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CORAL REEF MESOPREDATOR TROPHODYNAMICS

IN RESPONSE TO REEF CONDITION

Thesis submitted by

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for the degree of Doctor of Philosophy

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Townsville, Queensland, Australia
Acknowledgements

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Statement on the contribution of others

This thesis includes collaborative work from my supervisors Prof Nicholas Graham, Dr Aaron MacNeil, Dr Glenn Almany, Prof Geoffrey Jones, and Dr Andrew Hoey, as well as with Dr Shaun Wilson, Dr David Williamson, and Dr Nathalie Bodin. I led all collaborations and was responsible for the project designs, data collection, analysis and interpretation. My supervisors and co-authors provided intellectual guidance, equipment, assistance with fieldwork, technical and editorial assistance and financial support.

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## Contribution of authors to publications

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Abstract

Habitat degradation in coral reef ecosystems is occurring at an unprecedented rate and scale around the world. This habitat decline is driven by both intensifying local stressors and the escalating effects of global climate change. Concurrently, the ubiquitous loss of large consumers from ecosystems, known as trophic downgrading, has important ramifications for the function and resilience of both terrestrial and marine ecosystems. Mesopredators represent an important component of coral reef ecosystems, both economically, supporting large reef fisheries, and ecologically, as potentially important drivers of reef trophodynamics. While there has been substantial focus on the effects of habitat degradation on the small-bodied reef fish community, which is closely associated with the reef benthos, relatively little is known about the implications for piscivorous reef mesopredators. These large-bodied, mobile species are less directly reliant on the reef benthos, and likely to experience the strongest effects of habitat degradation mediated via the fish community on which they prey. This thesis addresses this important research gap by focusing on four key implications of habitat degradation for mesopredators and their role in coral reef trophodynamics.

Dietary adaptability is likely to be an important factor in determining the vulnerability of piscivorous mesopredators to changing prey availability associated with habitat degradation. In chapter 2, I use stable isotope analyses of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) to investigate whether coral trout (*Plectropomus maculatus*), in the Keppel Island group on the southern Great Barrier Reef (GBR), can switch their diet to exploit the altered prey base on degraded reefs. Coral bleaching and sediment-laden flood plumes have driven extensive live coral loss on these reefs. The resulting shift in dominant prey species from pelagic plankton-feeding damselfishes to benthic algal-
feeding species, represents a shift in the principal carbon pathways in the food web. The δ\(^{13}\)C signature in coral trout shifted from a more pelagic to a more benthic signal, reflecting the prey community shift, and demonstrating that trout appear to alter their diets as reefs degrade. Nitrogen signatures also indicated that trout with a more benthic carbon signature were feeding at a lower trophic level, indicating a shorter food chain on degraded reefs. Despite this apparent adaptability, mesopredator populations at this location are in steep decline, driven primarily by reduced total available prey biomass.

Thus, despite dietary flexibility conferring a degree of trophic resilience in the short term, mesopredators are nonetheless vulnerable to the effects of habitat degradation. Due the relative longevity of many mesopredator species, sublethal effects of changing prey resources may be difficult to detect. Chapter 3 investigates whether a common mesopredator species (Cephalopholis argus) in the Seychelles inner island group shows evidence of a loss of condition due to habitat degradation. Following extensive live coral loss during the 1998 mass bleaching event, some reefs have regained high coral cover, while others have experienced a regime shift to an algae-dominated state. Stable isotope analyses demonstrated that C. argus on regime-shifted reefs fed lower down the food chain, on a narrower range of carbon sources, than those on recovering reefs, suggesting a simplification of the food web. Histology of liver tissue showed reduced hepatocyte vacuolation in fish from regime-shifted reefs, and reduced lipid stores in spawning females. Reduced energy reserves can lead to decreased growth rates, fecundity and survivorship, ultimately resulting in long-term population declines.

Long-term effects of regime-shift in coral reef ecosystems can substantially alter the trophic structure of fish communities, yet understanding of how these changes manifest through time is limited. In chapter 4, I use a 20-year dataset documenting
changes in the benthic and reef fish communities on the Seychelles inner island reefs, to
examine how trophic structure has changed on recovering and regime-shifted reefs
following the 1998 mass bleaching event. I demonstrate how reef fish communities
become increasingly dissimilar, as the benthic states diverge with time since
disturbance. Trophic pyramids of relative biomass on regime-shifted reefs developed a
concave structure, with increased herbivore biomass supported by increased algal
resources, a loss of mid trophic level specialist species, including corallivores, and
biomass in the upper trophic levels maintained by large-bodied generalist species. In
contrast, on recovering reefs, after an initial loss of mid trophic level biomass, pyramids
developed a bottom-heavy structure, which is commonly predicted in stable ecosystems
by the theory of energy transfer efficiency in food webs.

Benthic habitat and associated fish communities can also be altered via climate-
driven shifts in coral assemblages. One of the predicted characteristics of novel future
coral ecosystems is a loss of thermally sensitive coral taxa and an increasing dominance
of taxa with higher thermal tolerance, many of which have low structural complexity. In
chapter 5, I used a patch reef experiment at Lizard Island on the northern GBR to
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communities which established naturally on the low structure ‘tolerant’ patch reefs had
lower diversity, abundance and biomass than ‘vulnerable’ reefs with higher structural
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cost to condition.
My research provides novel insight into the effects of habitat degradation on the
trophodynamics of coral reef mesopredators, mediated via the fish community on which
they prey. I demonstrate that while certain mesopredator species may be able to adapt
their diets to changing prey availability, their trophic niche becomes altered as they feed
further down the food chain, and they may experience sub-lethal costs due to reduced
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Chapter 1: General Introduction

CHAPTER 1
General Introduction

1.1 Background and State of Knowledge

Coral reefs around the world are degrading at an unprecedented rate due to the cumulative impacts of both local human disturbance and the escalating effects of climate change (Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Pandolfi et al. 2011, Ban et al. 2014, Graham et al. 2015). Despite the pervasive extent of this coral habitat decline, the implications for components of associated fish communities remain poorly understood. To date, most investigations of the effects of reef degradation on fishes have focused on small-bodied species, particularly corallivores, planktivores and herbivores, that are directly associated with the reef substrate (e.g. Wilson et al. 2006, Pratchett et al. 2008). In contrast, relatively little research has considered the effects of habitat degradation on higher trophic levels. Reef mesopredators, defined here as medium to large bodied piscivorous fishes that are resident on the reef (e.g. members of the families Serranidae and Lutjanidae), play an important ecological role in coral reef ecosystems, transferring energy up the food chain to apex predators (Polovina 1984). They may also have an important top-down and intermediate influence on coral reef food webs (Friedlander and DeMartini 2002, Graham et al. 2003, Palacios et al. 2016a), but their role remains poorly understood. Many of these species form a significant component of commercial, recreational and subsistence coral reef fisheries (Cinner et al. 2009, Lédée et al. 2012, GBRMPA 2014), as well as supporting an extremely lucrative global fishing tourism industry (World Bank 2012). Understanding whether and how mesopredators are impacted by habitat degradation is therefore of great ecological and
economic importance, particularly given the increasing scale, frequency, and intensity of stresses on coral reefs (Pandolfi et al. 2003).

Degradation from localised anthropogenic threats (e.g. overfishing, pollution, sedimentation) and natural perturbations (e.g. storms, disease, predator outbreaks), combined with increasing effects of climate change (e.g. coral bleaching, ocean acidification), impact on reef associated fish communities in a variety of ways. These impacts range from loss of live coral cover due to biological disturbances (e.g. predation by crown-of-thorns starfish (COTS), bleaching) that do not affect reef structural integrity in the short term (Sano et al. 1987, Sheppard et al. 2002), to the loss of both live coral cover and structural habitat due to physical disturbances (e.g. storm damage, destructive fishing practices). Both loss of live coral cover and reduced structural complexity uniquely alter the composition and abundance of the small-bodied reef fish community associated with the reef (Pratchett et al. 2011), thereby changing the prey base available to resident mesopredators.

The effect of disturbance on small-bodied reef fish communities has been the focus of a number of studies that have documented changes in fish abundance and diversity following reef degradation (e.g. Jones et al. 2004, Wilson et al. 2006, 2008, 2010, Pratchett et al. 2008, Graham et al. 2011). These have shown substantial variability in the specific responses of different taxa and functional groups, due largely to the type of disturbance and the degree of specialisation in their resource requirements (Munday 2004, Wilson et al. 2006, Pratchett et al. 2008). For example, declining live coral cover typically results in decreased abundance and diversity of coral feeding fishes (Pratchett et al. 2006), species that rely on live corals for shelter (Booth and Beretta 2002), or species whose recruitment depends on live coral for larval settlement cues (Öhman et al. 1998, Jones et al. 2004). Conversely, these degraded reefs can host
an increased abundance and diversity of herbivores, at least in the short–term, that take advantage of the increased algal cover that commonly follows disturbances that reduce live coral cover (Sheppard et al. 2002). Disturbance that results in a loss of habitat structural complexity (Graham and Nash 2013, Graham 2014), or changes in coral species assemblages (Marshall and Baird 2000, McClanahan et al. 2004) can detrimentally affect a wide range of small-bodied fishes by exposing them to increased predation (Graham et al. 2003) and density-dependant competition for limited shelter (Holbrook and Schmitt 2002, Boström-Einarsson et al. 2014, Bonin et al. 2015). Evidently, the effects of habitat decline on small-bodied species are relatively well studied.

However, comparatively little is known about the implications of degradation for higher trophic groups such as mesopredators. Changing prey availability is one of the primary ways in which habitat decline impacts mesopredator trophodynamics, and has been recognised as a leading driver of piscivore abundance (Graham et al. 2007, Wilson et al. 2008). However, few studies have empirically assessed the capacity of mesopredators to respond to these effects. This knowledge gap is clearly illustrated in a comprehensive review of the impacts of degradation on reef fishes by Wilson et al. (2006), who were unable to include any data or studies on piscivorous mesopredators due to lack of data available (Fig.1).
Fig. 1.1 Results of a meta-analysis illustrating mean responses of fish functional groups to biological and physical disturbance (error bars show 95% confidence intervals). The absence of data on piscivorous mesopredators highlights our lack of understanding about the effects of habitat degradation on this functional group (adapted from Wilson et al. 2006, see Appendix E for permissions).

Changes in coral assemblages on reefs due to climate change (McClanahan et al. 2007, Darling et al. 2013), is a further mechanism whereby associated fish community structure is likely to be affected. The response of coral reefs in the Indo-Pacific to the impacts of climate change has been observed to be non-random, with some species showing much higher susceptibility to coral bleaching and mortality than others (e.g. Marshall and Baird 2000, Loya et al. 2001). This is resulting in large-scale changes in coral species composition (McClanahan et al. 2007, Van Woesik et al. 2011), with a shift towards more thermally tolerant species that could result in reefs with reduced structural complexity (e.g. McClanahan et al. 2007, Graham et al. 2008, Riegl et al. 2012). The susceptibility of reef fish to this loss of niche space diversity is likely to vary with their body size and degree of specialization (Munday 2004, Pratchett et al. 2008,
While there is a degree of predictability associated with corals and smaller-bodied fish species based on what we know about their vulnerability to expected scenarios of climate change, little is known about the repercussions of these changes for larger piscivorous mesopredators.

To date, a substantial amount of research has focused on the top-down effects of exploitation on abundance and biomass of coral reef mesopredators (e.g. Dulvy et al. 2004), as well as examining the effectiveness of marine protected areas (MPAs) in conserving these species (e.g. McClanahan and Arthur 2001, Harrison et al. 2012, Varkey et al. 2012). The diet composition and feeding ecology of commercially important fisheries species (St John 1999, Greenwood et al. 2010, Wen et al. 2012), and the effect of MPAs on the trophic relationships of reef fish have also been addressed, but little effort has been explicitly focused on the effects of habitat degradation on piscivorous mesopredators. Being relatively large and mobile, mesopredators are less likely to be directly impacted by the loss of live coral cover or structure (Walters et al. 1999). However, altered abundance and composition of the available prey fish community due to habitat degradation may affect the condition and abundance of piscivorous mesopredators, thereby disrupting the transfer of energy from lower to higher trophic levels within the coral reef ecosystem (Polovina 1984, Munday et al. 2007).

