Regime shifts shorten food chains for mesopredators with potential sublethal effects

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Summary

1. Predator populations are in decline globally. Exploitation, as well as habitat degradation and associated changes in prey availability are key drivers of this process of trophic downgrading. In the short term, longevity and dietary adaptability of large-bodied consumers can mask potential sub-lethal effects of a changing prey base, producing a delayed effect that may be difficult to detect.

2. In coral reef ecosystems, regime shifts from coral- to algae-dominated states caused by coral bleaching significantly alter the assemblage of small-bodied reef fish associated with a reef. The effects of this changing prey community on reef-associated mesopredators remains poorly understood.

3. This study found that the total diversity, abundance and biomass of piscivorous mesopredators was lower on regime-shifted reefs than recovering reefs, 16 years after the 1998 mass coral bleaching event.

4. We used stable isotope analyses to test for habitat-driven changes in the trophic niche occupied by a key piscivorous fishery target species on reefs that had regime-shifted or recovered following climatic disturbance. Using morphometric indices, histology, and lipid analyses, we also investigated whether there were sub-lethal costs for fish on regime-shifted reefs.

5. Stable isotopes demonstrated that fish from regime-shifted reefs fed further down the food chain, compared to recovering reefs. Lower densities of hepatocyte vacuoles in fish from regime-shifted reefs, and reduced lipid concentrations in spawning females from these reefs, indicated a reduction in energy stores, constituting a sub-lethal and potential delayed effect on populations.

6. Reduced energy reserves in mesopredators could lead to energy allocation trade-offs, and decreased growth rates, fecundity, and survivorship, resulting in potential population declines in the longer term.

Key-words: coral bleaching, coral reef fish, food chain, habitat degradation, mesopredator, prey availability, trophic level

Introduction

Climate change poses a severe threat to coral reefs, with coral bleaching emerging as one of the most important drivers of habitat decline globally (Hughes *et al.* 2003; Sheppard 2003). While mass coral bleaching is expected to become frequent in coming decades (Hoegh-Guldberg *et al.* 2007), major bleaching events in the Indo-Pacific have already resulted in extensive loss of live coral cover, leading to erosion of habitat complexity and regime shifts to macroalgae-dominated states on some reefs (Graham *et al.* 2015). These habitat losses can undermine the foundation of a coral reef ecosystem (Pratchett *et al.* 2008), directly affecting small-bodied reef fish assemblages and coral-dependent species (Graham *et al.* 2006; Wilson *et al.* 2008). The effects of habitat degradation can also migrate up the food web, altering the composition and size structure of the prey fish community (Graham *et al.* 2007), and indirectly impacting piscivorous reef-associated predators (Wilson *et al.* 2008).

Mesopredators have high ecological, economic, and social value in coral reef ecosystems. They play a key role in transferring energy up the food chain to apex predators (Polovina 1984). Many reef mesopredators (e.g. Serranidae, Lutjanidae, Lethrinidae) support large commercial, recreational, and subsistence fisheries (Cinner *et al.* 2009; Lédée *et al.* 2012; GBRMPA 2014), as well as a lucrative global fishing tourism industry (World Bank 2012). Yet, we still know very little about the impacts of habitat degradation on this important functional group (Graham *et al.* 2011). In the short term, populations of large-bodied mesopredators appear to be notably more resistant to the effects of bleaching disturbance than smaller-bodied fish species (Graham *et al.* 2007), with declines often attributed more to fishing than habitat degradation (Wilson *et al.* 2010). However, we lack an understanding of the long-term effects of bleaching on mesopredators.

The apparent short-term resilience of mesopredators to coral bleaching disturbance can largely be attributed to their longevity (Graham *et al.* 2007). Many species have life expectancies in excess of 20 years (Froese & Pauly 2016), allowing populations to persist for many years following a disturbance event, masking failed recruitment (Warner & Hughes 1988) and producing a delayed effect that may last decades, suspending population decline (Bellwood *et al.* 2006; Graham *et al.* 2007). Mesopredators are also often more mobile than their prey (McCauley *et al.* 2012), with a broad dietary scope that allows them to adapt to changing prey availability (Shpigel & Fishelson 1989; Kingsford 1992; Hempson *et al.* 2017). This adaptability allows fish to persist in the short term, but may carry a physiological cost that manifests at a sub-lethal level (Pratchett *et al.* 2004).

Sub-lethal effects of habitat degradation can occur through multiple pathways. Alterations to the available prey base can lead to declining diet quality (Pratchett *et al.* 2004), due to either a reduced abundance of prey (e.g. Hondorp, Pothoven & Brandt 2005) or the lower nutritional value of less preferred prey sources (Berumen, Pratchett & McCormick 2005). Declines in prey availability may also result in intensified intra- and interspecific competition between predators, leading to increased energetic demands (Bonin *et al.* 2015). Further, as habitat structure degrades, ambush predators that rely on shelter for hunting may expend increased energy to capture prey (Kerry & Bellwood 2012). All organisms need to maintain a balance of energy allocation between growth, reproduction, and storage (Chapman, Jørgensen & Lutcavage 2011; Zudaire *et al.* 2014). Reduced energy reserves could therefore result in decreased body condition, growth rates (Kokita & Nakazono 2001), survivorship, and fecundity, leading to eventual population declines (Jones & McCormick 2002; Pratchett, Wilson & Baird 2006). Yet studies of the sub-lethal effects of habitat degradation reef mesopredatory fish are currently lacking.

This study aims to quantify habitat-driven sub-lethal effects in mesopredators by contrasting reefs that, 16 years after a major bleaching disturbance, have either undergone a regime shift to an algae-dominated state, or have recovered to a coral-dominated state

(Graham *et al.* 2015). We compare benthic habitats and fish assemblages associated with these reef states, to establish how piscivorous mesopredator populations and the prey community available to them become altered by habitat degradation. We then investigate the potential for sub-lethal effects on a mesopredator, using (i) lipid-extracted bulk stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ to describe their trophic niche; (ii) morphometric, growth and hepatosomatic indices to examine body condition at a coarse scale; and (iii) histology and lipid analysis to specifically examine differences in energy reserves at a finer scale.

