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Ecosystem Regime Shifts Disrupt Trophic Structure

RUNNING HEAD: Regime shifts disrupt trophic structure

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Abstract

Regime shifts between alternative stable ecosystem states are becoming commonplace due to the combined effects of local stressors and global climate change. Alternative states are characterised as substantially different in form and function to pre-disturbance states, disrupting the delivery of ecosystem services and functions. On coral reefs, regime shifts are typically characterised by a change in the benthic composition from coral- to macroalgal-dominance. Such fundamental shifts in the benthos are anticipated to impact associated fish communities that are reliant on the reef for food and shelter, yet there is limited understanding of how regime shifts propagate through the fish community over time, relative to initial or recovery conditions. 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 alternative reef ecosystem states (regime-shifted vs recovering) with time since disturbance. Regime-shifted reefs developed a concave trophic 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 moved towards a bottom-heavy pyramid shape, with a wide range of feeding groups (e.g. planktivores, corallivores, omnivores) represented at mid trophic levels. Given the importance of coral reef fishes in maintaining the ecological function of coral reef ecosystems and their associated 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 are large-scale transitions from one ecosystem state to another, characterised by changes in composition and function of ecological communities (Scheffer et al. 2001, Folke et al. 2004, Daskalov et al. 2007, Lindegren et al. 2012). Drivers such as rising temperatures, pollution or overharvesting, can act together as chronic stressors steadily eroding ecosystem resilience. Regime shifts can result from gradual increases in these chronic drivers over time, or in concert with a pulse disturbance event that pushes the system beyond a tipping point (Scheffer et al. 2001, Hughes et al. 2013). Regime shifts have been documented in a wide variety of ecosystems, from shallow lakes to deserts, savannahs, and the open ocean (van de Koppel et al. 1997, Watson and Estes 2011, Kosten et al. 2012, Staver et al. 2016). Such shifts can severely disrupt the provision of ecosystem services (Scheffer et al. 2001, Millenium Ecosystem Assessment 2005), yet it is often difficult to detect when a system is approaching a critical threshold (Scheffer et al. 2009). Identifying early warning indicators that signal a system may be in danger of shifting to an alternative state has thus been a primary focus of research into regime shifts (e.g. Scheffer et al. 2009, Carpenter et al. 2011, Graham et al. 2015, Hicks et al. 2016), with the hope that drivers can be reduced in time to maintain the current ecosystem state (Hughes et al. 2013).

In coral reef ecosystems, the first evidence of ecosystem regime shifts came from the Caribbean (Hughes 1994, Jackson et al. 2001). Subsequently, increasing local pressures such as fishing, coupled with global climate change, means reef systems elsewhere in the tropics are also at risk. For example, mass bleaching events have become a major driver of reductions in live coral cover and associated structure on coral reefs world-wide (Hoegh-Guldberg et al. 2007). Following large scale coral mortality, reefs can either recover back to coral dominance, or undergo a regime shift to another ecosystem state, for example fleshy macroalgal dominance (Nyström et al. 2008). This macroalgal state often represents an alternative stable state, with strong reinforcing feedbacks that make a return to coral dominance challenging (Mumby and Steneck 2008).

Two case studies highlight both the earlier vulnerability of Caribbean reefs, and the role of climate change increasing risk to coral reefs elsewhere. Fishing pressure and terrestrial run-off began to decrease coral reef resilience in Jamaica almost a century ago (Hughes 1994, Jackson et al. 2001). By the 1970s and 1980s, high densities of one species of sea urchin, *Diadema antillarum*, were primarily responsible for preventing macroalgal dominance on the overfished reefs (Hughes 1994, Steneck and Dethier 1994). When a disease outbreak in the early 1980s dramatically reduced urchin populations (Lessios et al. 1984), macroalgae blooms outcompeted many coral taxa and have persisted ever since (Gardner et al. 2003). In the Indo-Pacific region, regime shifts occurred on coral reefs of the Seychelles inner island group in response to the 1998 climate-driven mass coral bleaching event. Long-term monitoring of 21 sites found that 9 sites experienced a regime shift to macroalgal dominance, while 12 sites recovered pre-disturbance levels of coral dominance by 2011 (Graham et al. 2015). Reefs that followed a trajectory of recovery were those that had high structural complexity, were located in deeper water, had a high density of juvenile corals and herbivorous fishes, and where nutrient inputs into the system were low (Graham et al. 2015).