Trophic pyramids of biomass or numerical abundance have traditionally been used to represent food web structure (Lindeman 1942), providing a visually intuitive means of examining how habitat degradation is likely to affect energy flow among trophic levels (Trebilco et al. 2013). Bottom-heavy pyramids generally prevail in most ecosystems (Hatton et al. 2015) in the absence of energy subsidies (Mourier et al. 2016), due primarily to the principals of energy transfer efficiency (Trebilco et al. 2013).
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2013). Disruption of food webs either from top down drivers, such as extraction (e.g. fishing), or bottom up effects, such as habitat degradation (e.g. coral bleaching), is often evident through changes in this fundamental trophic pyramid structure. These changes highlight potential perturbations of food web dynamics, such as trophic replacement or trophic cascades (Pace et al. 1999, McClanahan and Muthiga 2016), and allow for comparison of trophic structure across gradients of disturbance (Graham et al. 2017, Fig.2). The widespread effect of human disturbance on marine ecosystems has generated intense interest in the intrinsic trophic structure of marine ecological communities (Sandin et al. 2008, Trebilco et al. 2013), yet the role of mesopredators has been largely ignored, despite their having top-down effects on prey and linking apex-predators to the forage base (e.g. Polovina 1984, Palacios et al. 2016). This pivotal ecological niche occupied by mesopredators means that loss of these species from ecosystems has the potential to have a disproportionately large effect on biodiversity and ecosystem function (Duffy 2003).

Trophic downgrading, which is the loss of high-level consumers from numerous ecosystems around the world, is becoming an issue of increasing global concern (Estes et al. 2011). This is often a cryptic process due to the long generation times of many larger predatory species, which masks the effects of habitat decline in the short term. Any impacts of altered prey availability on mesopredator abundance may take years to become evident. However, effects on mesopredator condition preceding a decline in abundance are likely to occur on shorter timescales. For example, degradation has indirect sub-lethal effects on condition in small-bodied reef fishes during the weeks and months following disturbance (Pratchett et al. 2004, 2006, Graham 2007, Feary et al. 2009). Studies on coral-feeding species have shown that decreased availability of food resources, or altered prey options, can result in depleted energy reserves (Pratchett et al.
2004, Berumen et al. 2005), reduced growth rates (Kokita and Nakazono 2001), survivorship, and fecundity (Pratchett et al. 2006). Despite loss of condition, these fishes can persist in the short term, but their populations are likely to decline in the long term due to decreased fitness (Jones and McCormick 2002). The potential exists for similar effects on piscivorous mesopredators when their prey populations are affected by habitat degradation, with the strength of such effects mediated by trophic linkages in the foodweb.

![Image of trophic pyramid structure of coral reef fish communities](image)

**Fig. 1.2** Change in relative biomass trophic pyramid structure of coral reef fish communities across a human-driven gradient of total community biomass, based on empirical data of 253 reefs, across nine countries in the Indian Ocean. Trend lines show the modelled mean proportion and 95% confidence interval of each trophic position category (adapted from Graham et al. 2017; see Appendix E for permissions).
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Diet specificity is likely to be an important predictor of disturbance effects on mesopredator condition. Specialist consumers depend on a few strong trophic relationships and are likely to be more vulnerable to changes in their preferred prey (Graham et al. 2011). In contrast, generalists can switch their diet in response to oscillations further down the food web in order to maintain condition, thereby increasing their capacity to adapt to ecosystem change (Munday 2004). Prey switching by generalist predators may assist in stabilising ecosystems affected by disturbance (McCann et al. 1998, 2005); by shifting their diets, predators can depress prey species advantaged by disturbance (e.g. benthic algal feeding species), allowing those disadvantaged by disturbance (e.g. pelagic plankton feeders) to recover. Understanding whether mesopredators on reefs can switch diets and how much reef predators rely on particular components of the reef ecosystem for their energy is therefore important for predicting how they will respond to changes in their prey base and how this will affect food web structure as a whole (Rooney et al. 2006, Gross et al. 2009).

The ability to adapt to changing prey availability may allow mesopredators to ameliorate the effects of changing prey availability in the short term, but in the long term, these altered dietary niches may carry a cost for both ecosystem function and predator condition. Detecting these sub-lethal effects before they manifest as lag effects in the food web is challenging (Graham et al. 2007), and requires an examination of consumer physiology. Habitat degradation is often associated with a loss of diversity (Pratchett et al. 2014), which can alter the dominant carbon pathways and mean trophic level within an ecosystem (Graham et al. 2017, Hempson et al. 2017). Stable isotope analyses provide an elegant tool for detecting changes in a consumer’s trophic niche, with $\delta^{13}C$ isotope signatures providing information on carbon sources within the food web (DeNiro and Epstein 1978, Wada et al. 1991), and
δ¹⁵N revealing the trophic level at which a consumer is feeding (Minagawa and Wada 1984, Post 2002a). Several techniques also exist for detecting a potential cost to mesopredator condition due to these altered trophodynamics. At a coarse level, growth rates or morphometric indices such as Fulton’s K provide a measure of a fish’s robustness, while the hepatosomatic index (HSI) and gonadosomatic index (GSI) compare liver and gonad mass to body mass respectively, as an indication of the liver energy stores and fecundity of an individual. Detecting costs to consumer condition may, however, require more subtle techniques, at least in the short term. Using histology to examine the density of hepatocyte vacuoles (lipid storage bodies) in the livers of fish, is a cost-effective means of assessing energy reserves (Pratchett et al. 2004), while more detailed lipid analyses of different tissues can provide extensive insight into consumer’s lipid physiology, condition and fecundity (Zudaire et al. 2014). Insights gained from these techniques allows managers and conservationists to adapt their approaches to better support the sustainability of mesopredator populations under stress, before they collapse.

As predators are widely considered to exert an important top-down effect in ecosystems (Duffy 2003, Palacios et al. 2016a), loss of these species could have extensive implications for ecosystem structure and function (McCauley et al. 2010). Improving our understanding of how mesopredators are affected by habitat degradation is thus of key importance for effective conservation and fisheries management. Given the widespread threats facing coral reefs and the increasing extent of habitat degradation from disturbance (Pandolfi et al. 2003), the lack of knowledge of how this decline affects mesopredators (Fig.1) and their role in the food web is cause for concern. As reef fish communities become increasingly altered in response to habitat degradation, it is important to (i) establish whether mesopredators are able to adapt their diets to
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exploit changing prey resources, and (ii) to determine if changing prey availability has sub-lethal effects on mesopredators that may impact their populations in the long term. Further, (iii) long-term investigations of the effects of habitat condition on coral reef food web structure, as well as (iv) experimental tests of how predator-prey dynamics are influenced by predicted habitat modifications, are key to improving our understanding of how the trophic roles played by mesopredators are affected by habitat degradation.

1.2 Aims and Thesis Outline

This objective of this study was to address the need to empirically assess how the effects of habitat degradation propagate through the reef fish community to reef associated mesopredators. To do so, this thesis focused on two key research aims: First, to understand how changes in prey availability due to coral reef habitat degradation affect the diet and condition of piscivorous reef mesopredators; and second, to investigate how changes in coral habitat affect the trophic structure of reef fish communities and what the implications are for reef mesopredators. To address these aims, four key research questions were identified:

1.) Do mesopredators switch their diet in response to changing prey availability due to reef degradation?

2.) Do mesopredators experience sub-lethal effects from changing prey availability due to habitat degradation?

3.) How does trophic structure change with reef condition and what are the implications for the trophic role of reef mesopredators?

4.) How do predicted changes in coral assemblages moderate mesopredator-prey dynamics?
Each question is addressed by a separate data chapter outlined below, and corresponds directly to the publications derived from this thesis. **Chapter 2** uses bulk stable isotope analysis of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) to investigate whether a mesopredator species (*Plectropomus maculatus*) can adapt its diet to changing prey availability, as reef prey fish communities shift from high abundances of planktivorous species, towards benthic algae-feeding species with a decline in live coral cover. This study was carried out in the Keppel Island group on the southern Great Barrier Reef (GBR), which has experienced extensive coral habitat degradation due to bleaching, sedimentation, and freshwater flood plumes (Williamson et al. 2016), and examines the key drivers of the large mesopredator population declines associated with this degradation. **Chapter 3** investigated the potential sub-lethal effects of habitat degradation and changing prey availability on an important mesopredator species (*Cephalopholis argus*) in the Seychelles granitic inner island group in the Western Indian Ocean. These reefs suffered extensive coral loss due to the 1998 mass bleaching event, with subsequent trajectories of recovery and regime-shift developing since (Graham et al. 2015). Using morphometric condition indices, histology, stable isotopes, and lipid analyses, this chapter investigates whether mesopredators on regime-shifted show signs of decreased energy reserves or an altered trophic niche. **Chapter 4** also compares the alternate reef states on the Seychelles reefs (recovering vs regime-shifted), using a 20-year dataset to examine how the trophic structure of reef fish communities has changed from a pre-bleaching state (1994) to post-bleaching (2005, 2014). It demonstrates how changing trophic structure associated with habitat degradation affects the functional composition of the reef fish community, and the likely implications of this change for piscivorous reef mesopredators and energy flow in the food web. **Chapter 5** then goes on to examine how predicted changes in the reef benthos due to
climate-driven shifts in coral assemblages may affect reef mesopredators and their prey fish community, using a patch reef array in the lagoon at Lizard Island on the northern GBR. Patch reefs represented both reefs consisting of coral taxa of all levels of thermal tolerance, and reefs dominated by coral taxa of high thermal tolerance. Fish communities were allowed to recruit naturally to the patch reefs, before the introduction of a mesopredator (*Cephalopholis boenak*). Using this experimental approach, this study assessed the likely effects of altered coral assemblages on mesopredators via condition indices and lipid analysis, and examined the effect of mesopredators on the prey fish communities associated with different assemblages. Finally, Chapter 6 provides a general discussion of the outcomes of the four data chapters. It integrates the results of the four studies and evaluates their contribution to the overall research aims of the thesis.
CHAPTER 2

Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation

2.1 Abstract

Diet specificity is likely to be the key predictor of a predator’s vulnerability to changing habitat and prey conditions. Understanding the degree to which predatory coral reef fishes adjust or maintain prey choice, in response to declines in coral cover and changes in prey availability, is critical for predicting how they may respond to reef habitat degradation. Here we use stable isotope analyses to characterise the trophic structure of predator-prey interactions on coral reefs of the Keppel Island Group on the southern Great Barrier Reef, Australia. These reefs, previously typified by exceptionally high coral cover, have recently lost much of their coral cover due to coral bleaching and frequent inundation by sediment-laden, freshwater flood plumes associated with increased rainfall patterns. Long-term monitoring of these reefs demonstrates that, as coral cover declined there has been a decrease in prey biomass, and a shift in dominant prey species from pelagic plankton-feeding damselfishes to territorial benthic algal-feeding damselfishes, resulting in differences in the principal carbon pathways in the food web. Using isotopes, we tested whether this changing prey availability could be detected in the diet of a mesopredator (coral grouper, *Plectropomus maculatus*). The $\delta^{13}C$ signature in grouper tissue in the Keppel Islands shifted from a more pelagic to a more benthic signal, demonstrating a change in carbon sources aligning with the change

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in prey availability due to habitat degradation. Grouper with a more benthic carbon signature were also feeding at a lower trophic level, indicating a shortening in food chains. Further, we found a decline in the coral grouper population accompanying a decrease in total available prey biomass. Thus, while the ability to adapt diets could ameliorate the short-term impacts of habitat degradation on mesopredators, long-term effects may negatively impact mesopredator populations and alter the trophic structure of coral reef food webs.

2.2 Introduction

Coral reef ecosystems are rapidly being degraded through multiple disturbances from human activities and the cumulative impacts of climate change (Hoegh-Guldberg et al. 2007, Ban et al. 2014, Graham et al. 2015). Such loss of habitat is predicted to be one of the most important drivers of marine defaunation in the next century (McCauley et al. 2015). Habitat degradation directly threatens coral-dependent species of coral reef fish, resulting in extensive changes in abundance and diversity within reef fish assemblages (e.g. Jones et al., 2004; Wilson et al., 2006, 2008, 2010; Pratchett et al., 2008). Reef fishes differ in their response to habitat degradation depending on both the type of disturbance and the degree of specialisation in resource requirements (Graham et al. 2011). Although reductions in live coral cover and habitat structural complexity often lead to declines in the abundances of many reef fishes, some species may increase, resulting in shifts in assemblage structure (Bellwood et al. 2006). For example, degraded reefs are typified by increases in algal cover that can benefit herbivorous fishes, at least in the short term (Pratchett et al. 2008). While there is a reasonable understanding of how coral reef fishes that are directly reliant on corals respond to reef habitat degradation (Wilson et al. 2006), relatively little is known about how indirect effects mediated via the foodweb affect higher trophic levels.
The long generation time of many larger predatory species at higher trophic levels means that the impacts of foodweb changes may take years or even decades to become apparent. This is one of the primary reasons cited by Estes et al. (2011) for the cryptic nature of ‘trophic downgrading’, a process whereby large consumers are being lost from ecosystems at a global scale. As high-level consumers are widely considered to exert important top-down effects in food webs (Duffy 2003), trophic downgrading could have wide-ranging implications for ecosystem structure and a broad suite of ecological processes (McCauley et al. 2010).