Materials and methods

STUDY SITE

This study was conducted in the Seychelles inner island group, one of the areas most severely impacted by the 1998 mass bleaching event, with live coral cover loss estimated to be in excess of 90% (Goreau *et al.* 2000; Lindén *et al.* 2002). Long-term monitoring of the reefs within this island group, both before (1994) and following the bleaching (2005, 2008, 2011, 2014) has shown that some reefs are recovering live coral cover, while others continue to decline, moving into an algae-dominated regime-shifted state (Graham *et al.* 2006, 2015; Wilson *et al.* 2012). For this study, we selected six of these monitoring sites; three recovering reefs and three regime-shifted reefs around the islands of Mahé and Praslin (see electronic supplementary material (ESM) for map, Fig. S1). Recovering sites were defined as those where post-disturbance coral cover was greater than macroalgae cover, with coral cover increasing or remaining high through time. Regime-shifted reefs were identified as those where post-disturbance macroalgae cover exceeded coral cover, and was increasing or remaining high (see Graham *et al.* 2015 for detailed site descriptions).

FISH AND BENTHIC SURVEYS

We surveyed reef fish and benthic communities at each site in April 2014 using the methods of Graham *et al.* (2015). At each site, the abundance of a potential 134 species of diurnal, non-cryptic, reef-associated fish was recorded within 8 replicate 7 m radius point counts along the reef slope, separated by > 15 m, over a distance of up to 0.5 km. Total length of each individual was estimated, and the biomass of each species calculated using published length-weight relationships (Froese & Pauly 2016). Species were assigned to functional groups based on their diet and feeding behaviour as defined in Graham *et al.* (2006) (Table S1). Benthic habitat composition within the area of each point count was measured as percent cover of live hard coral, soft coral, macroalgae, sand, rubble, and rock. Structural complexity was visually estimated using a six point scale (Wilson, Graham & Polunin 2007).

STUDY SPECIES

Based on long-term monitoring data from the inner Seychelles islands, *Cephalopholis argus*, an important Seychelles fishery species (Grandcourt 1999; Graham *et al.* 2007), was identified as a dominant and widespread reef mesopredator, occurring at all sites. This species is almost exclusively piscivorous, with 95% of its diet consisting of fish, and it has high site attachment (Shpigel & Fishelson 1989; Dierking, Williams & Walsh 2009; Froese & Pauly 2016).

MESOPREDATOR SAMPLING

In April 2014, 10 - 15 adult *C. argus* individuals were collected at each site using spearguns. Fish were euthanized per the methods prescribed by ANZCCART (Second Edition 2001), and placed on ice to preserve tissues. Total body weight (TW, kg), gutted weight (GW, kg), total length (TL, cm), body height (H, cm), gonad weight (GNW, g) and liver weight (LW, g) were recorded.

Sex was determined, except for fish not developed enough and considered as "immature". Female fish were further categorised according to reproductive status based on gonad appearance using conventional macroscopic criteria (West 1990) (see ESM for details).

Livers were collected; half the tissue deep-frozen (-80°C) for lipid analysis, and half fixed in 4% buffered formaldehyde for histological analysis. White muscle tissue (~ 1.5 cm^3) was sampled from between the dorsal fin and lateral line, and frozen for isotope and lipid analysis.

Sagittal otoliths were extracted and read to establish the age of the fish (Ferreira & Russ 1992) and calculate growth rates of each individual. Growth curves were fitted to the size-at-age data with the von Bertalanffy growth model (Beverton & Holt 1957):

$$L_t = L_\infty (1 - e^{-K*(t-t_0)})$$

where L_t is total length (TL, cm) at age t (years), L_∞ is the estimated maximum total length (cm), K is the growth rate coefficient (y^{-1}), and t_0 is the theoretical age at zero length.

STABLE ISOTOPE ANALYSIS

To test whether variability in isotopic signatures of *C. argus* could be attributed to differences in the baseline signatures between sites, we sampled 10 strands of *Sargassum* sp. algae at each site. Samples were thoroughly washed with fresh water to remove sediment, oven dried and ground to a fine homogenous powder in preparation for isotope analysis (see ESM for detailed methods).

Carbon and nitrogen stable isotope values for both fish muscle tissue and algae were calculated as delta (δ) values, equal to parts per thousand (‰) deviation from standard reference material (Pee Dee Belemnite carbonate for carbon, atmospheric nitrogen for nitrogen; see electronic supplementary material for detailed methods), using the equation:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where X is ^{13}C and R is the ratio ^{13}C:^{12}C for $\delta^{13}C$, or X is ^{15}N and R is the ratio ^{15}N:^{14}N for $\delta^{15}N$ (Peterson 1999). Due to low enrichment between trophic levels, $\delta^{13}C$ provides evidence as to the origin of the primary carbon source in a consumer's diet, while the greater enrichment of $\delta^{15}N$ between subsequent trophic levels provides a proxy measure of predator trophic position (Letourneur *et al.* 2013).

BODY CONDITION INDICES

Overall condition was assessed using the B′ index of morphometric body measurements (Richter *et al.* 2000). This index uses fish total length (TL), gutted body weight (GW), and body height (H) to provide a measure of condition (B′) that accounts for the tendency for allometric growth in many fish taxa.

$$B' = GW / (H \times TL^2)$$

At a finer scale, we calculated the hepatosomatic index (HSI); the ratio of liver weight (LW) to gutted body weight (GW), which serves as a measure of a fish's energy stores, with fish in better condition having larger livers (Stevenson & Woods 2006).

$$HSI = (LW/GW) \times 100$$

HISTOLOGY

Fish condition was also assessed using the density of hepatocyte vacuoles as an indicator of glycogen stores in the liver (Theilacker 1978). Preserved livers were embedded in paraffin wax, cut into 5 µm sections, stained using Mayer's haematoxylin and eosin, and hepatocyte vacuole densities quantified using a Weibel eyepiece at a magnification of 400x (Pratchett *et al.* 2001).

LIPID ANALYSIS

Total lipid content and lipid class composition of muscle, liver and gonad tissue were analysed to measure the allocation of energetic reserves to growth, storage, and reproduction respectively (Stallings *et al.* 2010; Zudaire *et al.* 2014) (see ESM for detailed methods). Concentrations of triacylglycerols (TAG), free sterols (ST), and phospholipids (PL) were measured as µg.mg^{-1} of wet weight (ww) of sample (Parrish 1999). Total lipids (µg.mg^{-1} ww) correspond to the sum of the concentrations of all lipid classes. The ratio of TAG (storage lipid class) to ST (structural lipid class) was also calculated, as an indication of a fish’s energy store (Amara *et al.* 2007; Isnard *et al.* 2015).