While our understanding of the factors that increase the likelihood of regime shifts on coral reefs is improving (Mumby et al. 2007, Graham et al. 2015), we lack an understanding of the effects of regime shifts on the wider 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). Regime shifts in dominant benthic organism/s 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 lack knowledge regarding effects on community trophic structure. Trophic pyramids provide a visually intuitive means of examining and comparing the structure of food webs (Lindeman 1942, Fath and Killian 2007, Hatton et al. 2015), helping to represent the likely transfer of energy among trophic levels (Trebilco et al. 2013). This simple, yet powerful tool has the potential to be used to identify disruption to trophic structure due to disturbance (Graham et al. 2017). With the expectation that bleaching events will become more frequent as atmospheric carbon levels increase, it is critical to improve our understanding of how coral reef fish communities restructure following climate-driven regime shifts or during recovery from such disturbances.

Coral reefs provide important goods 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 among upper and lower trophic levels, the implications of regime shifts for trophic structure and associated biomass storage, productivity, and trophic pathways become important. It has only recently become possible to investigate these long-term ecosystem changes with sufficient time having passed since the 1998 mass bleaching (Graham et al. 2015).

In this well-studied system, where climate-driven bleaching led to both regime-shifted and recovering reefs (Graham et al. 2015), we investigate how the trophic structure of associated reef fish communities has responded across two decades. 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 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 on recovering and regime-shifted reefs.

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 and after the bleaching event 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 macroalgal 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 coral cover in 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 underwater visual surveys on SCUBA at 8 to 16 replicate 7 m radius circular point counts. Each replicate point count was haphazardly located along the base of the reef slope, with adjacent surveys separated by a minimum of 15 m. At each point, the abundance of 134 potential species of diurnal, non-cryptic (>8 cm), reef-associated fish was recorded (of which 128 were observed), and the total length of each individual estimated to the nearest centimetre. Abundance estimates for each species were calculated as the number of individuals recorded within each point count area (153.94 m^2), and averaged over all point counts at each site. Length estimates were converted to biomass using published length-weight relationships for each species (Froese and Pauly 2016) according to the formula:

$$W = a \times L^b$$

where W is individual fish biomass (g), a and b are published species specific constants, and L is the visually estimated length recorded for an individual fish (See Graham et al. 2007 for a detailed description of fish community survey techniques used).

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). Trophic level estimates were obtained from Fish Base (Froese and Pauly 2015), which publishes trophic level estimates obtained from the scientific literature or based on their diet composition. Species were then assigned to one of five trophic level bins (TLB) for pyramid construction; TLB1: 2 - 2.5; TLB2: 2.5 – 3.0; TLB3: 3.0 – 3.5; TLB4: 3.5 – 4; TLB5: 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). While some variation due to sampling error is largely unavoidable in an ecological study such as this, it is not expected to bias the general patterns in the data.

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 Percentage (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 for each year to allow for comparison of the magnitude of difference in fish community functional structure among years.

Both the absolute (kg. ha^{-1}) and relative (%) biomass of reef fish within each of the five trophic level bins (TLB1 – TLB 5) was calculated for each reef state (recovering vs regime-shifted) to examine change in trophic structure within the fish community due to bleaching disturbance. Absolute biomass was calculated as the mean total biomass (kg. ha^{-1}) of all fish in each trophic level bin, averaged across all sites, within each reef state. Relative biomass (%) was calculated by dividing the absolute biomass within each TLB at each site, by the total biomass for that site, and then averaged over all sites within each reef state.

Differences in the trophic structure between recovering and regime-shifted reefs at each time point were tested using multinomial regression of the TLBs 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, and trophic level bin (TLB1 - TLB5), 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 accounted for 48.4 % of the total variation among sites. Following the disturbance (2005, 2014), there was a strong separation between reefs that were recovering from the bleaching and those moving into a regime-shifted state. In 2005, two of the regime-shifted 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 was 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 reflected this divergence between reef states in terms of the distribution of relative biomass among trophic level bins (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, Table S3). In 2005, seven years after mass bleaching, regime-shift reefs showed a large increase in relative and absolute biomass within the base trophic pyramid level (TLB1), 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 TLB1, 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 the expected triangular trophic pyramid structure, while regime-shifted reef pyramids had a concave shape, with biomass dominated by herbivorous species in TLB1, low biomass in mid trophic levels (TLB2 - TLB3) and comparatively high biomass at TLB4 (Fig. 2). The increase in TLB4 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 pyramid 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, recovering reefs were more similar to their pre-disturbance composition in 2014 than regime shifted reefs, with reduced variation in dissimilarity measures in all trophic pyramid levels except TLB2. The increased dissimilarity in this trophic pyramid level was due to an increase in the generalist damselfish species *Pomacentrus trilineatus* and a decrease in two rabbitfish species, *Siganus puelloides* and *Siganus stellatus* on recovering reefs (Appendix S1: Table S2). On regime-shifted reefs, mean dissimilarity and the degree of variation in community composition tends to increase for all trophic pyramid levels, again except for TLB2, 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. 3). Pre-disturbance (1994) fish communities had an overall dissimilarity (Bray-Curtis) of only 13.3% between reefs that subsequently either recovered or underwent regime shifts from the 1998 bleaching disturbance. 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 grazer/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 had a wide variety of functional groups from higher trophic levels, including corallivores, planktivores, and piscivores.

