more direct pathway between primary production and large piscivores (Graham et al. 2017). Conversely, on regime shifted reefs in Seychelles, the accumulation of upper trophic level fish is driven by an alternative energy pathway, with abundant mobile invertebrate species on degraded reefs supporting populations of upper trophic level invertivores.

While there may appear to be an abundance of available prey biomass in the base of the pyramid, unlike in temperate marine ecosystems (Jennings and Mackinson 2003), on coral reefs, herbivore biomass is largely made up of large bodied species, such as parrotfish, surgeonfish, and rabbitfish. Many adults of these fish are too large to be suitable prey for coral reef mesopredators which are limited by their gape size (Kingsford 1992, St John 1999). This likely explains the observed decreases in the abundance of predators that prey on small fish (e.g. *Parupeneus cyclostomus, Oxycheilinus digramma* and *Epibulus insidiator*; Froese and Pauly 2015) on regime-shifted reefs.

Examination of the species diversity of the reef fish communities on recovering and regime shift reefs confirms the trend of increasing dissimilarity between reef states over time. On recovering reefs, the return to a stable, coral-dominated state in the reef benthos is mirrored in the fish community, which shows an overall pattern of decreasing mean dissimilarity and variation, moving towards a pre-disturbance state. The deviation of trophic positions 2.5 - 3 from this trend, due to the increased abundance of the generalist, *Pomacentrus trilineatus*, is likely due to its association with both coral and rocky reef habitat (Allen 1991), giving it a competitive advantage over more specialised species when live coral cover habitat declined following the bleaching. The contrasting trend on regime-shifted reefs, whereby mean dissimilarity and variation increases with time since bleaching, indicates that the associated fish community is consistently moving further from its pre-disturbance state. On these reefs, it is again trophic positions 2.5 – 3 that deviate from the overall trend, with a relatively stable degree of dissimilarity attributable to a consistently high abundance of *Chlorurus sordidus*, a widespread excavating parrotfish species, that uses a broad range of habitat types (Hoey and Bellwood 2008).

The fact that the fish communities on recovering reefs have not yet reverted to their pre-disturbance state 16 years post-bleaching, despite the recovery of high coral cover, suggests that there may be a shift in the composition of the coral assemblages (Wilson et al. 2012). Changes in the coral community can lead to changes in composition of the closely associated reef fish communities, which may regain pre-disturbance abundances, but have altered species composition (Berumen and Pratchett 2006). Shifts in the composition of the reef fish community may represent a change in the prey base available to piscivorous mesopredators, requiring them to adapt their diets and alter their trophic niche (Hempson et al. *in press*), with potential sublethal effects (Hempson et al. *in review*)

Increasing divergence in the functional composition of the reef fish communities between states implies a disruption of ecological processes on regime-shifted reefs. The single strongest characteristic of this change is the increase in herbivorous species on these reefs, a pattern which has been observed on degraded algal reefs worldwide (e.g. Adam et al. 2011, Gilmour et al. 2013). While the proliferation of algal resources benefits many herbivorous species, both in terms of food availability (Rasher et al. 2013), and providing important nursery habitat for numerous reef species (Wilson et al. 2010b, Evans et al. 2014), the loss of coral cover transforms diverse reef habitat into a comparatively uniform landscape, unsuitable for the wide diversity of mid-trophic level species normally supported on a healthy reef (Chong-Seng et al. 2012, Nash et al. 2013). In 2005, the dissimilarity in mid-level trophic positions (2.5 – 3.5) is minimal. This may be because regime-shifted reefs still retained some degree of structural complexity, providing habitat for more adaptable mid-trophic level species, such as invertivores in trophic positions 3 – 3.5 (e.g. *Chaetodon guttatissimus*, *Chaetodon kleinii*). Also, at this stage, live coral cover on recovering reefs was still returning, so specialist species such as obligate corallivores in trophic position 3 – 3.5 (e.g. *Chaetodon trifascialis*) would still have been marginalised. By 2014, the dissimilarity between reef states in the mid-trophic levels had become clearly apparent, as habitat complexity declined on regime shifted reefs and recovering reefs regained increased live coral cover and complexity, resulting in a divergence in the fish species supported in trophic positions 2.5 - 3.5