STATISTICAL ANALYSES

Benthic habitat composition in 2014 was compared between reef states (recovering vs regime-shifted) using a canonical analysis of principal coordinates (CAP), based on a Bray-Curtis similarity matrix (Clarke & Warwick 2001; Anderson & Willis 2003). Data were square root transformed to reduce the influence of dominant cover types. Eigenvectors of all benthic categories were overlaid to examine their contribution to the separation between reef states. Differences in the percentage mean live hard coral cover, macroalgae cover, and structural complexity between reef states were each tested using Welch’s t-test, which adjusts the degrees of freedom to account for unequal variances between groups (Welch 1947).

Reef fish assemblages from the six sites were compared between reef states using non-metric multidimensional scaling (NMDS) based on Bray-Curtis similarity measures, and tested using one-way analysis of similarity (ANOSIM). A multivariate dispersion index (MVDISP) was also calculated from the similarity measures to quantify the level of dispersion or grouping of data points within each reef state (Clarke & Warwick 2001). Differences in mean total fish abundance (fish. ha^{-1}) were tested using Welch's t-test.

We used a SIMPER analysis (Clarke & Warwick 2001) to identify which fish species contributed most to average Bray-Curtis dissimilarity between reef states. These species were then categorised by functional group, and the percent contribution of all species within each functional group summed to provide an estimate of the relative measure of their importance in distinguishing recovering and regime-shifted assemblages.

The diet of *C. argus*, is considered to be largely limited by gape size to fish of TL ≤ 15 cm, and while they do have prey preferences, they are known to readily switch prey when preferred species are not available (Shpigel & Fishelson 1989; Dierking *et al.* 2009). The size of the prey fish community available to piscivorous mesopredators was therefore estimated as the total biomass of all fish of TL ≤ 15 cm (kg. ha^{-1}). To investigate differences in body size distributions between reef states, all individuals were assigned to six 5 cm size classes (5 cm to >30 cm) based on their total length (TL). Using a SIMPER analysis based on a Bray-Curtis similarity matrix, we examined which size classes contributed most to differentiating between reef states.

Differences in total mesopredator abundance (fish. ha^{-1}), biomass (kg. ha^{-1}), and diversity (Shannon-Weaver Index; H′) between reef states were tested using Welch's t-test.

The isotopic signatures of all *C. argus* were plotted in isotopic space using a δ^{13}C vs. δ^{15}N biplot. The relationship between δ^{13}C and δ^{15}N for fish on recovering and regime-shifted reef states was modelled using a linear mixed effects model (M) in R (R Core Team 2015), with site included as a random effect:

$$\delta^{15}\mathrm{N} \sim B_{0,s} + B_1 * \delta^{13}\mathrm{C} + B_2 * \mathrm{site} + \delta^{13}\mathrm{C} * \mathrm{site}$$

Differences in overall $\delta^{13}C$ and $\delta^{15}N$ values for *C. argus* sampled from recovering and regime-shifted reefs were assessed using notched boxplots, with non-overlapping notches providing strong evidence (95% confidence) that values differ (Zuur, Ieno & Smith 2007). To ensure that differences in isotopic signature were not due to ontogenetic dietary shifts, we used Welch's t-test to test for a difference in total length between *C. argus* sampled from recovering and regime-shifted reefs. Similarly, Welch's t-test was used to ascertain whether baseline isotopic signatures for *Sargassum* sp. algae differed between reef states.

Growth rate differences in *C. argus* from recovering and regime shifted reefs, measured using growth parameter estimates of the Von Bertalanffy growth model fitted to size-at-age data, were tested using a likelihood ratio test in the 'fishmethods' package in R (Nelson 2015). Differences in the condition of fish from recovering and regime-shifted reefs in terms of the B′ body condition index, the hepatosomatic index (HSI), and hepatocyte vacuole density counts were investigated using notched boxplots. To further test whether the difference in hepatocyte vacuole density was attributable to the effect of reef state (recovering vs regime-shifted), a hierarchical linear effects model was run, which included reef state, stage of maturity and total length as fixed effects, and site as a random effect. Model selection was based on the Akaike Information Criterion (AIC).

Due to the low number of sampled males (n: Recovering = 3, Regime-shifted = 3) and regressing females (n: Recovering = 0, Regime-shifted = 8), differences in tissue lipid composition between reef states were only tested for immature fish, and developing and spawning females, using notched boxplots (Fig. S2). Where boxplot quantiles did not overlap, suggesting substantial differences between reef states, the effect of regime shifts was further assessed using logistic regression, and parameter estimates generated using a bootstrap technique to account for low sample size.

Results

BENTHIC HABITAT

Benthic habitat composition in 2014 differed substantially between recovering and regime-shifted sites (Fig. 1a). The CAP analysis showed strong support for groupings between recovering and regime-shifted reefs, with 99.5% correct allocations ($p < 0.001$). Four PCO axes optimised the ordination, explaining 96.95% of the total variation in the data, with the first and second PCO axes (Fig. 1a, CAP1 and CAP2) accounting for 58.79% and 17.01% respectively. Regime-shifted reefs were most strongly characterised by high levels of macroalgae cover (mean ± standard error; Recovering: 0.00 ± 0.00%, Regime-shifted: 11.90 ± 2.77%, $t_{191} = 9.795$, $p < 0.001$). Recovering sites were characterised by high percentage live hard coral cover (Recovering: 36.92 ± 2.72%, Regime-shifted: 7.56 ± 0.80%, $t_{199.01} = -9.423$, $p < 0.001$), and high structural complexity (Recovering: 2.92 ± 0.08%, Regime-shifted: 2.17 ± 0.11%, $t_{308.9} = -3.008$, $p = 0.003$). The multivariate dispersion index (MVDISP) showed much greater variation in the composition of the benthic community on regime-shifted sites (1.25) compared to the more closely related recovering sites (0.75).

FISH COMMUNITY

The reef fish assemblages on recovering and regime-shifted reefs differed significantly (ANOSIM, global R = 0.467, $p < 0.001$), showing distinct separation between reef states (Fig. 1b). As with the benthic community composition, the multivariate dispersion index (MVDISP) showed much greater variation in the reef fish assemblage on regime-shifted sites (1.28) compared to recovering sites (0.72). Total fish abundance was significantly lower on regime-shifted reefs (mean ± standard error; Recovering: 11.72 ± 0.77 fish. ha^{-1}, Regime-shifted: 6.49 ± 0.53 fish. ha^{-1}, $t_{42.476} = -5.6191$, $p < 0.001$).