DISCUSSION

Regime shifts are increasingly common in a wide variety of ecosystems. In Seychelles, the long-term trajectories of regime shifts versus 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 (macroalgae-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.

Changes 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 1998 bleaching event, pyramids of relative biomass on all surveyed reefs were bottom heavy, with substantial biomass in the mid to upper trophic pyramid levels and the greatest amount of biomass located in the base trophic pyramid level (TLB1), as expected based on energetic theory (Trebilco et al. 2013, Hatton et al. 2015). Following bleaching, relative biomass in TLB1 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-shifted 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 suggests that increased total abundance of herbivores alone is insufficient for recovery. Rather, recovery is dependent on the size composition of the herbivore community and a combination of other factors including eutrophication, recruitment of corals, depth, and structural complexity (Graham et al. 2015, Nash et al. 2016).

Sixteen years post-bleaching, recovering reefs had developed a triangular biomass pyramid structure, representing an energetically stable food web (Hatton et al. 2015). This structure indicates that the fish community regained biomass in the mid trophic pyramid levels (TLB2 and TLB3), which includes various specialised species, such as corallivores, which are extremely sensitive to loss of coral cover (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). 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 pyramid levels, particularly TLB4, 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. 2017). Another possibility is that they may benefit from decreased competition from other mesopredators with different 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, Cephalopholis 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 on coral reefs - unlike in temperate marine ecosystems (Jennings and Mackinson 2003) - 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 that are limited by their gape size (Kingsford 1992, St John 1999). This may explain 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-shifted 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 TLB2 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 TLB2 that deviates 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. 2017). Switching to a less preferred diet can be associated with potential sublethal effects, such as decreased energy reserves, condition, growth rates, survivorship and fecundity (Kokita and Nakazono 2001, Jones and McCormick 2002, Pratchett et al. 2004, Berumen et al. 2005).

Increasing divergence in the functional composition of the reef fish communities between states suggests potential disruption of ecological processes on regime-shifted reefs. The single strongest characteristic of this change is the increase in herbivores, a pattern that 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 (Wilson et al. 2010b, Evans et al. 2014), the loss of coral cover transforms the previously diverse reef habitat into a comparatively uniform landscape, unsuitable for the wide diversity of mid trophic level species normally supported by a healthy reef (Chong-Seng et al. 2012, Nash et al. 2013). In 2005, the dissimilarity in mid trophic pyramid levels (TLB2 and TLB3) appeared 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 TLB3 (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 TLB3 (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 TLB2.

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 feed 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 suggests 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. There is increasing recognition that the structure of coral reef ecosystems is likely to become progressively altered in the Anthropocene (Norström et al. 2016, Hughes et al. 2017). The inevitable resulting change in reef fishery catch composition could substantially alter the market available to fishers to sell their catch (Cinner et al. 2013). Similarly, as coral reefs move into a new era, the tourism appeal of these aesthetically attractive ecosystems may decline, with severe implications for an industry estimated to account for a large proportion of global coastal tourism value (Spalding et al. 2017). To sustainably manage these novel ecosystems and ensure the continued delivery of key ecosystem services, it is essential that we improve our understanding of the likely ecological structure and function (Graham et al. 2014), and dramatically rethink coral reef fisheries management to adapt to these changes. This study provides important insight into how regime shifts are likely to affect the fundamental structure of coral reef ecosystems, and the distribution of energy within them. This information 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. Alternatively, increased abundance within lower trophic levels and herbivorous species may offer new opportunities for fishers. 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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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the James Cook University Tropical Data Hub:

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

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 TLB1 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 Level Bin (TLB)**	**Model Coefficient**	**2.5%**	**97.5%**
1994				
	TLB 2	-0.429	-0.522	-0.336
	TLB 3	0.720	0.649	0.790
	TLB 4	-1.495	-1.617	-1.372
	TLB 5	-2.468	-2.681	-2.255
2005				
	TLB 2	0.317	0.200	0.435
	TLB 3	-0.241	-0.334	-0.148

	TLB 4	0.448	0.308	0.588
	TLB 5	-0.011	-0.287	0.266
2014				
	TLB 2	-0.161	-0.290	0.033
	TLB 3	0.007	-0.084	0.098
	TLB 4	0.419	0.274	0.564
	TLB 5	-0.587	-0.919	-0.255

TABLE 3. Mean percentage dissimilarity (± standard error; SE) in the fish community composition in each trophic level bin (TLB) 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.

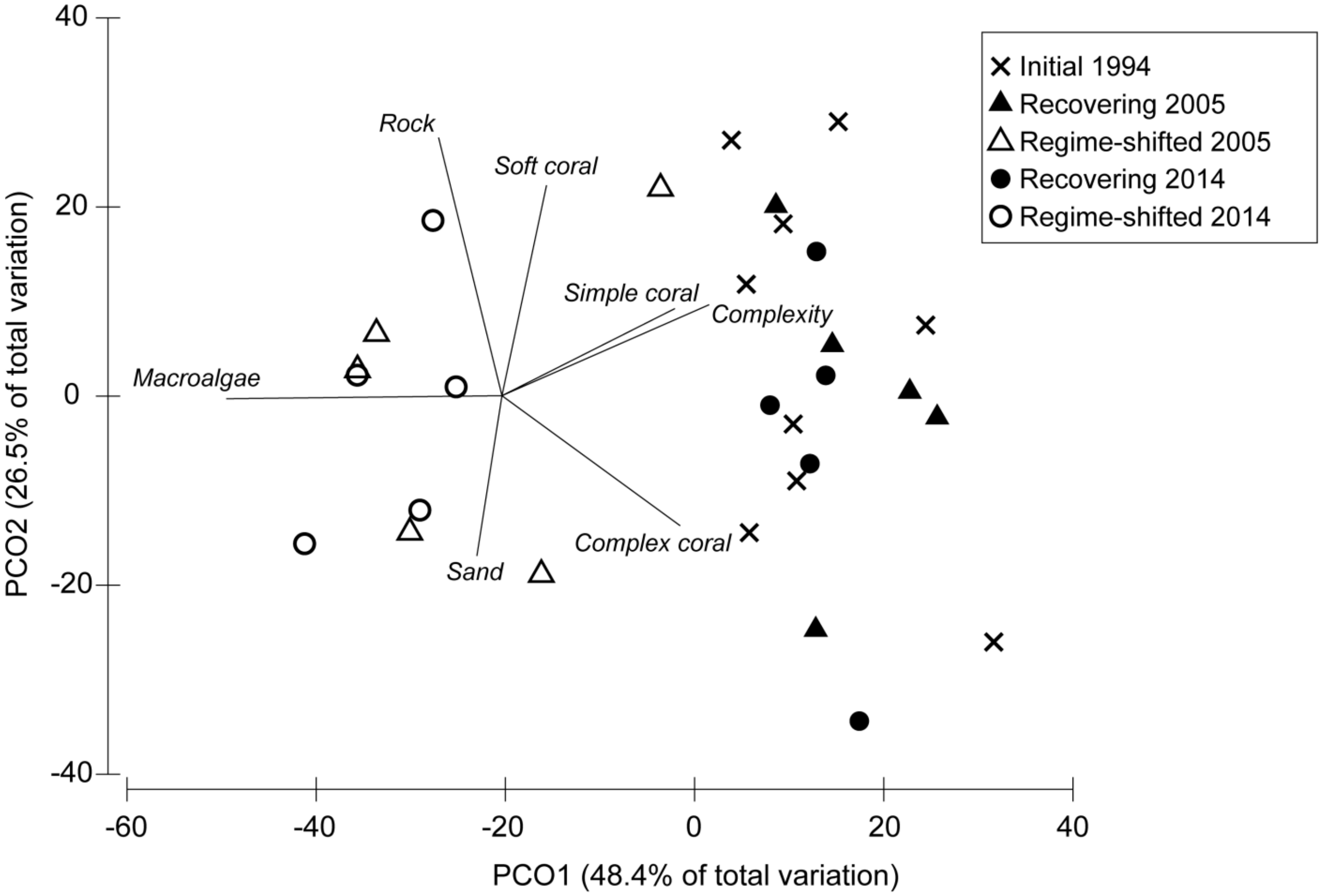
		Recovering		**Regime-Shifted**				
Years	**Trophic Level Bin**	**Mean % dissimilarity**	**±SE**	**Mean % dissimilarity**	**±SE**	**t**	**df**	***p***
1994 vs 2005	TLB 1	34.99	2.32	45.13	3.38	-2.47	7.09	0.04
	TLB 2	28.59	4.46	44.50	4.20	-2.60	7.97	0.03
	TLB 3	38.57	3.56	48.03	4.33	-1.69	7.71	0.13
	TLB 4	54.77	4.46	44.09	6.67	1.33	6.98	0.23
	TLB 5	52.33	19.53	58.68	6.73	-0.31	4.94	0.77
1994 vs 2014	TLB 1	35.29	1.84	62.72	2.71	-8.36	7.05	0.00
	TLB 2	44.18	5.68	37.82	4.94	0.85	7.85	0.42
	TLB 3	32.45	3.72	53.10	5.60	-3.07	6.96	0.02
	TLB 4	39.40	4.69	57.05	7.89	-1.98	6.38	0.09
	TLB 5	41.87	9.39	71.40	12.75	-1.87	7.35	0.10