Changes in the lower trophic levels carry important consequences for mesopredators in the upper trophic levels of the reef fish community. In 2005, there was a higher abundance of generalist mesopredators (e.g. *Parupeneus cyclostomus, Aethaloperca rogaa*) that fed on both invertebrates and fish on regime-shifted than recovering reefs, while exclusively piscivorous species characterised recovering reefs (e.g. *Cephalopholis argus*, *Cephalopholis miniata, Epinephelus merra*). However, by 2014, even the generalist mesopredators were more abundant on recovering reefs. This provides strong evidence that the high abundance of herbivorous species on regime shifted reefs were not a suitable prey source for mesopredators. Predation in the coral reef food web is therefore disrupted by the shift of the coral reef fish community associated with a benthic regime-shift.

The disruption of trophic structure within the coral reef fish community has long-term ecological, social and economic implications for the reefs and the people that rely on them. This study provides important insight into how regime shifts are likely to affect this structure, that can support better management of commercial, recreational and subsistence coral reef fisheries. For example, placing greater fisheries restrictions on piscivorous species, than those with more generalist invertebrate diets could help to sustain predatory guilds in post disturbance systems. As climate-driven disturbance events and ecosystem regime shifts become increasingly common, it is essential that we continue to improve our understanding of the impacts on trophic structure to inform decisions that enhance ecological resilience, food security and economic sustainability.

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DATA ACCESSIBILITY

Supporting data can be accessed in the following external repositories:

- Coral reef benthic and fish surveys in the Inner Seychelles

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

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FIGURE & TABLES

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

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

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

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

TABLE 3. Mean percentage dissimilarity (± standard error; SE) in the fish community composition in each trophic level on recovering and regime-shifted reefs, between 1994 (pre-bleaching), and 2005 and 2014 (post-bleaching), calculated from SIMPER analyses of species abundance, showing results of Welch two sample t-tests for difference in mean dissimilarity between reef states.