Functional groups that contributed most to the difference in fish communities between reef states were planktivores (17.38%) and corallivores (15.54%), which were strongly associated with recovering reefs (Fig. 2a). The next most influential group were grazing and browsing herbivores (13.28%) that were more abundant on the algae-dominated regime-shifted reefs. The only other group to increase on regime-shifted reefs were detritivores. The species composition of invertivores, scraping/excavating herbivores and piscivores differed between reef states, but all three groups were more abundant on recovering reefs.

SIMPER analysis of the size class composition of the fish community revealed that fish with TL ≤ 15 cm accounted for 76.4% of the total difference between recovering and regime-shifted reefs (Fig. 2b; 6 – 10 cm = 49.57%, 11 – 15 cm = 26.82%, ESM Table S2). Total available prey biomass for piscivorous mesopredators such as *C. argus* was thus significantly higher on recovering reefs than regime-shifted reefs (Fig. 2c; $t_{43.386} = -8.95$, $p < 0.001$). Slight differences in larger size categories between reefs was attributed to a higher abundance of larger herbivorous species from the parrotfish family on regime-shifted reefs where macroalgae dominated the benthos (Fig. 2b; 16 – 20 cm = 8.90%, 26 – 30 cm = 5.61%).

PISCIVOROUS MESOPREDATORS

Total diversity (Shannon-Weaver Index, H′; $t_{27.364} = 3.542$, $p = 0.001$), abundance ($t_{184.45} = 3.75$, $p < 0.001$), and biomass ($t_{261.9} = 2.20$, $p = 0.029$) of piscivorous mesopredators was lower on regime-shifted reefs than on recovering reefs (ESM, Table S3).

STABLE ISOTOPES

The isotopic signature for the base of the food web, derived from *Sargassum* sp. (ESM, Table S4), showed no significant difference between reef states in terms of either $\delta^{13}C$ (Recovering: -13.56 ± 0.27 ‰, Regime-shifted: -16.6 ± 0.24 ‰, $t_{2.664} = 2.680$, $p = 0.085$) or $\delta^{15}N$ (Recovering: 5.20 ± 0.21 ‰, Regime-shifted: 4.07 ± 0.18 ‰, $t_{2.492} = 1.309$, $p = 0.298$). Due to the potential relationship between intraspecific body size and $\delta^{15}N$ (Greenwood, Sweeting & Polunin 2010), we evaluated mean total length of *C. argus* sampled between reef states (Table S5), finding it did not differ significantly (Recovering: 25.40 ± 1.14 cm, Regime-shifted: 25.80 ± 1.04 cm, $t_{66.322} = -0.260$, $p = 0.796$). This suggests that neither of these two potential sources of variation in isotopic signal where likely to confound the isotope results for *C. argus*.

The linear relationship between $\delta^{13}C$ and $\delta^{15}N$ for *C. argus* sampled on recovering and regime-shifted sites differed primarily in terms of their slopes (Fig. 3a; Recovering: -0.122 ± 0.160, Regime-shifted: -0.533 ± 0.238). This indicates that fish on regime-shifted had a lower trophic position (i.e. lower $\delta^{15}N$) than fish sampled on recovering reefs for the same $\delta^{13}C$ signature, where a consistently higher trophic position was maintained. The mean $\delta^{13}C$ signature for *C. argus* did not differ between reef states (Fig. 3b; $t_{55.597} = 0.235$, $p = 0.815$). However, there was greater variation in $\delta^{13}C$ signature for fish from recovering reefs than those from regime-shifted reefs (Coefficient of variation [95% confidence interval]; Recovering: -7.354 [-5.890, -9.795], Regime-shifted: -4.696 [-3.797, -6.158]). In contrast, mean $\delta^{15}N$ signature differed significantly between reef states (Fig. 3b; $t_{66.678} = -5.012$, $p < 0.001$), indicating that *C. argus* sampled from recovering sites are feeding higher up the food chain than fish on regime-shifted reefs.

BODY CONDITION INDICES

The morphometric index, B′ showed no distinction in the body condition of *C. argus* between reef states (Fig. 4a, ESM Table S6). Sagittal otolith data also indicated no difference in growth rates, measured as size-at-age (ESM, Fig. S3), with growth rate parameter estimates for the von Bertalanffy growth model for fish from recovering reefs ($L_\infty = 41.19$ cm, $K = 0.19y^{-1}$, $t_0 = -2.02$) and regime-shifted reefs ($L_\infty = 39.89$ cm, $K = 0.19y^{-1}$, $t_0 = -2.06$) showing no significant difference between states ($\chi^2 = 1.38$, df = 3, $p = 0.71$).

The hepatosomatic index (HSI, Fig. 4b, ESM Table S6) also indicates little difference in energy stores between fish sampled from different reef states. However, at a finer scale, histological assessments of liver tissue found densities of hepatocyte vacuoles were significantly higher in liver sections from fish sampled on recovering sites (Fig. 4c, ESM Table S6), indicating higher lipid stores in these individuals. The results of the hierarchical linear mixed effects models indicated that, based on AIC value, a model containing only 'reef state' best described the variation in hepatocyte vacuole density (AIC = 209.6), with the addition of 'stage of maturity' and 'total length' decreasing model performance (AIC = 261.2).

TISSUE LIPID COMPOSITION

Low sample sizes due to ethical and logistical constraints on sampling, resulted in substantial uncertainty in the overall results of the lipid analyses. However, we found a few clear results, which we present here. Firstly, it was evident that *C. argus* in the spawning phase sampled from recovering reefs had higher concentrations of triacylglycerol (TAG) storage lipids in their gonad tissue than those on regime-shifted reefs (Fig. 5a), suggesting that these fish have more energy available to channel into their gonads for spawning. A similar trend is evident in the ratio of concentrations of TAG (storage lipid class) to sterols (structural lipid class) in both the liver (Fig. 5b) and gonad (Fig. 5c) tissue for spawning females, implying a cost to condition for fish living on regime-shifted reefs. While the result in Fig. 5c is not independent of that in Fig. 5a, the comparison of storage lipids (TAG) to structural lipids (sterols) is valuable in gaining insight into differences in energy allocation. Detailed results for all tissues, lipids and maturity categories are available in the ESM (Table S7).