Medium- to large-bodied reef fishes that are mesopredators (e.g. Serranidae, Lutjanidae and Lethrinidae) are important for mediating energy flow between herbivores and apex predators on coral reefs (Polovina 1984). Many mesopredators are also targeted by commercial, recreational, and subsistence fisheries (Friedlander and DeMartini 2002, Cinner et al. 2009, Lédée et al. 2012, GBRMPA 2014). However, our understanding of the effects of habitat disturbance on these species is relatively poor. Changing prey availability is one of the primary mechanisms through which habitat disturbance can affect mesopredator trophic dynamics, and can be an important driver of total piscivore abundance (Graham et al. 2007, Wilson et al. 2008). While large mobile apex predators may have the capacity to respond to localized degradation by moving to remnant healthy and productive habitats, less mobile reef-associated mesopredators may need to modify their prey selection in degraded habitats in order to fulfil their energetic requirements (Shpigel and Fishelson 1989). Consequently, the persistence of reef-associated mesopredator populations will depend to a large extent on their ability to adapt their diets as reef habitats become increasingly altered.

Gut content analysis has been traditionally used to collect dietary data in marine predators (Cortés 1997). However, this technique has a number of limitations, including
being only a snapshot view of a consumer’s diet (Pinnegar and Polunin 1999), loss of
regurgitated prey during capture, unidentifiable stomach contents, and differential
digestion rates among prey types (Baker et al. 2014). Stable isotope analyses of tissue
samples are a powerful tool for understanding the trophic ecology of consumers
(Boecklen et al. 2011, Letourneur et al. 2013) that provide a dietary signal integrated
over extended time periods (Pinnegar and Polunin 2000, Phillips and Gregg 2003). A
consumers’ \( \delta^{15}N \) isotopic signature is typically enriched relative to their food source,
making it possible to calculate a predator’s trophic position (Post et al. 2000, Post
2002a, Layman et al. 2007). In contrast, \( \delta^{13}C \) signatures remain relatively unchanged up
the food web, providing a means to identify carbon sources (Peterson 1999, Fry 2006,
McMahon et al. 2016). In the marine environment, the primary sources of variation in
predator \( \delta^{13}C \) signatures include geographic position (i.e. latitude or inshore vs. offshore
production; McMahon et al., 2016), alternative carbon pathways (i.e. benthic vs. pelagic
production; Hobson et al., 1994), and prey choice (Fry and Sherr 1984).

Stable isotopes can also uniquely quantify changes in total food web structure (Post
2002a). Food chain length (FCL) is a central concept in trophic ecology and a widely
accepted metric used to describe changing trophic interactions in ecological
communities (Post et al. 2000, Post 2002b, Schriever 2015). Habitat degradation can
alter the trophic structure of an ecosystem (Dobson et al. 2011), with a high frequency
and intensity of disturbance predicted to result in shorter food chains (Menge and
Sutherland 1987). However, empirical understanding of how FCL responds to
disturbance has been limited by the inability to quantify this key property of trophic
ecology. Stable isotope techniques offer an opportunity to investigate changes in
trophodynamics from the perspective of discrete trophic levels, while still capturing the
dynamics of energy flow in the food web (Post 2002a).
In this study, we use stable isotope analysis to investigate whether changes in prey availability due to habitat degradation affects the trophic niche of a coral reef mesopredator. The specific objectives of the study were to (i) map food web trophic structure in terms of both carbon source ($\delta^{13}$C) and trophic level ($\delta^{15}$N) on degraded and healthy reefs; (ii) quantify changes in the prey fish community associated with habitat degradation; (iii) use stable isotopes to determine whether coral grouper altered their diets in response to changing prey availability; (iv) assess whether food chain length is affected by habitat degradation, and (v) investigate how grouper populations are responding to changes in trophic structure.

2.3 Methods

2.3.1 Study site

The study was carried out in the Keppel Island Group (Fig. 2.1) in the southern section of the Great Barrier Reef (GBR), Australia. Coral reefs surrounding the Keppel Island Group were characterised by exceptionally high coral cover up until the early 2000’s (Elvidge et al. 2004). A localised bleaching event in 2006 reduced coral cover by 27% (Williamson et al. 2014) and, despite these reefs demonstrating the potential for fast recovery from this acute disturbance (Diaz-Pulido et al. 2009), long-term monitoring over the past decade has documented steady habitat degradation associated with both coral bleaching and freshwater river flood plumes (Williamson et al. 2014). A major flooding event occurred between December 2010 and January 2011 (Berkelmans et al. 2012), resulting in an overall decline in live hard coral cover of 37% (Williamson et al. 2014) and an increase in dead coral, rubble and macroalgal cover (for details of site level changes, see Table S1). In 2009, after several years of recovery and prior to the flood plume disturbances, 75% of monitored reefs in the Keppel Islands supported
at least 50% cover of live coral. In 2013 however, only 10% of monitored reefs had retained above 50% live coral cover, and 15% of reefs supported less than 5% live cover (Williamson et al. 2016). Accompanying this habitat decline, was a change in the associated prey-fish community, from an assemblage characterised by large schools of plankton-feeding damselfishes (e.g. *Chromis nitida*), to one dominated by territorial algal-feeding damselfishes (e.g. *Pomacentrus wardi*; Williamson et al., 2014). Coral grouper (*Plectropomus maculatus*) are the dominant coral reef mesopredator in the Keppel Islands, with mean densities of 150 individuals per hectare (Williamson et al. 2014).

2.3.2 Fish and benthic surveys

Reef fish and benthic communities in the Keppel Islands were surveyed prior to the flood event (2009, pre-disturbance), and twice after the flood event (2011 and 2013, post-disturbance). These surveys were conducted at four fringing reef sites (Clam Bay, Big Peninsula, Halfway Island, Middle Island; Fig. 2.1) as part of a long term monitoring program, using underwater visual census (UVC) on SCUBA according to the methods established in Williamson et al. (2014). The fish community was quantified along 5 replicate UVC transects laid at a depth of 3-9 m parallel to the reef crest at each site. Coral grouper (*P. maculatus*) were counted in 50 m x 6 m transects (300 m² survey area) and assigned into 5 cm length classes. Small-bodied prey species (Pomacentridae and small Labridae), were counted on the return swim within a 2 m wide transect (100 m² survey area). The benthic composition of the sites was surveyed using a line intercept method, with benthic point samples recorded every 1 m along the 50 m transect lines.
2.3.3 **Mesopredator sampling**

Coral grouper dorsal muscle tissue was sourced from 36 archived biopsy probe samples collected from the five reef sites in the Keppel Islands between 2009 and 2013 (Table S2). Samples were stored in 100% high-grade ethanol. Ethanol has been shown to have less effect on isotopic signatures than other preservatives (Sarakinos et al. 2002, Ruiz-Cooley et al. 2011). However, preservation in ethanol can increase mean $\delta^{13}$C and $\delta^{15}$N values, as it acts as a fat solvent, removing isotopically light lipids from muscle.
samples (Sarakinos et al. 2002, Sweeting et al. 2004, Carabel et al. 2006). The magnitude of effect is likely to be species-specific (Kelly et al. 2006) and may depend on the concentration of preservative used, the duration of preservation, and the tissue preserved (Ruiz-Cooley et al. 2011). For a congener species (*Plectropomus leopardus*), we found that after lipid extraction, δ¹³C did not differ significantly between muscle tissue samples that had been frozen for 9 months and samples that had been stored in 100% ethanol (*t*₇.₃ = 0.03, df = 7.3, *p* = 0.98; unpublished data, see electronic supplementary material for details). However, to reduce any potential bias, we lipid-extracted muscle tissue samples using chloroform-methanol (2:1) extraction prior to performing stable isotope analyses (Ruiz-Cooley et al. 2011).

Coral grouper (*Plectropomus* spp.) undergo a marked ontogenetic diet shift once they reach approximately 20 cm standard length (SL; total length (TL) = 23.9 cm), when their diet changes from a combination of benthic invertebrates and fish to almost exclusively fish (Kingsford 1992, St John 1995, 1999). For this reason, we only took muscle tissue samples from coral grouper > 20 cm SL (Table S2). A broad range of prey fishes have been identified in the diets of coral grouper > 20 cm SL, with small-bodied, locally abundant damselfishes (Pomacentridae) most often dominating gut content samples (Kingsford 1992, St John 1995, 1999, Wen et al. 2012). Labridae (including Scarids), and Caesionidae are also common in coral grouper diets, as well as small schooling fishes (e.g. Clupeidae and Engraulidae) when available (Kingsford 1992, St John 1995, 1999).

### 2.3.4 Foodweb sampling

To characterise the carbon pathways and trophic structuring at our study sites, we collected samples from lower trophic level fish, invertebrate species and turf algae
in May and August 2013. Samples of white muscle tissue were collected from
damsels with different dietary niches, including the dominant algal-feeding species
(*Pomacentrus wardi*), the dominant plankton-feeding species (*Chromis nitida*), and two
species with a mixed diet of algae and plankton (*Pomacentrus australis* and
*Pomacentrus moluccensis*). A coral grouper congener (*Plectropomus leopardus*) is
reported to opportunistically prey upon pelagic schools of baitfish (Kingsford 1992), so
we also sampled hardyhead silversides (*Atherinomorus lacunosus*) in order to account
for this potential pelagic isotopic signal. Finally, to provide a baseline for the
interpretation of isotope results, we collected samples of benthic turf algae and muscle
tissue from filter-feeding rock oysters to characterise the basal isotopic signatures of
benthic versus pelagic carbon sources in the food web at each site.

Prey fishes were collected by SCUBA divers using handspears. All sampled
fishes were euthanized using a concentrated clove oil in seawater emulsion and
immediately stored on ice to preserve tissues. Tissue samples of approximately 0.5 cm³
were cut from the white muscle tissue between the dorsal fin and the lateral line of all
fish, taking care not to include any bone or skin tissue. Turf algae samples were
collected from the blades of macro algae (*Lobophora variegata*). For oysters, all
connective tissue was removed and samples taken from the main adductor muscle
tissue, ensuring that samples did not contain any calcareous shell. All samples were
thoroughly rinsed with distilled water, and muscle tissue samples were soaked in
distilled water for 5 minutes, to remove salt that could cause problems with the mass
spectrometry equipment. Samples were frozen in 1.5 ml plastic vials and freeze dried at
-50°C, 0.16 mBar for 24 hours. Dried samples were subsequently ground to a fine
homogenous powder in preparation for analyses.


2.3.5 Stable isotope analyses

Bulk stable isotope analysis of carbon and nitrogen for all samples was carried out at the Great Lakes Institute for Environmental Research (GLIER) laboratory at the University of Windsor, Canada. Lipids were extracted using chloroform-methanol extraction for all muscle tissue samples to ensure that differences in the fat content between species did not confound the $\delta^{13}$C results (Post et al. 2007). Algal samples were acid washed with hydrochloric acid (HCl) to dissolve any calcareous matter from corals or sediment that may have contaminated the samples. Isotope ratios were calculated from 400-600$\mu$g of each sample added to tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, California, USA).

Stable isotope values for both carbon and nitrogen are expressed as delta ($\delta$) values, equal to parts per thousand (‰) deviation from the standard, using the equation:

$$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

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 and Fry 1987). The standard reference material used for carbon and nitrogen were Pee Dee Belemnite carbonate and atmospheric nitrogen respectively. Food chain length (FCL) can be approximated by assessing the trophic position (TP) at which high-level consumers in the ecosystem are feeding. Trophic position of all consumers was calculated from the $\delta^{15}$N stable isotope results according to the equation below (Hussey et al. 2014). The mean $\delta^{15}$N signature of all filter-feeding oysters sampled was used as the trophic level 2 baseline, with a mean TP = 2, from which to calculate the relative positions of all other groups.
\[ TP = -\log \left( \frac{\log(\delta^{15}N_{lim} - \delta^{15}N_{base}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{TP})}{k} \right) + TP_{base} \]

Where,
\[ \delta^{15}N_{base} \] is the isotope value for a known baseline consumer in the food web, 
\[ k \] is the rate at which \( \delta^{15}N_{TP} \) approaches \( \delta^{15}N_{lim} \) per TP step,

And, estimates of \( k \) and \( \delta^{15}N_{lim} \) are given by:

\[ k = -\log \left( \frac{\beta_0 - \delta^{15}N_{lim}}{-\delta^{15}N_{lim}} \right) \]

\[ \delta^{15}N_{lim} = \left( \frac{\beta_0}{\beta_1} \right) \]

With intercept \( \beta_0 = 5.924 \) and slope \( \beta_1 = -0.271 \) characterizing the change in \( \delta^{15}N \) as dietary \( \delta^{15}N \) values increase, given by the meta-analysis in Hussey et al. (2014).