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

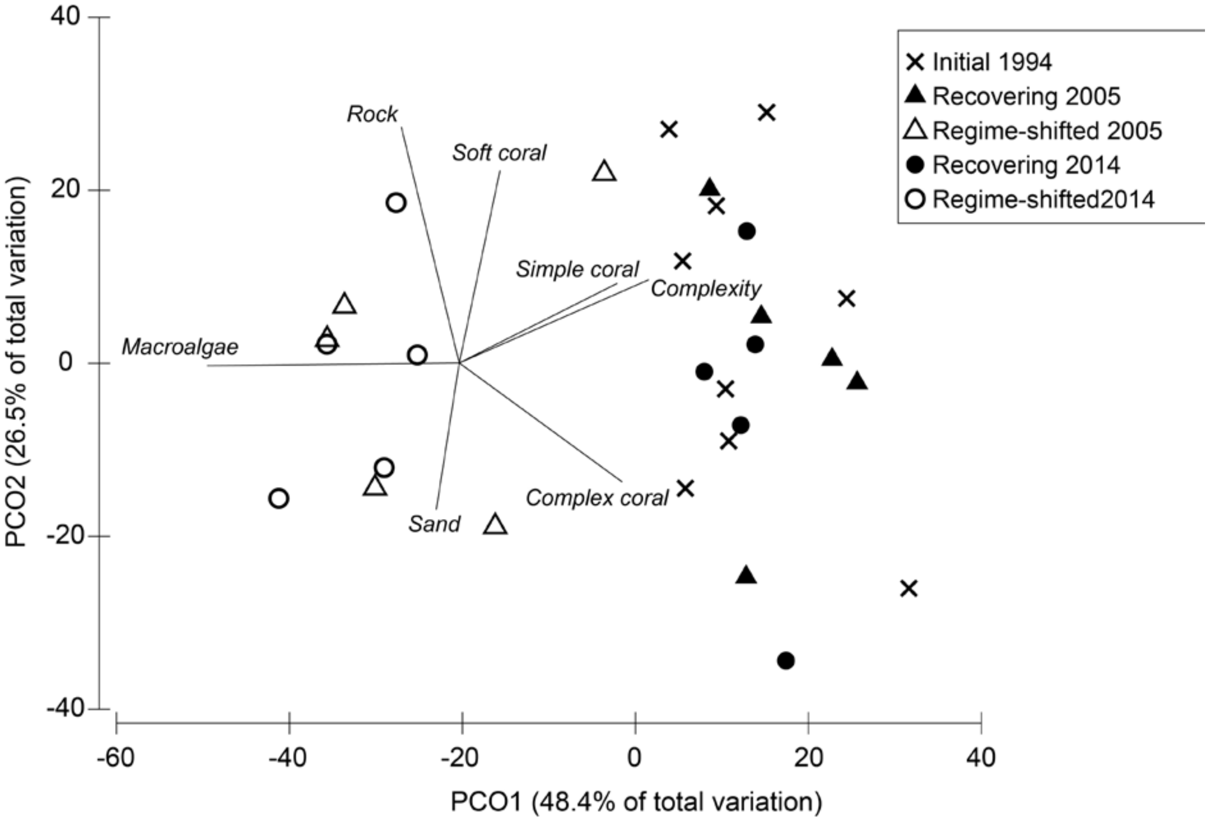

FIG. 1. Principal coordinates analysis of the composition of benthic cover of ten reefs surveyed in the Seychelles inner island group based on Bray-Curtis similarity (data square-root transformed). Crosses represent all reef sites surveyed in 1994, prior to the bleaching 1998 mass bleaching event. Black symbols represent those reefs that were surveyed in 2005 (triangles) and 2014 (circles) and considered to be recovering to a pre-disturbance state (n = 5), and open symbols represent those reefs that in 2005 (triangles) 2014 (circles) had moved into a regime-shifted, algae-dominated state (n = 5).