Discussion

Mass coral bleaching can cause extensive habitat degradation, triggering regime shifts to algae-dominated states, and distorting the trophic structure and dynamics of coral reef ecosystems (Graham *et al.* 2015). Many of the long-term consequences of such disturbance remain poorly understood, particularly with respect to the indirect effects on higher trophic levels. Trophic downgrading, which is the loss of high-level consumers in an ecosystem, is typically a cryptic process, owing to the extended life spans of apex consumers and the large time and spatial scales over which downgrading can occur (Estes *et al.* 2011). This study provides some of the first empirical evidence of habitat driven trophic downgrading on coral reefs that, 16 years after bleaching, remain in an algae-dominated state. Abundance and diversity of mesopredators has begun to decline, and the *Cephalopholis argus* that have persisted occupy an altered trophic niche, with some signs of reduced energy reserves in fish on regime-shifted reefs.

Size structure in reef fish communities can be considerably altered by habitat degradation following bleaching (Graham *et al.* 2007). The reduction of small fish (< 15 cm TL) on regime-shifted reefs in Seychelles, likely driven by loss of live coral and rugosity as reef structure degrades following bleaching (Munday & Jones 1998; Dulvy *et al.* 2004; Graham *et al.* 2006), represents a decrease in the prey base available to mesopredators (ESM, Table S2). Despite their feeding adaptability (Shpigel & Fishelson 1989; Kingsford 1992; Hempson *et al.* 2017), reef mesopredators are physically limited in their prey choice by their gape size (Mumby *et al.* 2006), making them vulnerable to reduced biomass of suitably sized prey. Piscivorous mesopredators are therefore prone to experience deleterious effects of habitat degradation, mediated via their small-bodied prey base.

Stable isotopes show that, on regime-shifted reefs, *C. argus* are feeding lower down the food chain, and thus occupying a different trophic niche to those on recovering reefs. This altered trophic position is likely attributable to differences in the composition of the available prey fish assemblages between reef states. On recovering reefs, there is higher potential prey biomass (i.e. fish < 15 cm TL), and a higher diversity of species within the prey fish community, than on regime-shifted reefs. This diverse prey assemblage, includes higher trophic level consumers from various functional groups (e.g. corallivores, planktivores), increasing the trophic level at which mesopredators feed, as evidenced by higher $\delta^{15}N$ values. In contrast, on regime-shifted reefs, lower trophic level consumers (e.g. grazers, browsers and detritivores) dominate the fish community, and *C. argus* had a reduced $\delta^{15}N$ signature, indicative of a lowered trophic position (Greenwood *et al.* 2010). This supports the prediction that declining reef fish biodiversity may result in reduced energy transfer to higher trophic levels (Munday *et al.* 2007).

The altered trophic position of *C. argus* on regime-shifted reefs is also associated with lower hepatocyte vacuole densities, signalling reduced lipid stores and potential energetic costs to piscivorous mesopredators persisting on these reefs (Pratchett *et al.* 2004). In addition to lower prey availability; reduced structural complexity of the reef habitat can result in suboptimal hunting conditions for *C. argus*, an ambush predator that relies on complex habitat to conceal itself to wait for prey to pass by (Shpigel & Fishelson 1989). On regime-shifted reefs, not only are there less prey targets, but decreased habitat structure reduces potential concealment for ambush hunting (Kerry & Bellwood 2012), potentially resulting in higher energy expenditure for prey capture.

Limited energy budgets demand that all organisms make trade-offs in how they allocate resources between growth, reproduction, maintenance and storage (Reznick & Yang 1993; Kozlowski & Teriokhin 1999; Zudaire *et al.* 2014). On recovering reefs, where energy demands are likely to be met by ample prey availability, *C. argus* have sufficient energy to allocate to storage, as evidenced by the higher densities of hepatocyte vacuoles in their livers, and the higher ratio of storage to structural lipids (TAG: sterols) in the gonads of spawning females. However, on regime-shifted reefs, decreased energy intake and potentially higher energetic costs for *C. argus* would require an altered energy allocation scheme (Kozlowski & Teriokhin 1999). Fish on these reefs may need to mobilise lipid stores to meet their energetic requirements for reproduction or growth, as indicated by the low hepatocyte vacuole densities in their livers and the reduced concentrations of storage lipids (TAG).

Chronically compromised energy reserves in mesopredators can cause population decline in the long term through decreased fecundity and survivorship (Jones & McCormick 2002). If mesopredators have insufficient energy stores to allocate to reproduction, they may produce fewer or less viable gametes, compromising their fitness, resulting in reduced recruitment rates and long term population declines (REF). Similarly, if met with adversity, without sufficient energy stores, their own survivorship is likely to be compromised. The finding that *C. argus* that are persisting on regime-shifted reefs show no decrease in size-at-age or in coarse measures of body condition despite the deterioration of habitat and prey options may signal that *C. argus* has an energy allocation strategy that prioritises growth over reproductive output, or it could be as a result of the low number of individuals sampled. It could also be that a lower carrying capacity equilibrium has been established, with the decreased abundance of mesopredators on regime-shifted reefs (Table S3), allowing the remaining competitors to persist in this resource-depleted habitat (Cooney & Brodeur 1998), despite a depletion of energy reserves at a fine scale.

Sub-lethal effects of habitat degradation in mesopredator populations have important implications for the management of coral reef fisheries and conservation. The finding that the effects of bleaching on important fishery species, such as *C. argus*, may only manifest at a very fine scale at an individual level, means that they may go unnoticed for decades, only resulting in population declines in the long term, with potential delayed loss of fisheries production. It is essential that conservation and fisheries managers bear this in mind when managing reef fisheries in post-bleaching habitats, and consider closer monitoring of piscivorous mesopredator populations to detect fine scale signs of reduced condition (e.g. hepatocyte vacuolation). High-level consumers are also widely considered to play a critical role in exerting top-down control in ecosystems (Heithaus, Wirsing & Dill 2012), facilitating coexistence (Wallach, Ripple & Carroll 2015), and stabilising community dynamics (Duffy 2003; Myers *et al.* 2007). Delayed long-term decline in mesopredator populations could therefore precipitate fluctuations in prey populations, causing ecosystem instability. To better understand and predict the implications of coral bleaching on mesopredators, future research should focus on the effect of habitat degradation on the lipid metabolisms of these species, and how to detect potentially important fine scale physiological effects.