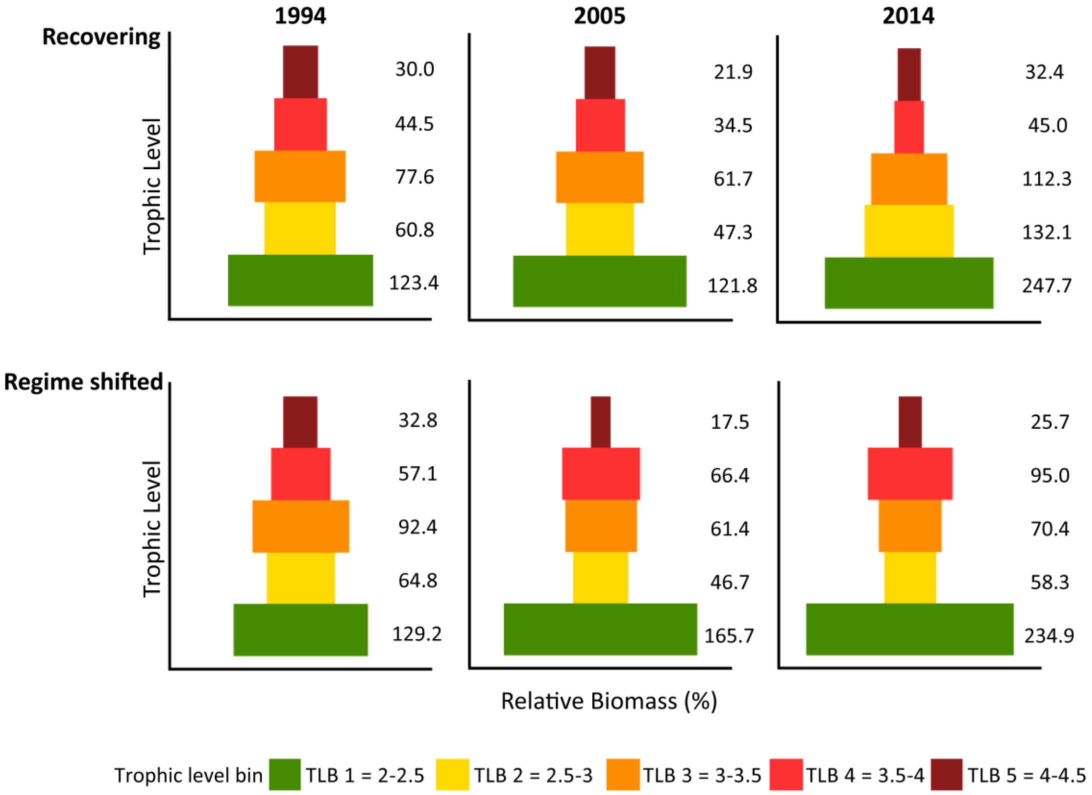
Figure Legends

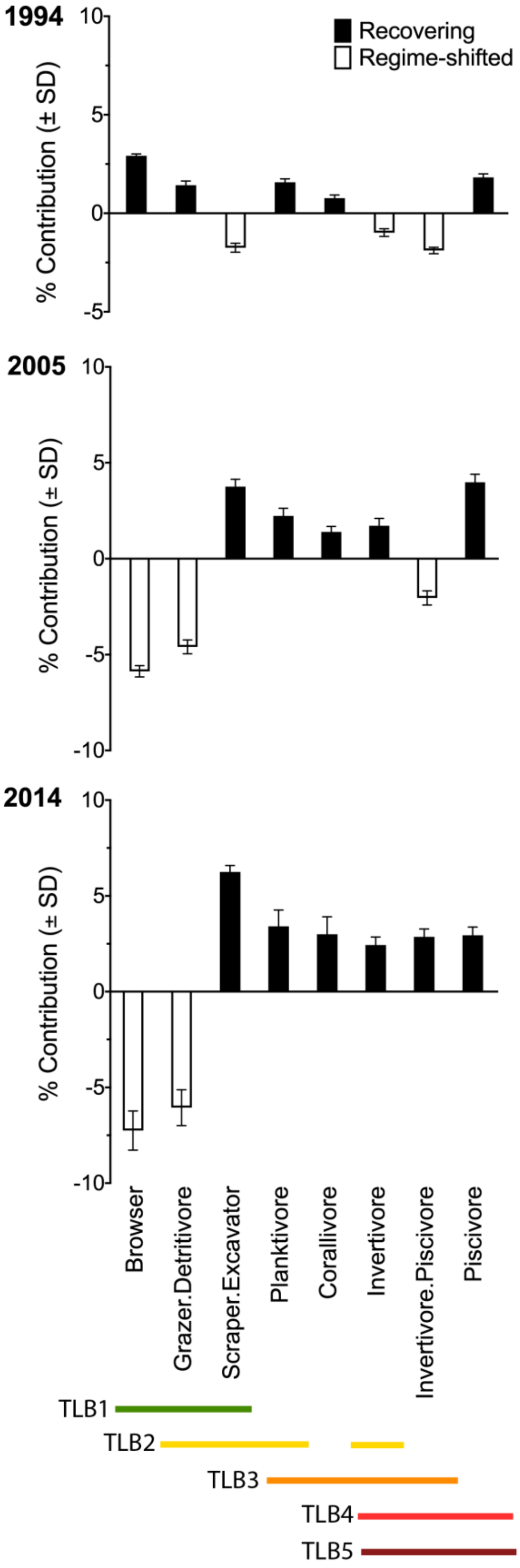
FIG. 1. Principal coordinates analysis of the composition of benthic cover of ten reefs surveyed in the Seychelles inner island group based on Bray-Curtis similarity (data square-root transformed). Crosses represent all reef sites surveyed in 1994, prior to the bleaching 1998 mass bleaching event. Black 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. Differences in the functional group composition between fish communities on regime-shifted (white) and recovering sites (black). The mean (± standard deviation; SD) percentage contribution of each functional group to Bray-Curtis dissimilarity between reef states in Seychelles in 1994, 2005 and 2014, based on a SIMPER analysis. Values are weighted by the overall dissimilarity between states for that year (1994: 13.13 %; 2005: 25.61 %; 2014: 34.2 %). Bars represent the percentage contribution for the functional group that had a higher contribution in either reef state.