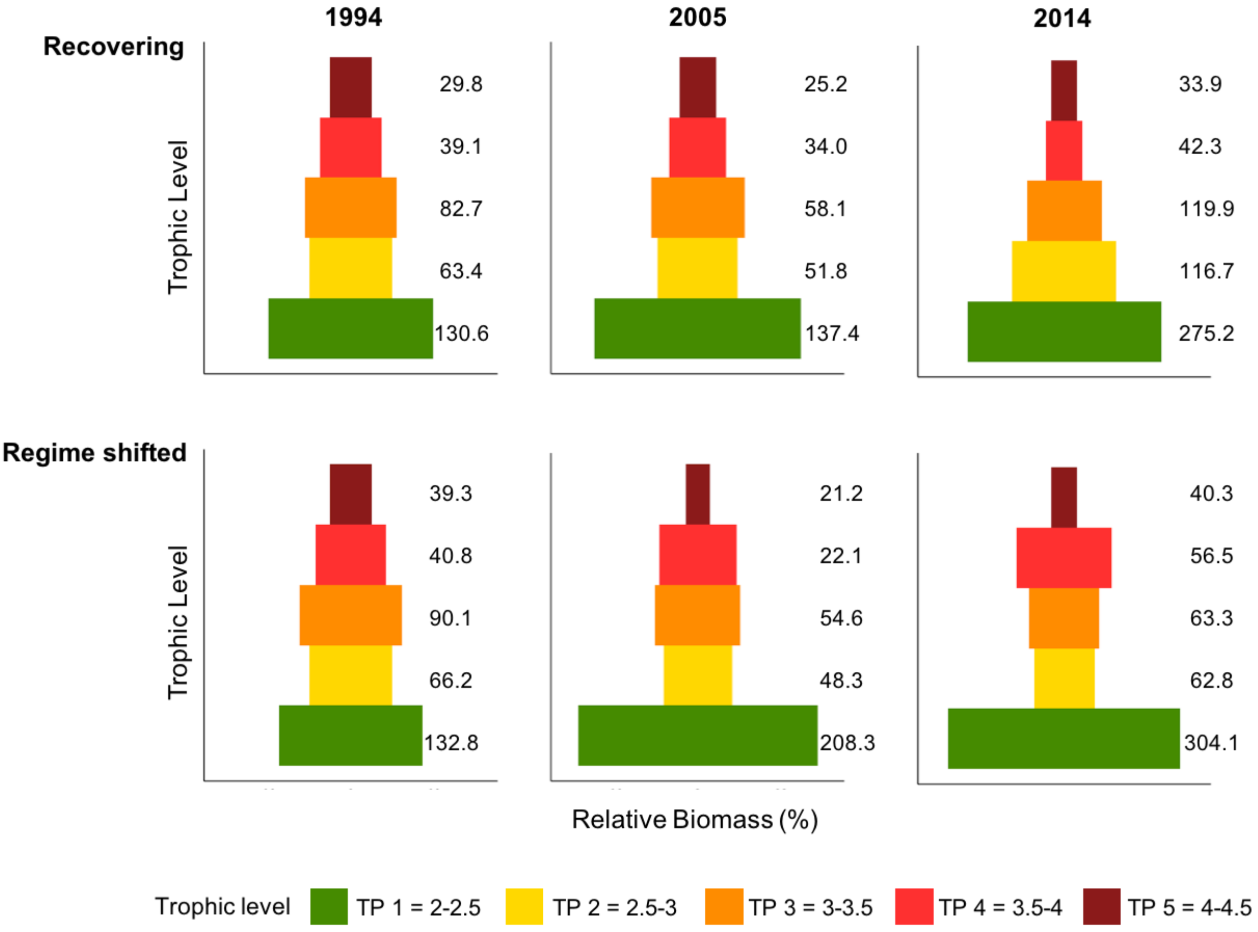

FIG. 2. Trophic pyramids showing the distribution of relative biomass (%) between five trophic positions in the reef fish communities on recovering (n = 5) and regime-shifted (n = 5) reefs in the Seychelles inner island group, both before the 1998 mass bleaching (1994) and after it (2005, 2014). Numbers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

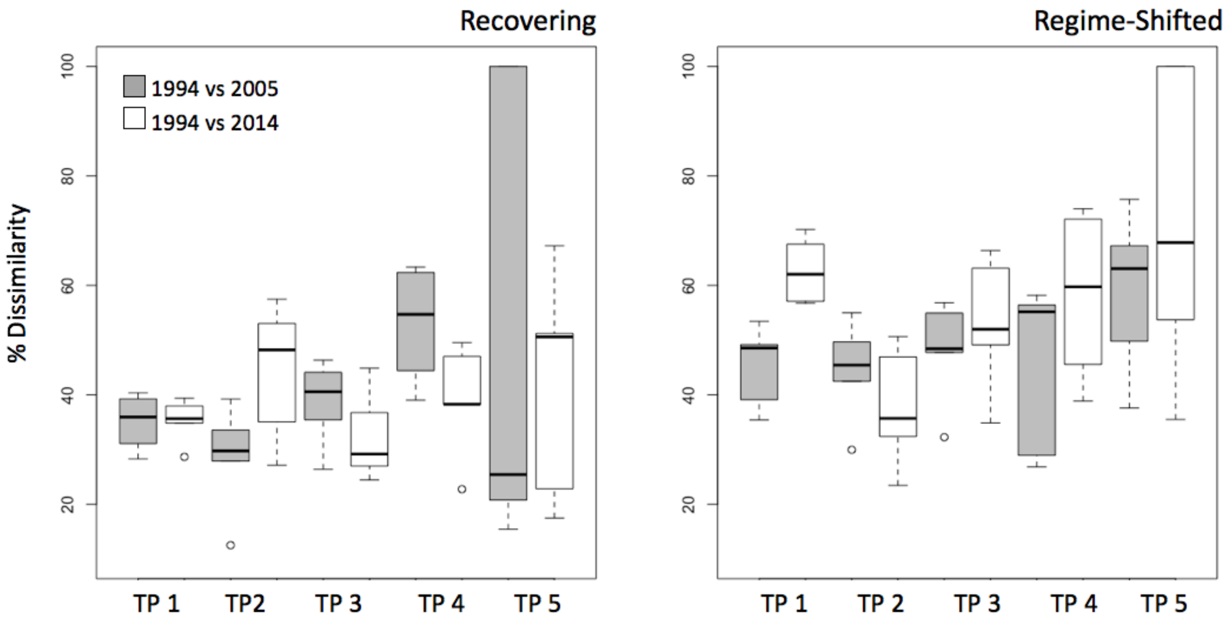

FIG. 3. Percentage dissimilarity (SIMPER analysis) in fish community species composition within reef states and trophic positions between pre-bleaching reefs (1994), and post-bleaching reefs in 2005 (grey bars), and in 2014 (white bars). Data were square root transformed and dissimilarity measures calculated using a Bray-Curtis resemblance matrix. Dark horizontal bars indicate the medians of the data, box height shows the interquartile range, whiskers span minimum and maximum values, with open circles indicating outliers.

state.