This study provides insight into how the complex trophic dynamics of food webs may respond to regime shifts following disturbance, with important implications for mesopredators, a group with high ecological and economic value. We show how, as habitat degrades, the composition of the available prey community changes, resulting in mesopredators feeding lower down the food chain and experiencing reduced energy reserves. The decline in mesopredator abundance and diversity on regime-shifted reefs in Seychelles maintained after a period of over a decade, illustrates the extended time scales required to understand the full effect of disturbance and habitat degradation in ecosystems. As climate-driven disturbance becomes more frequent, effective conservation and ecosystem management depends on our ability to anticipate how communities will respond.

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Figures and Tables

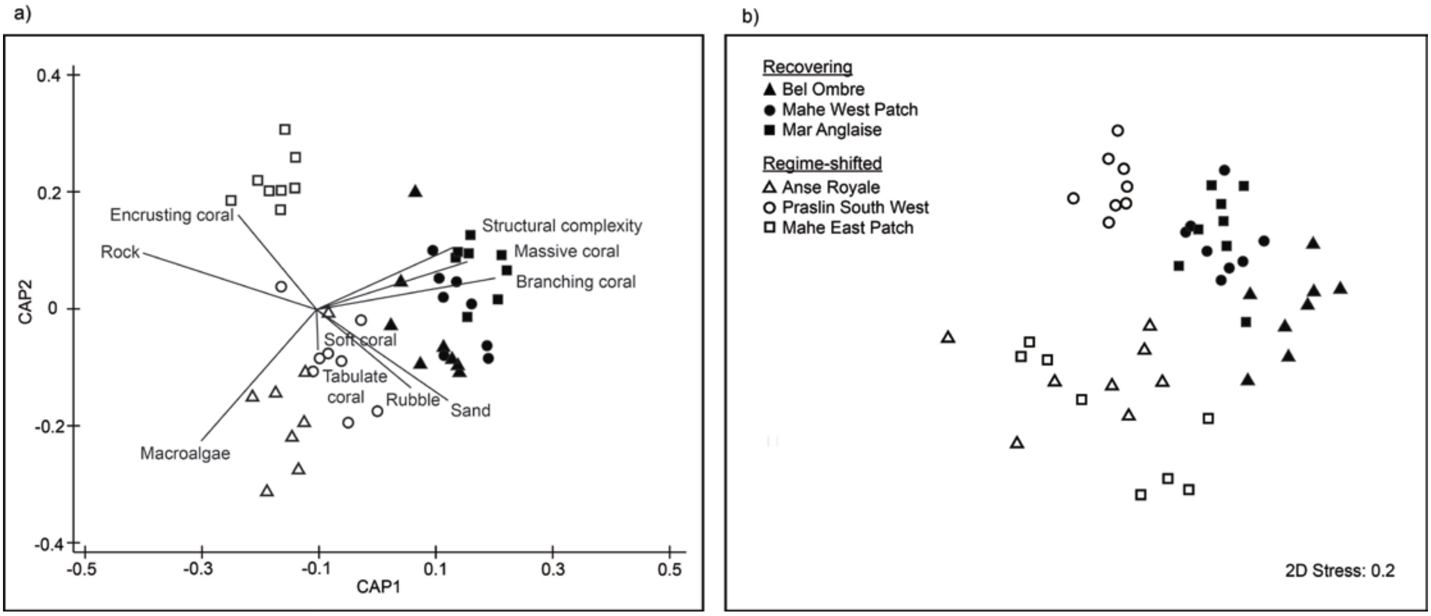

Fig. 1. Composition of the reef community on six sites surveyed in the Seychelles inner island group in April 2014, with sites designated by symbols, and reef state indicated by colour (Recovering = black, Regime-shifted = white). (a) Canonical analysis of principal coordinates (CAP) ordination plot of benthic communities based on Bray-Curtis similarity measures, and (b) Non-metric multidimensional scaling plot (MDS) of the fish community on recovering and regime-shifted sites.