### 2.3.6 Data analyses

To characterise trophic structure within the food web in terms of both carbon sources and trophic levels, the isotopic signatures of all samples were plotted in isotopic space using a \( \delta^{13}C \) by TP biplot. For all subsequent analyses, grouper sampled from Egg Rock were excluded due to the lack of data on prey fish and benthic communities from this offshore site.

To investigate the source of variability in the \( \delta^{13}C \) and \( \delta^{15}N \) signal among coral grouper tissue samples, we constructed a set of hierarchical (mixed-effects) linear models. Covariates of interest included percentage live hard coral cover (as a measure of habitat condition), abundance of planktivorous pomacentrids (the prey fish which dominate on reefs with higher coral cover; Table S3), abundance of territorial benthic-
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feeding pomacentrids (prey fish which dominate on more degraded reefs with lower coral cover; Table S3), and a ratio of the logged abundances of planktivorous pomacentrids to territorial pomacentrids (to examine the effect of their relative dominance on a reef). To ensure that any changes in isotopic signature were not simply due to ontogenetic diet shifts, total length (TL) of individual fish was included as a covariate. Location can also be an important driver of isotope ratios, particularly in an inshore system that is under strong terrestrial influence from river outflow and flooding events, we included a covariate for distance from shore, measured as the straight-line distance from the middle of each site to the highwater mark due west on the mainland. Model variables extracted from long term monitoring data were averaged over the 2-3 monitoring sites closest to the location and date at which each grouper tissue sample was taken. A random factor was also included for site and year to account for any unexplained variance in the data.

Rather than relying on arbitrary methods for model selection, we calculated a model-averaged estimate for each standardised variable across all models using multimodel inference (Burnham and Anderson 2002) to estimate a weighted average of parameter estimates based on model uncertainty (Akaike weights) of all models.

Finally, we looked at how coral grouper abundance changed over the study period, again using a hierarchical linear (mixed effects) model, to test what factors may be responsible for driving any observed changes, including the same covariates tested in the previous isotope model, with the exception of TL. Total available prey biomass was added as an additional covariate to account for the different body sizes of prey species, which would not be captured in abundance data alone. Based on what is known about the diet of the congener, *Plectropomus leopardus* (Kingsford 1992), we included all species from the families Labridae (including juvenile parrotfishes) and Pomacentridae,
with a maximum total length of 20 cm or less (Froese and Pauly 2016), and for which at least three individuals had been recorded in the fish community monitoring dataset. Individual biomass estimates for each species were calculated according to the equation

\[ W = aL^b \]

where \( W \) is the weight, \( L \) is maximum total length for the species, and \( a \) and \( b \) are species-specific volumetric constants sourced from FishBase (Froese and Pauly 2016). This was then multiplied by the total number of individuals recorded for any given species, site, and year, and summed to provide an estimate of the total biomass available to mesopredators.

All data exploration was carried out in R following the protocol described in Zuur et al. (2010). Cleveland dotplots were used to inspect the variables for outliers. Pairplots and variance inflation factors (VIF) values were used to assess colinearity, and multi-panel scatterplots were used to visualize relationships. Model selection was based on the Akaike information criterion (AIC).

### 2.4 Results

#### 2.4.1 Shifts in prey availability

Loss of live hard coral cover with habitat degradation in the Keppel Islands between 2009 and 2013 (Table S1) was associated with a change in the dominant prey fish species (Fig. 2.2), from planktivorous damselfishes (\textit{Chromis nitida}) to territorial benthic-feeding damselfishes (\textit{Pomacentrus wardi}) (0.008 [0.004, 0.012]; Maximum Likelihood Estimate [95% Confidence Interval]). This likely represents a shift in the principal carbon source available to piscivores such as coral grouper.
**Chapter 2: Prey switching**

**Fig. 2.2** Relationship between percent live hard coral cover and ratio of the dominant prey fish species available to mesopredators in the fish community. At higher percentage live hard coral cover, planktivorous damselfishes (*Chromis nitida*) dominate the available prey fish community, while at low coral cover, territorial benthic-feeding species (*Pomacentrus wardi*) are relatively more abundant.

**2.4.2 Community Trophic Structure**

Stable isotopes identified distinct trophic structuring within the Keppel Islands’ coral reef foodweb (Fig. 2.3) associated with distinct carbon pathways ($\delta^{13}C$). Oysters, which as filter feeders, were considered to characterise the pelagic carbon signal in the system, had a mean $\delta^{13}C$ value of -18.19%o ($\pm$ 0.10 SE), a signal that was tracked by that of *Chromis nitida*, the pelagic plankton-feeding damselfish (-18.69%o $\pm$ 0.07). The benthic basal carbon signal of the algae was less negative and considerably more
variable (-17.21‰, ± 0.43) than the planktonic signal. As a producer, the trophic position (TP) of turf algae should be 1, but our results show an inflated TP for these samples (1.31 ± 0.02). This variability in both δ¹³C and TP (calculated from δ¹⁵N) could be due to contamination of algal samples from other carbon sources from reef and land-based sediment and detritus. This benthic basal carbon signal was reflected in the isotopic signatures of benthic algal-feeding damselfish *Pomacentrus wardi* (-16.88‰ ± 0.35). The TP values for all other groups sampled concurred with what is known about the ecological niches of these species (Fig. 2.3).

### 2.4.3 Variation in coral grouper δ¹³C

There was a substantial amount of variability in isotopic signals among the coral grouper sampled, with δ¹³C values ranging from -17.07‰ to -12.46‰ (Fig. 2.3). The abundance of planktivorous damselfishes was the strongest driver of this variation in coral grouper δ¹³C values (-0.69 [-0.79, -0.58]; see Table S4 standardised parameter estimates). Grouper sampled at sites dominated by planktivorous damselfishes had a more negative (pelagic) δ¹³C signal, while fish from more degraded sites where territorial damselfishes are more dominant, had a less negative (benthic) δ¹³C signal in their muscle tissue (Fig. 2.4a), with an overall enrichment towards a benthic signature in grouper δ¹³C over time (Fig. S1).

Percentage live hard coral cover was highly correlated with the abundance of planktivorous pomacentrids (Pearson correlation coefficient; r = 0.8), as were the abundance of territorial pomacentrids (r = -0.7), and the ratio of the abundances of planktivorous pomacentrids to territorial pomacentrids (r = 0.7). These covariates were therefore excluded from the final model. Fish size (TL) was a poor predictor of grouper δ¹³C signature, (0.00 [-0.01, 0.01]), as was distance from shore, (-0.04 [-0.11, 0.04])
indicating that, among the fish sampled for this study, there was no confounding effect of either individual size or terrestrial influence on $\delta^{13}\text{C}$.

**Fig. 2.3** Isotope biplot showing the trophic structuring within the Keppel Islands’ coral reef foodweb in terms of carbon source ($\delta^{13}\text{C}$) and trophic position, which is a function of $\delta^{15}\text{N}$. Sampling sites are indicated by different shaped symbols, and species are designated by colour.
2.4.4 Variation in coral grouper $\delta^{15}N$

The isotopic signature of coral grouper ($P. maculatus$) placed them at the highest trophic position of the species sampled (TP = 3.13 ± 0.02 SE), as would be expected for a reef mesopredator, but there was also a great deal of variation in TP between individuals, with values ranging from 2.72 to 3.41. The fish with the highest TPs were also those with the most negative (pelagic) $\delta^{13}C$ signals (Fig. 2.4b). This indicates that coral grouper that were feeding predominantly on planktivorous prey species were also on reefs with greater trophic complexity and longer food chains.

AIC-based model averaging of hierarchical linear mixed effects models showed the two strongest predictors of $\delta^{15}N$ to be the abundance of territorial pomacentrids (0.396 [-0.17, 0.96]), and grouper TL (0.013 [0.001, -0.03]).

Fig. 2.4 (a) The marginal change in $\delta^{13}C$ signature of coral grouper ($P. maculatus$) sampled from the Keppel Islands between 2009 and 2013 was best explained by the decrease in planktivorous prey species in the fish community. (b) Relationship between $\delta^{13}C$ (carbon source) and trophic position (calculated from $\delta^{15}N$) in coral grouper.
2.4.5 Coral grouper population response

Adult coral grouper (*P. maculatus*, SL > 20 cm) abundance decreased steadily with time over the years examined in this study (Fig. 2.5a), from a mean (± SE) of 2.077 ± 0.209 fish.100m⁻² in 2009, to 1.170 ± 0.192 in 2011, and 0.449 ± 0.082 in 2013. The total prey biomass available to mesopredators also diminished over the course of the study (Fig. S2) and was the most important factor associated with the grouper population decline (0.634 [0.480, 0.788]) (Fig. 2.5b). The abundance of planktivorous pomacentrids was strongly correlated with total available prey biomass (Pearson correlation coefficient = 0.7). Percentage live hard coral cover (0.017 [0.010, 0.024]), the abundance of territorial pomacentrids (0.0254 [0.013, 0.038]), and distance from shore (0.029 [-0.145, 0.202]) were all much weaker predictors of coral grouper abundance.

**Fig. 2.5** (a) Mean abundance of adult (SL>20 cm) coral grouper (*Plectropomus maculatus*) on the reefs of the Keppel Island Group in (n=165). The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile range past these points. (b) Relationship of adult coral grouper abundance to the total logged biomass (log(kg.ha⁻¹)) of prey fishes available to them in the reef fish community.
2.5 Discussion

Fluctuations in prey availability linked to environmental change are becoming increasingly common, and a predator’s dietary plasticity may be critical to their persistence in a given ecosystem (Berumen et al. 2005, Peers et al. 2014). Increased knowledge of how coral reef mesopredators respond to changing prey availability is therefore key to predicting how coral reef trophic dynamics will be affected by widespread habitat degradation. This study presents some of the first empirical evidence that piscivorous mesopredators may be able to adapt their diets in response to such changes.

Prey switching often occurs when the relative abundance of prey species is altered and predators modify their diets to exploit this change in available resources (Berumen et al. 2005). In the present study, differences in the δ\textsuperscript{13}C signature of coral grouper in the Keppel Island Group suggest that they are capable of adapting their diets in response to changes in prey availability due to habitat degradation. While this may appear to be an effective strategy, costs associated with shifts in diet may not be evident in the short term. Previous studies documenting prey switching in marine and terrestrial species have linked facultative dietary shifts to detrimental effects (e.g. Pratchett et al., 2004; Cohen et al., 2014; McNamara & Lonsdale, 2014). For example, when switching to less preferred prey species there may be a loss of condition due to reduced nutritional quality (Pratchett et al. 2004, Berumen et al. 2005), or due to increased energetic costs involved in capturing alternative prey (Cohen et al. 2014). Such sub-lethal effects are not immediately evident in the population and may result in reduced fecundity (Jones and McCormick 2002), growth rates (Kokita and Nakazono 2001, Feary et al. 2009), or delayed age of maturity (Jonsson et al. 2013); all of which can have a significant impact on the population in the longer term (Graham et al. 2007). Dietary adaptability may
therefore only ameliorate the effects of habitat degradation in the short term. If a consumer’s habitat recovers rapidly following disturbance, then prey switching could be an effective way for longer-lived mesopredators to survive until the system recovers, despite loss of condition in the short term.

Shortening of food chains is often symptomatic of deterioration of ecosystem function, frequently driven by a loss of top consumers in an ecosystem (Estes et al. 2011). Dobson et al. (2011) also highlight an important process called trophic downgrading, whereby a thinning of the food web due to a loss of species diversity results in a decrease in the mean trophic level of consumers. Such changes in food chain length therefore have the potential to influence key ecological dynamics such as rates of primary productivity, nutrient cycling, and carbon flow (Pace et al. 1999, Persson 1999, Oksanen and Oksanen 2000). With the loss of live coral cover in the Keppel Islands followed by a decline in fish diversity (Williamson et al. 2014), we document that a species of mesopredator (coral grouper, *P. maculatus*) shows variation in its trophic position, indicating differences in food chain length, associated with an increase in territorial benthic pomacentrids. These effects were matched by those of increasing body size, a well-known driver of increasing isotope-derived TL among fishes (Jennings et al. 2001).