40
20
0
-20
-40
PCO2 (26.5% of total variation)
-60
-40
-20
0
20
40
PCO1 (48.4% of total variation)
Rock
Soft coral
Simple coral
Complexity
Macroalgae
Complex coral
Sand
× Initial 1994
▲ Recovering 2005
△ Regime-shifted 2005
● Recovering 2014
○ Regime-shifted 2014


1994
2005
2014
Recovering
Trophic Level
30.0
44.5
77.6
60.8
123.4
21.9
34.5
61.7
47.3
121.8
32.4
45.0
112.3
132.1
247.7
Regime shifted
Trophic Level
32.8
57.1
92.4
64.8
129.2
17.5
66.4
61.4
46.7
165.7
25.7
95.0
70.4
58.3
234.9
Relative Biomass (%)
Trophic level bin
TLB 1 = 2-2.5
TLB 2 = 2.5-3
TLB 3 = 3-3.5
TLB 4 = 3.5-4
TLB 5 = 4-4.5


1994
2005
2014
% Contribution (± SD)
10
5
0
-5
-10
■ Recovering
☐ Regime-shifted
Browser
Grazer.Detritivore
Scraper.Excavator
Planktivore
Corallivore
Invertivore
Invertivore.Piscivore
Piscivore
TLB1
TLB2
TLB3
TLB4
TLB5