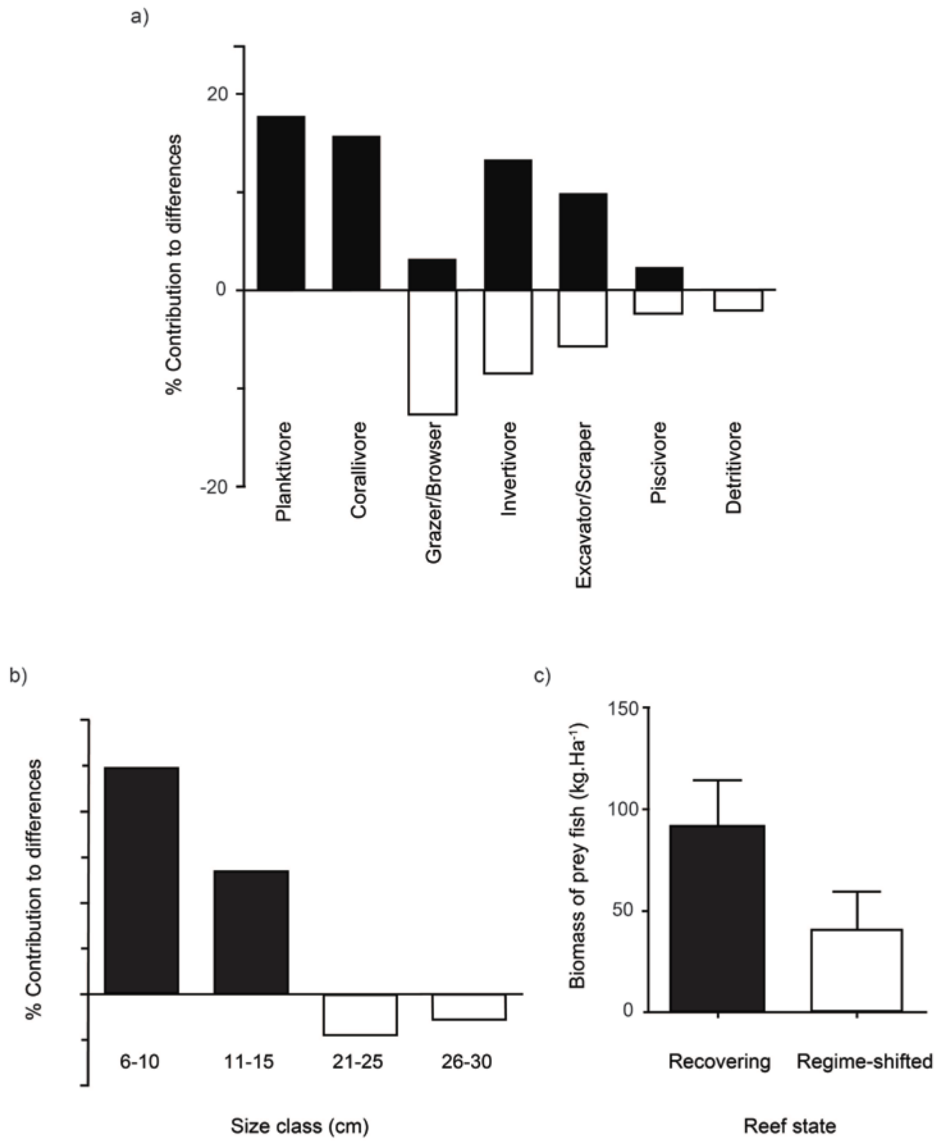

Fig. 2. Differences in the fish community composition between regime-shifted (white) and recovering sites (black). (a) The percentage contribution of fish functional groups to the difference between reef states in Seychelles in 2014, based on the summed percentage contribution of each functional group from a SIMPER analysis of the species assemblages. Bars represent the percentage contribution for each species that was higher on either reef state. (b) The percentage contribution of the 5 cm TL size classes that accounted for 90% dissimilarity between reef states from a SIMPER analysis of size class composition. (c) Total mean prey biomass (± standard error; kg.Ha^{-1}) available, calculated as the total biomass of fish of TL ≤ 15 cm on regime-shifted and recovering reefs.

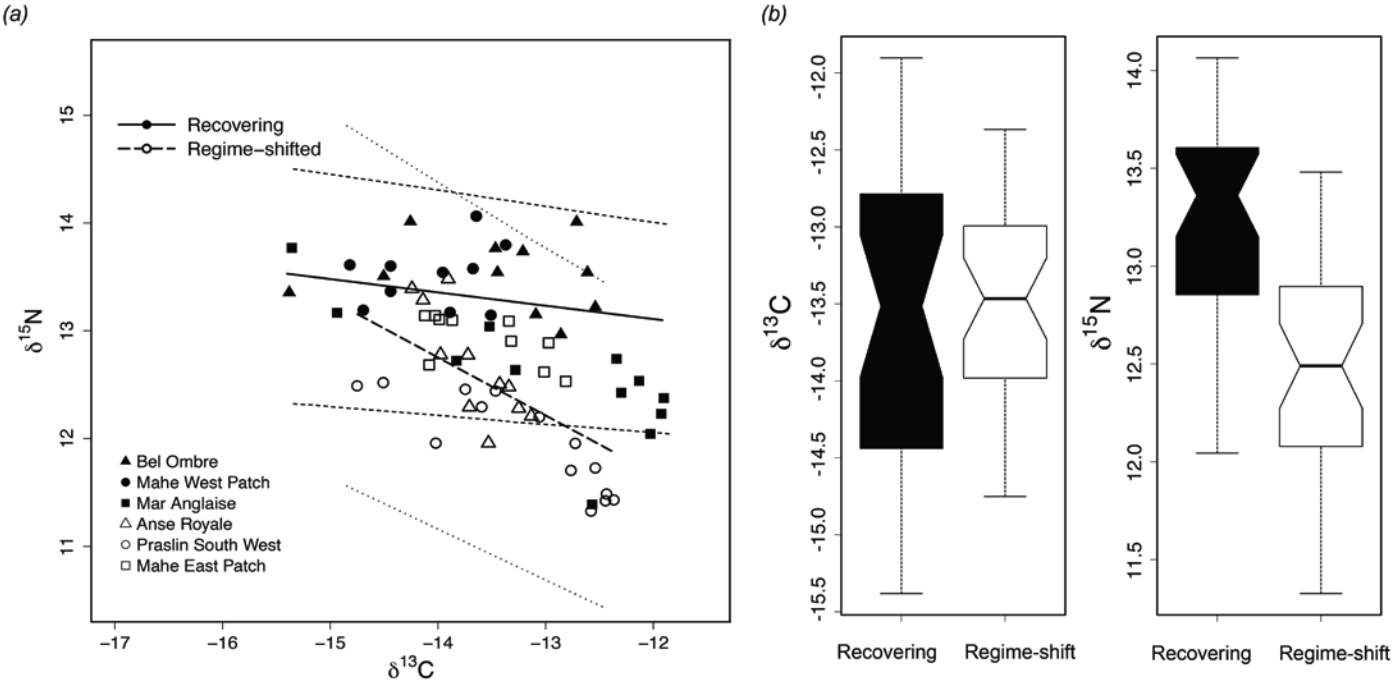

Fig. 3. Stable isotope signatures of *Cephalopholis argus* sampled from recovering and regime-shifted reefs in the Seychelles inner island group. (a) Biplot of δ^{13}C and δ^{15}N values from white muscle tissue, showing the differences in trophic niche of fish from different reef states in terms of their carbon food sources (δ^{13}C) and trophic level (δ^{15}N). Sampling sites are indicated by different shaped symbols, and reef states are designated by colour. Bold lines indicate the best-fit linear model for fish sampled from recovering (solid line) and regime-shifted (dashed line) reefs. Finely dashed lines indicate the 95% confidence interval around each model fit. (b) Notched boxplots of δ^{13}C and δ^{15}N for fish sampled from regime-shifted (n = 35) and recovering reefs (n = 34). Whiskers indicate maximum and minimum values, box height shows the interquartile range, the bold centre line is the median, and diagonal notches in the boxes illustrate the 95% confidence interval around the median.