Grouper feeding at lower trophic levels also had a more enriched δ¹³C signature, indicative of a diet rich in benthic herbivorous species. These species (e.g. *P. wardi*) were found to be dominant on reefs with decreased live coral cover and low fish species diversity (Williamson et al. 2014), suggesting a thinning of the foodweb on the degrading Keppel Island reefs. According to Dobson et al. (2011), a subsequent stage is a rapid shortening of the food chain as trophic levels are lost from top to bottom, leading to a simplification of the food web. Coral grouper populations in the Keppel
Islands are already in decline, a trend that appears to be primarily related to a decrease in the total available biomass of prey, supporting the suggestion by Williamson et al. (2014) that the reduction in prey fish abundance is largely responsible for the decreased abundance of mesopredators.

While disturbance has already impacted the reef fish community in the Keppel Islands considerably, the habitat degradation on these reefs is relatively recent, with the majority of live coral loss occurring since 2011 (Diaz-Pulido et al. 2009, Williamson et al. 2014). It is therefore possible that these effects may become more pronounced in the longer term (Graham et al. 2007) as intact skeletons from dead coral that were maintaining a degree of structural complexity on the Keppel reefs will be lost as these reefs degrade further. Structural complexity is crucial in not only supporting coral reef fish communities (Syms and Jones 2000, Graham and Nash 2013, Nash et al. 2013), but also in facilitating successful predation by mesopredators such as coral grouper that rely on shelter for ambush predation (Kerry and Bellwood 2012). Mesopredators may therefore decline further as their prey base is increasingly altered, and predation becomes more challenging, requiring greater energy investment.

The effects of widespread habitat degradation on long-lived reef mesopredators remain poorly understood, as sub-lethal effects may not be apparent in the short-term. These species are often of great economic and social value (Cinner et al. 2009, GBRMPA 2014) and play a key functional role in the trophodynamics of coral reef ecosystems, transferring energy up the food chain (Polovina 1984), and potentially offering a stabilising effect in post disturbance communities (McCann et al. 1998, Loeuille 2010). Improving our understanding of how habitat degradation impacts this functional group, particularly at a sub-lethal level is therefore a high priority for future research.
This study provides evidence that the trophodynamics of mesopredators could become altered due to habitat degradation and altered prey availability. Our results also illustrate the utility of stable isotope analyses in detecting the early stages of trophic downgrading in a marine ecosystem. We conclude that while the ability of mesopredators to modify their diets may be effective at ameliorating the effects of habitat degradation on coral grouper in the short term, altered trophic structure, decreased total prey availability, and sub-lethal effects may have detrimental consequences for mesopredator populations in the longer-term. This study contributes to improving forecasts about how coral reef ecosystems will respond to habitat degradation and environmental change in the future, facilitating better-informed management decision-making, particularly with respect to coral reef fisheries.
3.1 Abstract

Predator populations are in decline globally. 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 lag effect that may be difficult to detect based on population data alone. 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. We used stable isotope analyses to test for evidence of habitat-driven changes in the trophic niche occupied by a key piscivorous fishery target species on reefs that had either 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. Stable isotopes demonstrated that fish from regime-shifted reefs fed on shorter food chains across a narrower range of carbon sources 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 lag effect on populations. Reduced energy reserves in mesopredators could lead to decreased growth rates, fecundity, and survivorship, resulting in population declines in the longer term. Current stock assessments of mesopredators may therefore not

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accurately reflect the true long-term carrying capacity of a regime-shifted ecosystem, resulting in unsustainable management strategies.

3.2 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 prey fish community and indirectly impacting piscivorous reef-associated predators (Wilson et al. 2008).

Mesopredators have high ecological, economic, and social value in coral reef ecosystems, playing a key role in transferring energy up the food chain to apex predators (Polovina 1984). Many reef mesopredators (e.g. Serranidae, Lutjanidae, Lethrinidae) also 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. 2010c). However, our understanding of the long-term effects of bleaching on mesopredators remains limited.

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 and Pauly 2016), allowing populations to persist for many years following a disturbance event, masking failed recruitment (Warner and Hughes 1988) and producing a lag effect that may last decades (Bellwood et al. 2006, Graham et al. 2007). Mesopredators are also often more mobile than their prey, with a broad dietary scope that allows them to adapt to changing prey availability (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), with long-term implications.

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) while increased energetic demands can result from intensified competition and difficulty hunting as habitat structure degrades (Kerry and Bellwood 2012). Reduced energy reserves could result in decreased body condition, growth rates (Kokita and Nakazono 2001), survivorship, and fecundity, leading to eventual population declines (Jones and McCormick 2002, Pratchett et al. 2006). Yet studies of the sub-lethal effects of habitat degradation on reef fish have focused exclusively on obligate corallivores; their occurrence in reef mesopredatory fish is not known.

This study aims to quantify the presence of habitat-driven sub-lethal degradation effects in mesopredators by comparing and contrasting reefs that, 16 years after a major bleaching disturbance, have either entered an algae-dominated state following a regime shift, or have recovered to a coral-dominated state (Graham et al. 2015). We compare
the 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 δ\(^{13}\)C and δ\(^{15}\)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.

### 3.3 Methods

#### 3.3.1 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. 2012b). 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 macroalgal cover, with coral cover increasing or remaining high through time. Regime-shifted reefs were identified as those where post-disturbance macroalgal cover exceeded coral cover, and was increasing or remaining high (see Graham et al. 2015 for detailed site descriptions).
3.3.2 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 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 and Pauly 2016). Species were assigned to functional groups based on their diet and feeding behaviour as defined in Graham et al. (2006). 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 et al. 2007).

3.3.3 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 and Fishelson 1989, Dierking et al. 2009, Froese and Pauly 2016).

3.3.4 Mesopredator sampling

The mesopredator C. argus was sampled during the monitoring trip in April 2014. At each site 10 - 15 adult C. argus individuals were collected using spearguns. Paired sampling of regime-shifted and recovering reefs ensured that reproductive potential data
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were not confounded by cyclic changes in reproductive state. 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 cm³) was sampled from between the dorsal fin and lateral line, and frozen for isotope and lipid analysis. Stomachs were dissected, and gut content recorded and identified where possible.

Sagittal otoliths were extracted and read to establish the age of the fish (Ferreira and 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 and Holt 1957):

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

where \( L_t \) is total length (TL, cm) at age \( t \) (years), \( L_\infty \) 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.
3.3.5 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.

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 (see ESM for detailed methods), using the equation:

\[ \delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \]

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).

3.3.6 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.

\[ B' = \frac{GW}{(H \times TL^2)} \]

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 and Woods 2006).

\[ \text{HSI} = \frac{(LW/GW)}{100} \]
3.3.7 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).

3.3.8 Lipid analysis

Total lipid content and lipid class composition of muscle, liver and gonad tissue from the sampled C. argus 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).

3.3.9 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 (Anderson and 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 and Warwick 2001). Differences in mean total fish abundance (fish.500 m$^{-2}$) were tested using Welch’s t-test.

We used a SIMPER analysis (Clarke and 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 $\leq$ 15 cm, and while they do have prey preferences, they are known to readily switch prey when preferred species are not available (Shpigel and 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 $\leq$ 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.500 m^-2), 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 $\delta^{13}C$ vs. $\delta^{15}N$ biplot. The relationship between $\delta^{13}C$ and $\delta^{15}N$ 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:

$$M = \text{lmer}(\delta^{15}N \sim \delta^{13}C \ast \text{state} + (1 \mid \text{site}))$$

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 et al. 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.

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. 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. The point at which lipid concentrations or TAG:ST ratio transitioned between the two reef states was estimated from the point corresponding to half way between the two states (i.e. 0.5).

3.4 Results

3.4.1 Benthic habitat

Benthic habitat composition in 2014 differed substantially between recovering and regime-shifted sites (Fig. 3.1a). The CAP analysis showed strong support for the 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. 3.1a, 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).
Fig. 3.1 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.
3.4.2 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. 3.1b). 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: 234.54 ± 15.42 fish.500m\(^{-2}\), Regime-shifted: 129.72 ± 10.50 fish.500m\(^{-2}\), \( t_{42.476} = -5.6191, p < 0.001 \)).

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. 3.2a). 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. 3.2b; 6 – 10 cm = 49.57%, 11 – 15 cm = 26.82%). Total available prey biomass for piscivorous mesopredators such as \( C. \) argus was thus significantly higher on recovering reefs than regime-shifted reefs (Fig. 3.2c; \( t_{43.386} = -8.95, p < 0.001 \)). 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. 3.2b; 16 – 20 cm = 8.90%, 26 – 30 cm = 5.61%).

3.4.3 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 S1).

Gut content analysis of all *C. argus* ($n = 69$) found the majority (62.3 %) of the dissected stomachs were empty ($n$: Recovering = 23, Regime-shifted = 20). Gut contents from the remaining fish showed few clear difference in the diets of *C. argus* between reef states, although only fish from regime-shifted sites having invertebrate remains in their stomachs (Recovering: 9 fish remains, 0 invertebrate, 2 unknown; Regime-shifted: 12 fish remains, 3 invertebrate, 0 unknown). This supports the assertion that *C. argus* is predominantly piscivorous. However, the fact that invertebrate remains were only found in fish from regime-shifted reefs, suggests that fish on these reefs may be supplementing their diets.
Fig. 3.2 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.
3.4.4 **Stable isotopes**

The isotopic signature for the base of the food web, derived from *Sargassum* sp., showed no significant difference between reef states in terms of either $\delta^{13}C$ (Recovering: $-13.56 \pm 0.27 \%e$, Regime-shifted: $-16.6 \pm 0.24 \%e$, $t_{2.664} = 2.680$, $p = 0.085$) or $\delta^{15}N$ (Recovering: $5.20 \pm 0.21 \%e$, Regime-shifted: $4.07 \pm 0.18 \%e$, $t_{2.492} = 1.309$, $p = 0.298$). Due to the potential relationship between intraspecific body size and $\delta^{15}N$ (Greenwood et al. 2010), we evaluated mean total length of *C. argus* sampled between reef states, finding it did not differ significantly (Recovering: $25.40 \pm 1.14$ cm, Regime-shifted: $25.80 \pm 1.04$ cm, $t_{66.322} = -0.260$, $p = 0.796$). This suggests that neither of these two potential sources of variation in isotopic signal were 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. 3.3a; Recovering: $-0.122 \pm 0.160$, Regime-shifted: $-0.533 \pm 0.238$). This indicates that fish on regime-shifted reefs that fed on more benthic carbon pathways (less negative $\delta^{13}C$ signature) 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. 3.3b; $t_{55.597} = 0.235$, $p = 0.815$). 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: $-4.696 [-3.797, -6.158]$), suggesting a greater diversity of carbon sources on recovering sites. In contrast, mean $\delta^{15}N$ signature differed significantly between reef states (Fig. 3.3b; $t_{66.678} = -5.012$, $p < 0.001$), indicating that *C.*
argus sampled from recovering sites are feeding higher up the food chain than fish on regime-shifted reefs.

**Fig. 3.3** Stable isotope signatures of *Cephalopholis argus* sampled from recovering and regime-shifted reefs in the Seychelles inner island group. (a) Biplot of $\delta^{13}$C and $\delta^{15}$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 ($\delta^{13}$C) and trophic level ($\delta^{15}$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 $\delta^{13}$C and $\delta^{15}$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. 3.4 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.
3.4.5 **Body condition indices**

The morphometric index, $B'$ showed no distinction in the body condition of *C. argus* between reef states (Fig. 3.4a). Sagittal otolith data also indicated no difference in growth rates, measured as size-at-age (ESM, Fig. S2), 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. 3.4b) 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. 3.4c), indicating higher lipid stores in these individuals.

3.4.6 **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. 3.5a), suggesting that these fish have more energy available to channel into their gonads for spawning. Logistic regression estimated that lipid concentrations transitioned between reef states at approximately $24.85 \mu g.mg^{-1}$, with fish from regime-shifted reefs on average having lower concentrations of TAG lipids, and fish from recovering reefs having concentrations above this point. 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. 3.5b; transition point = 15.36) and gonad (Fig. 3.5c; transition point = 13.06) tissue for spawning females, implying a cost to condition for fish living on regime-shifted reefs. Detailed results for all tissues, lipids and maturity categories are available in the ESM (Table S3).

3.5 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 following a lag effect of more than a decade (Graham et al. 2007), 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.