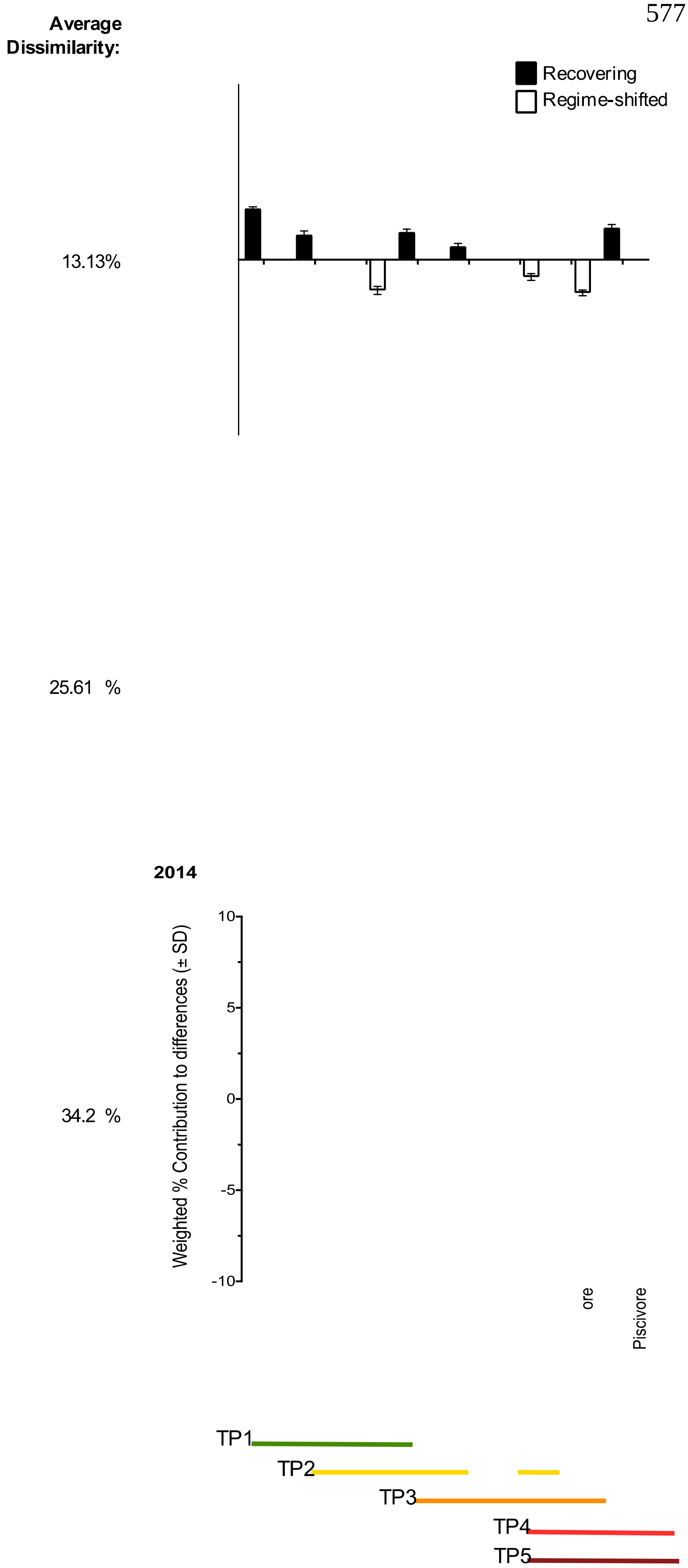

FIG. 4. Differences in the fish community composition between regime-shifted (white) and recovering sites (black). The mean (± standard deviation; SD) percentage contribution of fish functional groups to the difference between reef states in Seychelles in 1994, 2005 and 2014, based on the percentage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