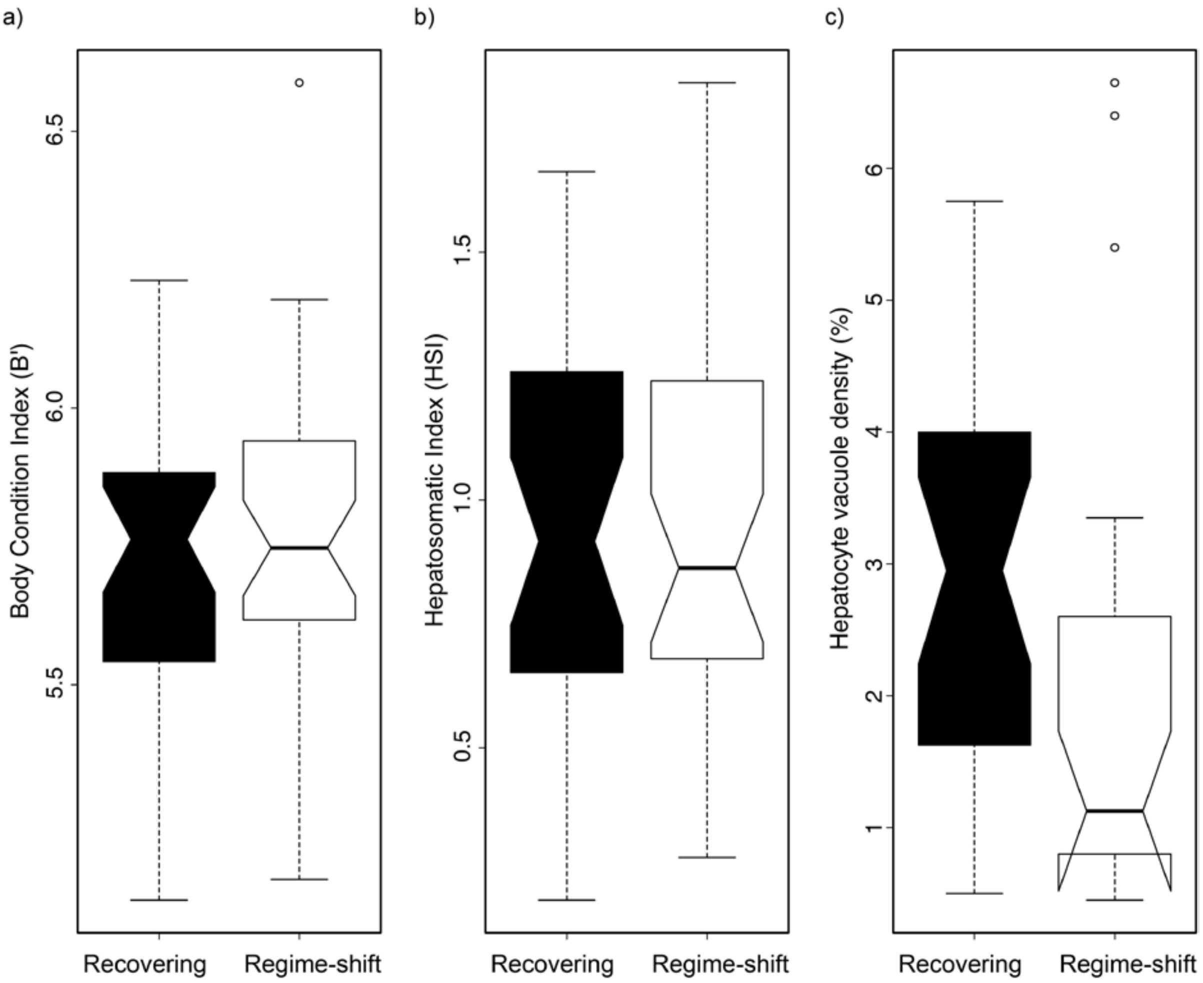

Fig. 4. Body condition indices of *Cephalopholis argus* sampled from regime-shifted (n = 35) and recovering (n = 34) reefs in Seychelles. Notched boxplots of (a) body condition in B’, (b) hepatosomatic index (HSI), and (c) hepatocyte vacuole density from liver sections, show an increasingly fine scale level of detection of differences in body condition between fish from different reef states.

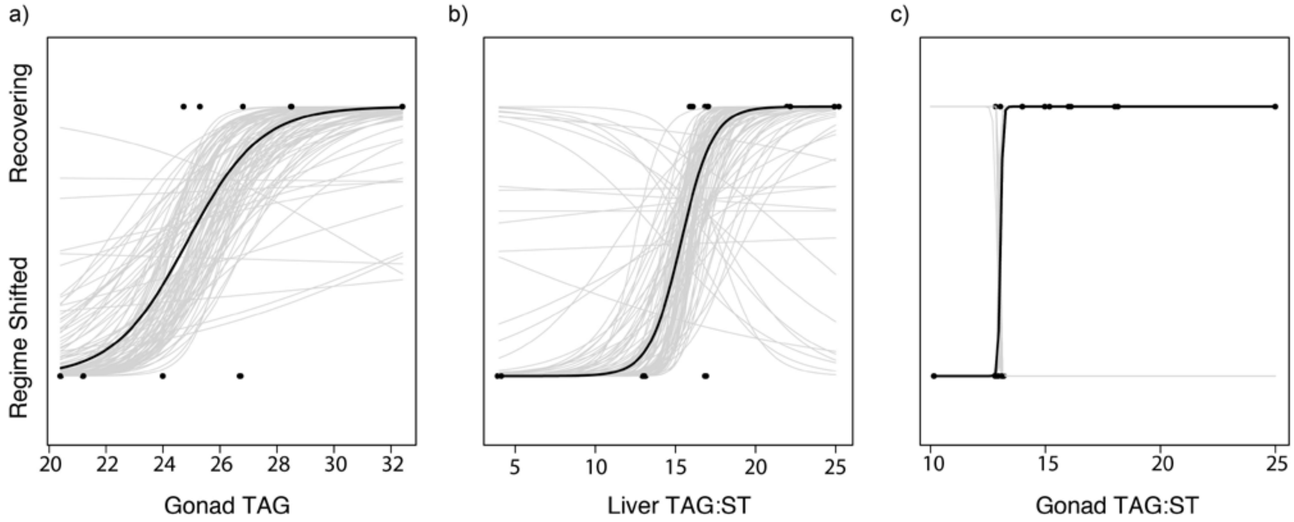

Fig. 5. Lipid composition and logistic regression results showing a lower concentration of (a) triacylglycerols (TAG; μg.mg^{-1} ww) in the gonads of spawning female *Cephalopholis argus* sampled from regime-shifted reefs, than for fish sampled from recovering reefs (Bootstrap parameter point estimate [95% confidence interval]: 0.741, [0.436, 1.047]). Similarly, the ratio between TAG and sterol concentrations (TAG:ST) was lower in the (b) liver (1.086, [0.659, 1.513]) and (c) gonad (18.809, [18.439, 19.178]) tissues of spawning females from regime-shifted sites. Grey lines represent variability in potential model fits.