Stable isotopes show that, on regime-shifted reefs, food-chains below *C. argus* are shorter, such that the trophic niche of mesopredators differs from that on recovering reefs. The broader range of $\delta^{13}C$ values for *C. argus* on recovering reefs is unlikely to be due to underlying variability in baseline carbon signals, as this is not reflected in the $\delta^{13}C$ signatures of algae sampled (ESM, Table S2). It more likely reflects the greater diversity of prey from various functional groups that feed on a broad spectrum of carbon sources. This diverse prey assemblage, includes higher trophic level consumers (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, which is why *C. argus* from these reefs have a narrower range of $\delta^{13}C$ values, and 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, and a decrease in the biomass of high order predators a reef is able to support (Munday et al. 2007).
Size structure in reef fish communities can also be considerably altered by habitat degradation following bleaching (Graham et al. 2007). The significant reduction of small fish (< 15 cm TL) on regime-shifted reefs in Seychelles represents an important decrease in the prey base available to mesopredators. Despite their feeding adaptability (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. The reduction in small-bodied species is likely primarily driven by loss of live coral and rugosity as reef structure degrades following bleaching (Munday and Jones 1998, Dulvy et al. 2004, Graham et al. 2006), causing increased competition and mortality from predation (Hixon and Jones 2005).

The *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. This is possibly due to the decreased competition for resources following the decline in mesopredator abundance, as the population reaches a new carrying capacity (Cooney and Brodeur 1998). However, the reduced density of hepatocyte vacuoles in *C. argus* from regime-shifted reefs indicates reduced lipid stores, suggesting an energetic cost to piscivorous mesopredators persisting on these reefs. These energetic costs may result from suboptimal hunting conditions; not only are there less prey targets on regime-shifted reefs, but the loss of habitat structure reduces potential concealment for ambush hunting (Kerry and Bellwood 2012). It is also possible that there is a difference in the nutritional quality of prey available on algae- and coral-dominated reefs. Irrespective of cause, reduced energy reserves in mesopredators can have long-term implications for population decline through decreased fecundity and survivorship (Jones and McCormick 2002).
Sub-lethal effects of habitat degradation in mesopredator populations have important implications for the management of coral reef fisheries and conservation. Reduced energy reserves in mesopredators on regime-shifted reefs may not appear in traditional stock assessments or surveys for several years, despite the potential to cause unexpected population crashes in the longer term. It is essential that conservation and fisheries managers bear this in mind when setting catch and size limits for targeted species where regime shifts have occurred, as current stocks may not be representative of population levels that the system will be able to support in coming years. To better understand and predict these dynamics, future research should focus on further investigation of the effect of habitat degradation on the lipid metabolisms of reef predators.

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 can change, resulting in shorter food chains and reduced energy reserves in mesopredators. The decline in mesopredator abundance and diversity on regime-shifted reefs in Seychelles 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, particularly to effects that are detrimental in the long term.
CHAPTER 4

Ecosystem regime shifts disrupt trophic structure

4.1 Abstract

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 moved towards a bottom-heavy 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

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communities is essential to inform decisions that enhance ecological resilience and economic sustainability.

4.2 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, Staver 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
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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. 2017). 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 1998.

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 across 2 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 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.

4.3 Methods

4.3.1 Study sites

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. 2012b). 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.

4.3.2 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 base of the reef slope, 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 2016). 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 trophic levels estimates published in Fish Base (Froese and Pauly 2015), species were also assigned to one of five trophic level bins (TP) for pyramid construction; 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).

4.3.3 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 pyramid levels (TP1 – TP 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. Differences in the trophic structure between recovering and regime-shifted reefs at each time point were tested using multinomial regression of the TP bins 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 pyramid 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.

4.4 Results

4.4.1 Benthic habitat

There was a distinct shift in the benthic composition of regime shifted reefs following disturbance in relation to recovering reefs (Fig. 4.1). 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.
Fig. 4.1 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).
4.4.2 *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 4.1). The trophic structure of the fish community also reflects this divergence between reef states in terms of the distribution of relative biomass among trophic pyramid levels (Fig. 4.2). 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. 4.2, 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 pyramid 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 4.2). 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, 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).
**Fig. 4.2** 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.)
Table 4.1 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.

<table>
<thead>
<tr>
<th>Average % Dissimilarity</th>
<th>1994</th>
<th>2005</th>
<th>2014</th>
</tr>
</thead>
<tbody>
<tr>
<td>Functional Groups</td>
<td>13.13</td>
<td>25.61</td>
<td>34.2</td>
</tr>
<tr>
<td>Biomass (kg. ha⁻¹)</td>
<td>45.21</td>
<td>57.49</td>
<td>66.32</td>
</tr>
<tr>
<td>Abundance (fish. 500m⁻²)</td>
<td>39.05</td>
<td>48.69</td>
<td>61.23</td>
</tr>
</tbody>
</table>

Table 4.2 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). Coefficients are the difference between regime-shifted and recovering estimates, where positive values indicate more relative biomass in regime-shifted reefs, and negative values indicate less.

<table>
<thead>
<tr>
<th>Year</th>
<th>Trophic Position (TP)</th>
<th>Model Coefficient</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>2</td>
<td>-0.429</td>
<td>-0.522</td>
<td>-0.336</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.720</td>
<td>0.649</td>
<td>0.790</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>-1.495</td>
<td>-1.617</td>
<td>-1.372</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-2.468</td>
<td>-2.681</td>
<td>-2.255</td>
</tr>
<tr>
<td>2005</td>
<td>2</td>
<td>0.317</td>
<td>0.200</td>
<td>0.435</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>-0.241</td>
<td>-0.334</td>
<td>-0.148</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.448</td>
<td>0.308</td>
<td>0.588</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.011</td>
<td>-0.287</td>
<td>0.266</td>
</tr>
<tr>
<td>2014</td>
<td>2</td>
<td>-0.161</td>
<td>-0.290</td>
<td>0.033</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.007</td>
<td>-0.084</td>
<td>0.098</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.419</td>
<td>0.274</td>
<td>0.564</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>-0.587</td>
<td>-0.919</td>
<td>-0.255</td>
</tr>
</tbody>
</table>
Table 4.3 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.

<table>
<thead>
<tr>
<th>Years</th>
<th>Trophic Level</th>
<th>Recovering Mean % dissimilarity ±SE</th>
<th>Regime-Shifted Mean % dissimilarity ±SE</th>
<th>t</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994 vs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2005</td>
<td>TP 1</td>
<td>34.99 ± 2.32</td>
<td>45.13 ± 3.38</td>
<td>-2.47</td>
<td>7.09</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>TP 2</td>
<td>28.59 ± 4.46</td>
<td>44.50 ± 4.20</td>
<td>-2.60</td>
<td>7.97</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>TP 3</td>
<td>38.57 ± 3.56</td>
<td>48.03 ± 4.33</td>
<td>-1.69</td>
<td>7.71</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>TP 4</td>
<td>54.77 ± 4.46</td>
<td>44.09 ± 6.67</td>
<td>-1.33</td>
<td>6.98</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>TP 5</td>
<td>52.33 ± 19.53</td>
<td>58.68 ± 6.73</td>
<td>-0.31</td>
<td>4.94</td>
<td>0.77</td>
</tr>
<tr>
<td>1994 vs</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2014</td>
<td>TP 1</td>
<td>35.29 ± 1.84</td>
<td>62.72 ± 2.71</td>
<td>-8.36</td>
<td>7.05</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td>TP 2</td>
<td>44.18 ± 5.68</td>
<td>37.82 ± 4.94</td>
<td>0.85</td>
<td>7.85</td>
<td>0.42</td>
</tr>
<tr>
<td></td>
<td>TP 3</td>
<td>32.45 ± 3.72</td>
<td>53.10 ± 5.60</td>
<td>-3.07</td>
<td>6.96</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>TP 4</td>
<td>39.40 ± 4.69</td>
<td>57.05 ± 7.89</td>
<td>-1.98</td>
<td>6.38</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>TP 5</td>
<td>41.87 ± 9.39</td>
<td>71.40 ± 12.75</td>
<td>-1.87</td>
<td>7.35</td>
<td>0.10</td>
</tr>
</tbody>
</table>

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 4.3). 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 pyramid levels except TP2. The increased dissimilarity in this trophic pyramid 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 pyramid 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. 4.3). 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 levels, including corallivores, planktivores and piscivores.
Fig. 4.3 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.
4.5 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 pyramid levels and the greatest amount of biomass located in the base trophic pyramid level, as expected based on energetic theory (Trebilco et al. 2013, Hatton et al. 2015). Following the bleaching, relative biomass in the base trophic pyramid level (TP1) 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 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 had regained biomass in the mid trophic pyramid levels (TP2 and TP3), 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 pyramid levels, particularly TP4, 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 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 TP2 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
Chapter 4: Trophic structure

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 TP2 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. 2012b). 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), with potential sub-lethal effects (Chapter 2).

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. 2012b).
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 trophic pyramid levels (TP2 and TP3) 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 TP3 (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 TP3 (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 TP2.

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*; Carassou et al. 2008). 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.
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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.
CHAPTER 5
Trophodynamics in novel coral reef ecosystems

5.1 Abstract

Ecosystems are becoming vastly modified through disturbance. In coral reef ecosystems, the differential susceptibility of coral taxa to climate-driven bleaching is predicted to shift coral assemblages towards reefs with an increased relative abundance of taxa with high thermal tolerance. Many thermally tolerant coral species are characterised by low structural complexity, with reduced habitat niche space for the small-bodied coral reef fish communities on which piscivorous mesopredators feed. This study used a patch reef array to investigate the potential impacts of climate-driven shifts in coral assemblages on the trophodynamics of reef mesopredators and their prey communities. The ‘tolerant’ reef treatment consisted only of coral taxa of low susceptibility to bleaching, while ‘vulnerable’ reefs included species of moderate to high thermal vulnerability. ‘Vulnerable’ reefs had higher structural complexity, and the fish communities that established on these reefs over 18 months had higher species diversity, abundance and biomass than those on ‘tolerant’ reefs. Fish communities on ‘tolerant’ reefs were also more strongly influenced by the introduction of a mesopredator (*Cephalopholis boenak*). Mesopredators on ‘tolerant’ reefs had lower lipid content in their muscle tissue by the end of the six-week experiment. Such sub-lethal energetic costs can compromise growth, fecundity and survivorship, resulting in unexpected population declines in long-lived mesopredators. This study provides valuable insight into the altered trophodynamics of future coral reef ecosystems, highlighting the potential increased vulnerability of reef fish communities to predation as reef structure declines, and the cost of changing prey availability on mesopredator condition.

Submitted for publication as: Trophodynamics in novel coral reef ecosystems. Hempson TN, Graham NAJ, MacNeil MA, Hoey AS, Almany GR. Coral Reefs
5.2 Introduction

Climate change is increasingly recognised as a key driver of ecosystem structure and trophic dynamics in marine and terrestrial ecosystems worldwide (Hoegh-Guldberg and Bruno 2010, Byrnes et al. 2011, Buitenwerf et al. 2012, Brandt et al. 2013, Wernberg et al. 2016). Coral reefs are one of the most vulnerable ecosystems due to the high thermal sensitivity of habitat-forming scleractinian corals (e.g. Hoegh-Guldberg et al. 2007). Indeed, climate-driven increase in ocean temperature is emerging as the greatest driver of large scale disturbance and regime-shifts in these ecosystems, with mass coral bleaching events becoming more frequent, widespread and sustained (Hughes et al. 2017). The degree of vulnerability to bleaching, however, varies substantially among coral taxa (Marshall and Baird 2000, Loya et al. 2001, Grottoli et al. 2006, McClanahan et al. 2007). This differential susceptibility to bleaching is predicted to result in large-scale changes in the composition of coral assemblages, with an expected overall shift towards more thermally tolerant species (Riegl et al. 2009, Van Woesik et al. 2011, Pratchett et al. 2014). As the frequency and severity of bleaching increases, the composition of future coral assemblages will depend not only on the thermal tolerance of coral taxa, but also how they respond to changing disturbance regimes (Fabina et al. 2015), and their ability persist or to re-establish in the post-disturbance environment (Darling et al. 2013, Graham et al. 2014).

Many of the coral taxa predicted to have high thermal tolerance, and therefore likely to characterise many future coral reef assemblages, are also species with low structural complexity (Loya et al. 2001, Alvarez-Filip et al. 2013). Habitat structure is known to be a key determinant of coral reef fish species diversity, abundance, and biomass (Graham and Nash 2013, Darling et al. 2017), with a loss of complexity
resulting in a decline in habitat niche space and refugia, leading to increased competition and predation (Beukers and Jones 1997, Holbrook and Schmitt 2002, Kok et al. 2016). The predicted changes in coral assemblages in response to ocean warming are therefore likely to lead to a shift in coral reef fish community composition (Graham et al. 2014).

Small-bodied species of fish are vulnerable to changes in the composition and structure of the coral reef benthos (e.g. Alvarez-Filip et al. 2011, Nash et al. 2013), particularly those species that are directly reliant on live coral for food or shelter (Munday et al. 2008, Coker et al. 2014). While these changes are expected to result in long term reductions in fisheries yields (Graham 2014, Rogers et al. 2014), there remains a lack of understanding of how these changes in the fish community will affect piscivorous reef mesopredators. These larger bodied, more mobile species are less likely to be directly affected by changes in coral assemblages, but may be vulnerable through alterations in the fish community on which they predate (Hempson et al. 2017). Due to the longevity of many piscivores, relative to their small-bodied prey, the impacts of changing prey availability may initially manifest at a sub-lethal level, resulting in a loss of condition due to reduced nutritional value (Pratchett et al. 2004, Berumen et al. 2005), or higher energetic demands associated with hunting alternate prey (Cohen et al. 2014). Reduced energy reserves can reduce resource allocation to important life history functions such as growth (Kokita and Nakazono 2001, Feary et al. 2009), fecundity (Jones and McCormick 2002), age of first reproduction (Jonsson et al. 2013) and survivorship, resulting in potential population decline in the long term (Graham et al. 2007).

Change in the benthic composition of coral reefs therefore has the potential to have a substantial impact on reef mesopredator populations, yet there remains little
known about how mesopredator trophodynamics will respond to climate-driven shifts in coral assemblages. To address this knowledge gap, this study used an array of patch reefs with varying coral compositions that simulated both undisturbed and predicted climate altered configurations. This experimental setup was then used to investigate (1) the prey base among reefs in terms of diversity, abundance, and biomass, (2) the role of mesopredators in shaping these prey communities, and (3) the effect of differing reef compositions on the condition of mesopredators.

5.3 Methods

5.3.1 Study site & patch reefs

This study was conducted at Lizard Island, a high continental island on the mid-shelf of the northern Great Barrier Reef (14°41'31.5"S 145°27'39.3"E), using a patch reef array positioned on the south-eastern side the island’s lagoon between October 2013 and July 2015. The experimental setup consisted of twenty large (1.5 m diameter) patch reefs, with two distinct coral assemblages (i.e., thermally tolerant and thermally sensitive or vulnerable) constructed in October 2013. The 10 x 2 array was built at a depth of 3 - 5 m on the sandy lagoon flat, parallel to the surrounding reef, with a distance of at least 15 m separating the patch reefs from each other and from the main reef. Each patch reef consisted of a coral rubble base, stabilised with nylon line, and populated with equal numbers of colonies of six local coral species collected from the reefs surrounding the lagoon. ‘Vulnerable’ reefs included coral taxa that are currently abundant on reefs across the full range of thermal tolerance, including those that are sensitive to increasing ocean temperatures and prone to coral bleaching (bottlebrush Acropora sp., branching Acropora sp., Porites cylindrica, Porites sp. massive, Stylophora pistulata, Turbinaria reniformis; Fig. 5.1a). ‘Tolerant’ reefs consisted only
of coral taxa that have high thermal tolerance and low vulnerability to bleaching, to simulate predicted future coral assemblages (*Fungia* spp., *Goniastrea retiformis*, *Goniopora* sp., *Porites* sp. massive, *Symphyllia radians*, *Turbinaria reniformis*; Fig. 5.1b). Species were chosen based on the current best knowledge of their susceptibility to bleaching recorded during previous natural mass bleaching events in the Indo-Pacific (e.g. Marshall and Baird 2000, Loya et al. 2001, McClanahan et al. 2007).

The same number of taxa was used in each treatment to exclude species diversity as a variable, the number and size of coral colonies kept as consistent as possible among reefs, and the distribution of treatments randomised within the array. Once built, the live coral cover, average height, and structural complexity of each patch reef was measured along three haphazard 1.5 m transects across the reef, passing through the centre. Percentage live coral cover was estimated by recording the benthos (live coral cover vs alternative substrate) at 12 random points along each transect. Reef height was measured as the distance from the sand to the top of the coral at nine random points on each reef. Structural complexity was measured using a standard rugosity index for each transect, calculated as the ratio of the linear straight line distance across the reef, to the same diameter measured using a fine-linked (8 mm diameter) chain draped across the surface of the reef (Luckhurst and Luckhurst 1978).

### 5.3.2 Fish communities

Fish communities were allowed to establish on the patch reefs over the following 18 months, which included two periods of peak settlement (2014 - 13, 2014 – 15), which occur annually between late October and late January at Lizard Island (Milicich and Doherty 1994). In April 2015, the composition of the fish community resident on each reef was surveyed. Each reef was systematically searched and all fishes identified to species and their total length estimated to the nearest 0.5 cm.
Chapter 5: Novel trophodynamics

Fig. 5.1 Photos illustrating the two reef treatments in the patch reef array immediately after construction in 2013, prior to recruitment of fish communities. All reefs were constructed on a 2 m diameter base of coral rubble, with live colonies of six coral taxa each. a. Vulnerable reefs were composed of coral taxa from the entire spectrum of predicted vulnerability to increasing ocean temperatures (bottlebrush *Acropora* sp., branching *Acropora* sp., *Porites cylindrical*, *Porites* sp. massive, *Stylophora pistulata*, *Turbinaria reniformis*). b. Tolerant reefs consisted only of coral taxa that are expected to have high thermal tolerance (*Fungia* spp., *Goniastrea retiformis*, *Goniopora* sp., *Porites* sp. massive, *Symphyllia radians*, *Turbinaria reniformis*).
5.3.3 Mesopredator caging experiment

To examine the effect of the different fish assemblages from the two coral treatments on the trophodynamics of coral reef mesopredators, mesopredators were introduced in April 2014. The chocolate grouper, *Cephalopholis boenak*, was selected as the study mesopredator species as it is both locally abundant on the Lizard Island reefs, predominantly piscivorous (Beukers-Stewart and Jones 2004), and relatively site-attached. Fourteen grouper were collected from the reefs surrounding the lagoon using baited hook and line underwater, and placed in aquaria at the Lizard Island Research Station. Only adult fish (17.1 – 21.3 cm TL) were collected to avoid any confounding effects of ontogenetic diet shifts (Chan and Sadovy 2002), and to ensure that there were minimal differences in the prey sizes available to the introduced mesopredators, as grouper are known to be limited by their gape size.

Prior to the introduction of the *C. boenak* to the patch reefs, all mesopredators that had recruited naturally to the patch reefs were removed using a net and clove oil anaesthetic, and relocated to the reef habitat surrounding the lagoon. Using the same method, all members of the family Apogonidae were also removed, as these species tend to recruit to reefs in large clouds of hundreds of fish, that could confound measures of both fish community composition and predation. The reefs were then enclosed using cages constructed from 2.5 cm x 2.5 cm wire mesh attached to a 2 m x 2 m x 1.2 m frame of PVC piping. A skirt of 2.5 cm mesh nylon netting was attached to the base of the cage, and weighted with metal chain that was buried in the sand to ensure that fish could not escape from the reefs.

All mesopredators (*C. boenak*) were individually tagged with a unique subcutaneous fluorescent elastomer tag in their pectoral fins. Their total length (TL) and
wet weight (WW) were recorded immediately before introducing them to the caged patch reefs. A single *C. boenak* was introduced to seven randomly selected reefs within each treatment, while the remaining six caged reefs (three for each coral treatment) were used as controls. The experiment was then allowed to run for six weeks before the mesopredators were removed. During this period, the cages were monitored daily and cleaned of algae and any other fouling organisms. Immediately prior to removing the *C. boenak*, the fish community on each reef was again surveyed as per the start of the caging experiment.

Mesopredators are physically limited in the prey they are able to consume by their gape size (Mumby et al. 2006). Therefore, to estimate the relative difference in prey biomass available to the *C. boenak* introduced to the patch reefs, their gape height (cm) was measured (mean ± standard error; 3.68 ± 0.07 cm, max = 4.15 cm, min = 3.30 cm). A prey size cut-off of 5 cm (TL) was consequently used to calculate the prey biomass available to all mesopredators. This slightly longer size was based on the assumption that mesopredators will not always consume their prey side-on, but rather head or tail first.

### 5.3.4 Mesopredator sampling

After six weeks of enclosure, *C. boenak* were removed from the reefs using a net and clove oil anaesthetic, and then euthanised by immersion in ice water. Total wet weight (WW), gutted weight (GW), total length (TL), body height (H), gape height (GH) and liver weight (LW) were recorded for each fish. The livers were excised and fixed in 4% buffered formaldehyde for histological analysis. Samples of white muscle tissue (~ 2.5 cm³) were collected from between the lateral line and dorsal fin of each fish, and frozen for lipid analysis.
5.3.5 **Body condition indices**

Morphometric body measurements were used to calculate the overall body condition index B’ (Richter et al. 2000). This index specifically accounts for the tendency for allometric growth in numerous fish taxa by incorporating body height (H) in its calculation:

\[
B' = \frac{GW}{(H \times TL^2)}
\]

Short-term changes in energy stores are often first detected in the liver (Ostaszewska et al. 2005), as this is both the primary site of lipid storage in fish (Stallings et al. 2010), and the tissue with the highest metabolic turnover rate (MacNeil et al. 2006). Therefore, we examined the potential for a treatment effect in the livers of caged mesopredators using both the hepatosomatic index and density of liver vacuoles. The hepatosomatic index (Stevenson and Woods 2006) is the ratio of liver weight (LW) to gutted body weight (GW):

\[
HSI = \frac{(LW/GW) \times 100}{100}
\]

To examine the potential difference in glycogen stores in the livers of *C. boenak* more closely, the density of hepatocyte vacuoles in transverse liver sections were examined using histology. Preserved livers were embedded in paraffin wax, then cut into 5 μm sections and stained with eosin and Mayer’s haematoxylin. A Weibel eyepiece was then used to count vacuole densities at a magnification of 400x (Pratchett et al. 2001).

Finally, total lipid content of white muscle tissue samples was quantified using a chloroform-methanol mixture to dissolve all lipids from the tissues (Bligh and Dyer 1959). The solvent was then evaporated off, and the total lipid mass weighed and expressed as a percentage of the total sample.
5.3.6 Statistical analyses

Differences in the structural complexity of the benthic habitat between patch reef treatments (vulnerable vs tolerant) was tested using Welch’s t-test, which adjusts degrees of freedom to account for unequal variances between groups (Welch 1947). Similarly, differences in the diversity (Shannon-Weaver Index; H), abundance (fish.reef\(^{-1}\)) and total biomass (kg.reef\(^{-1}\)) of the entire fish assemblage, as well as the available prey fish biomass (kg.reef\(^{-1}\), based on a 5 cm body size cut off ), were compared between coral treatments.

To examine how the fish communities on the patch reefs shifted in terms of their composition over the duration of the 6-week mesopredator caging experiment, a principal coordinates analysis (PCO) was used, based on a Bray-Curtis similarity matrix. Data were square root transformed to reduce the influence of highly abundant species. Eigenvectors of the species accounting for the largest separation in the fish communities (> 0.7 Pearson correlation co-efficient) were then overlaid to show the key distinguishing taxa. The change in species composition was measured in terms of the Bray-Curtis dissimilarity between the fish community on each reef at the end of the caging experiment compared to the start. A linear mixed effects model was then used to test for a difference in Bray-Curtis dissimilarity between reef treatments (vulnerable vs tolerant), with the predator treatment (control vs C. boenak) included as a random effect.

Differences in the condition of mesopredators caged on vulnerable and tolerant reefs in terms of their B’ condition index, hepatosomatic index (HSI) and the density of hepatocyte vacuoles in liver sections were all tested using notched boxplots and associated 95% confidence intervals.
5.4 Results

5.4.1 Benthic habitat & fish community

In April 2015, immediately prior to the introduction of the mesopredator caging experiment, patch reefs of the ‘tolerant’ treatment had significantly lower structural complexity than those of the ‘vulnerable’ treatment (RI; Vulnerable: 2.46 ± 0.14, Tolerant: 1.87 ± 0.10, t_{11.72} = 4.154, \(p < 0.001\), mean ± standard error; Fig. 5.2a). The reef fish communities that established over 18-month period differed significantly between treatments in terms of their Shannon-Weiner Diversity (H'; Vulnerable: 2.32 ± 0.12, Tolerant: 1.70 ± 0.09, t_{17.48} = - 5.01, \(p < 0.001\), Fig. 5.2b). Fish communities on vulnerable reef treatments also had higher overall abundance (fish.reef\(^{-1}\); Vulnerable: 47.45 ± 3.83, Tolerant: 29.4 ± 2.71, t_{17.64} = - 4.712, \(p < 0.001\)), and biomass (kg.reef\(^{-1}\); Vulnerable: 0.34 ± 0.03, Tolerant: 0.20 ± 0.05, t_{16.10} =, \(p < 0.005\)) than those on tolerant reefs. There was more available prey biomass (<5cm) on vulnerable patch reefs than on tolerant reefs (kg.reef\(^{-1}\); Vulnerable: 0.054 ± 0.003, Tolerant: 0.030 ± 0.005, t_{13.03} = 4.87, \(p < 0.001\); Fig. 5.2c).

The PCO analysis showed a clear separation of fish community composition between vulnerable versus tolerant reefs (Fig. 5.3a). Fish communities on vulnerable reefs were characterised by high abundances of Pomacentrus moluccensis, Dascyllus aruanus, Gobiodon ceramensis, and Halichoeres melanurus. Tolerant reef fish communities were distinguished by higher abundances of Canthigaster papua and Balistoides viridis, while Pomacentrus chrysurus was equally abundant across both treatments.
5.4.2 Effect of mesopredators on fish communities

A greater shift was evident in the composition of reef fish communities on tolerant reefs than vulnerable reefs following the introduction of the mesopredator (Fig. 5.3a). Bray-Curtis dissimilarity of the fish assemblages between the start and end of the caging experiment was somewhat greater on tolerant reefs (Vulnerable: 12.40 [6.24, 18.56], Tolerant: 19.73 [13.57, 25.89]; Fig. 5.3b). On vulnerable reefs, there was little difference in mean Bray-Curtis dissimilarity between control reefs and those with C. boenak introduced, while on tolerant reefs, mean Bray-Curtis dissimilarity in fish community composition was higher for reefs with mesopredators than for controls (Fig. S1).
5.4.3 Effect of fish communities on mesopredators

The morphometric body condition index (B’) showed no difference in the robustness of *C. boenak* at the start of the experiment, prior to being introduced to the patch reefs (Vulnerable: 0.056 ± 0.001, Tolerant: 0.057 ± 0.002, *t*<sub>10.89</sub> = -0.988, *p* = 0.344). By the end of the 6-week mesopredator caging experiment, there was still no evidence of a difference in this body condition factor (B’) between patch reef treatments (Vulnerable: 0.052 ± 0.001, Tolerant: 0.053 ± 0.001, *t*<sub>9.81</sub> = -0.555, *p* = 0.591).
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The hepatosomatic index (HSI) showed no difference in the liver to body mass ratio in *C. boenak* between the two patch reef treatments (Fig. 5.4a). Similarly, the results of the liver histology analyses showed no significant difference in the hepatocyte densities in *C. boenak* caged on the two patch reef treatments (Fig. 5.4b). However, there was a much higher variance in the density of hepatocyte vacuoles in the livers of mesopredators caged on tolerant reefs than those from vulnerable reefs (Variance; Vulnerable: 0.676, Tolerant = 79.246). At a finer physiological scale, the results of the total lipid extraction showed a higher percentage lipid composition in the white muscle tissue of *C. boenak* caged on vulnerable reefs than those from tolerant reefs (Fig. 5.4c).

**Fig. 5.4** Notched boxplots of (a) hepatosomatic index (HSI), (b) hepatocyte densities from liver tissue sections, and c. percentage total lipid content in white muscle tissue of *C. boenak* after removal from mesopredator caging experiment on vulnerable and tolerant patch reef treatments. Bold centre line indicates the median, whiskers span maximum and minimum values, box height shows the interquartile range, and diagonal notches in the boxes illustrate the 95% confidence interval around the median.
5.5 Discussion

Novel coral reef ecosystems emerging due to climate change are expected to vary substantially, in terms of both structure and function, from the structurally complex, diverse assemblages we associate with current day healthy coral reefs (Graham et al. 2014). This study suggests that these changes are likely to affect the trophodynamics between reef mesopredators and the reef fish communities on which they prey. Critically, it provides evidence that mesopredators could experience a loss of condition associated with decreased energy reserves. It also shows that the prey fish communities on which they feed on tolerant reefs are less diverse, and prone to greater impacts from piscivore predation. Disruption of trophodynamics on future reefs is thus likely to have repercussions for both mesopredators and their prey.

Reduced lipid energy stores in the *C. boenak* caged on tolerant reef treatments could be attributable to several factors, including altered prey species availability or reduced available prey biomass. Like many reef mesopredators, *C. boenak* are ambush predators, that rely on structure for shelter to hunt from (Shpigel and Fishelson 1989). They may therefore need to expend more energy in hunting and capturing prey on tolerant reefs due to the decreased structural complexity. In this experiment, we excluded the effects of competition, by only including a single mesopredator on each reef. On a contiguous coral reef, it is possible that the depletion of lipid stores may be exacerbated as mesopredators experience increased competition for shelter and prey, both factors negatively affected by a loss of structural complexity (Hixon and Beets 1993, Beukers and Jones 1997, Syms and Jones 2000, Kerry and Bellwood 2012).

Sub-lethal effects, such as the loss of condition and energy reserves, in mesopredators can compromise not only their ability to withstand periods of stress (Jones and McCormick 2002), but also the resources they are able to allocate to
important life history components, such as growth, age of first reproduction and fecundity (Kokita and Nakazono 2001, Pratchett et al. 2006). This study was too short to empirically detect these effects, but previous field studies have shown that despite mesopredators being able to adapt their diets to a changing prey base, this altered trophic niche carried a cost to their condition (Chapter 2). Due to the relative longevity of many reef mesopredators, sub-lethal costs may not be easily detected in the short term, but may result in unexpected population crashes in the long term (Graham et al. 2007). This has implications for fisheries management, as mesopredators are often highly targeted species, and if catch rates are not managed when populations are stressed and experiencing reduced recruitment rates, fisheries could face severe declines.

Changes in the broader fish community associated with predicted shifts in coral assemblages are also likely to have wide-ranging ecological and economic implications. This study suggests that the abundance and diversity of reef fish communities will decline as coral communities become dominated by taxa with higher thermal tolerance and low structural complexity. This is not surprising, as a reduction in structural complexity decreases available habitat niche space for fish species (Darling et al. 2017). The overall reduction in reef fish biomass also supports previous findings that biodiversity and biomass are closely related, with high biomass reefs supporting a high diversity of species (McClanahan et al. 2011), and biomass found to scale with biodiversity (Mora et al. 2011). Reduced diversity and biomass in coral reef fish communities would compromise the sustainability of multispecies reef fisheries, with severe repercussions for the food security of some of the world’s poorest coastal populations (Cinner et al. 2013a).
High species diversity is frequently predicted to confer ecological stability to communities, by increasing the functional diversity represented among species (McCann 2000, Gross et al. 2014, Duffy et al. 2016). Greater functional diversity can increase community resilience, allowing them to better respond to perturbation (e.g. Nash et al. 2016), an attribute which may become increasingly important in responding to new future disturbance regimes (Nyström et al. 2008). In this study, fish communities on tolerant patch reefs were both less diverse and more strongly affected by the introduction of a mesopredator, suggesting that they may be less resilient to predation than fish communities on vulnerable patch reefs.

The species that distinguished fish communities on vulnerable reefs from those on tolerant reefs represent a variety of different functional groups (e.g. planktivores, coral dwellers, mixed-feeding mid-trophic level wrasses). These species also included habitat specialists that rely on complex live corals (*Dascyllus aruanus, Gobiodon ceramensis*) (Froese and Pauly 2016). Tolerant reefs were characterised by species of the order Tetraodontiformes (*Canthigaster papua, Balistoides viridescens*), which are known to associate with rubble bottoms as juveniles, and have broad habitat use (Froese and Pauly 2016). Species that were ubiquitous between treatments were omnivorous habitat generalists (e.g. *Pomacentrus chrysurus*). This suggests that degree of habitat specialisation likely to be a strong driver of future reef fish communities, with generalist species potentially emerging as the successful species on future novel reef assemblages due to their adaptability.

As atmospheric carbon concentrations continue to rise, it is improbable that coral reef ecosystems will return to their pre-disturbance state. It is therefore essential that we improve our understanding of how these novel configurations in future ecosystems are likely to function. This study provides insight into how the
trophodynamics of piscivorous mesopredators and their prey communities could be affected as coral assemblages shift with rising ocean temperatures. Predation is one of the fundamental ecological processes in food webs (Legović 1989), and therefore of key importance to understanding how ecosystem function may be disrupted or maintained in future reef ecosystems. Mesopredators are also important target species in many reef fisheries (Cinner et al. 2009, Mumby et al. 2012, GBRMPA 2014). To ensure the best possible management of these ecologically and economically valuable species, is crucial that we improve our understanding of the probable effects of changing prey bases and habitats on mesopredators, to maintain ecological function and provision of ecosystem services.
6.1 Introduction

Habitat degradation in both marine and terrestrial ecosystems is becoming increasingly widespread, causing significant disruption of ecosystem structure and function (Hoekstra et al. 2005, Pratchett et al. 2014). Climate change is one of the most significant drivers of this degradation, and coral reefs are disproportionately vulnerable to its effects (Hoegh-Guldberg et al. 2007), with rising ocean temperatures causing coral bleaching and associated loss of live coral cover (Hughes et al. 2017), and potential regime shifts (Graham et al. 2015).

Changes in the benthic composition and structure of coral reefs leads to changes in associated reef fish communities (Chong-Seng et al. 2012, Darling et al. 2017). This is also the prey base replied upon by resident piscivorous mesopredators (e.g. Serranidae, Lutjanidae). Many of these mesopredator species have high ecological, economic and social value (Bell et al. 2013, Cinner et al. 2013b, Sadovy de Mitcheson et al. 2013), making it imperative that we expand our relatively limited understanding of the repercussions of habitat degradation for this group.

This thesis addresses this key research gap, investigating how the prey fish communities of mesopredators change in response to habitat degradation (Chapter 1), regime shifts (Chapters 2 and 3), and expected climate-driven changes in coral assemblages (Chapter 4). It examines changing trophic structure and functional composition within reef fish communities, and using observation, tissue sampling and
experimental techniques, examines the effects of these changes on mesopredator populations and their physiology.

Through addressing these questions in various locations affected by different drivers of change, it also provides the opportunity to compare the commonalities and differences between study sites.

6.2 Integration of research outcomes

6.2.1 Habitat degradation

Habitat destruction has been predicted to become an important driver of marine defaunation and species extinction in the next century (McCauley et al. 2015). Disturbance and habitat degradation in coral reef ecosystems is driven by a broad suite of drivers, often acting synergistically, each producing different effects in the reef benthos (Ban et al. 2014). This thesis considers the effects of various types of degradation resulting from different disturbances and drivers on the trophodynamics of coral reef mesopredators. In the Keppel Island Group on the southern Great Barrier Reef (GBR), the study site for chapter 1, extensive loss of live hard coral habitat and increase in macroalgae cover was due to a localised bleaching event in 2006, followed by disturbance from sediment-laden flood plumes in 2011 and 2013 (Williamson et al. 2016, Chapter 1). In the Seychelles Inner Island Group, the 1998 mass bleaching event lead to the regime shift of numerous reefs from a coral- to algae-dominated state (Graham et al. 2015, Chapters 2 and 3). Finally, in chapter 4, a patch reef experiment simulated predicted altered coral assemblages expected as reefs become increasingly dominated by taxa that are less susceptible to rising ocean temperatures (Loya et al. 2001, Pandolfi et al. 2011, Chapter 4).
The key factor in changes in the benthos of reef systems across all studies, was the loss of structural complexity, an attribute of coral reef ecosystems that is emerging as a critical determinant of small-bodied reef fish communities (Nash et al. 2013, Darling et al. 2017). While lower structural complexity is often associated with a reduction in live hard coral cover (Graham and Nash 2013), it is also a characteristic of many coral taxa with low susceptibility to bleaching (Loya et al. 2001, Alvarez-Filip et al. 2013). It is therefore a concern that while certain reefs may be able to maintain high levels of live coral cover as thermal stress increases through shifting assemblages this may nonetheless reduce structural complexity, with detrimental effects for the associated reef fish community.

6.2.2 Changes in prey communities

Coral reef fish community composition is very closely linked to the benthic coral habitat, and therefore vulnerable to habitat degradation (e.g. Pratchett et al. 2014). While loss of live coral cover affects specialised species that are directly reliant on live coral for food, habitat, or settlement (Wilson et al. 2006, Pratchett et al. 2008), it is loss of structural complexity that has been shown to have the most far-reaching effects on the reef fish community, including large reef mesopredator species (Cinner et al. 2009, Wilson et al. 2012a), many of which are ambush hunters, associating strongly with high structure habitat which they use to hunt (Kerry and Bellwood 2012). These large-bodied, mobile mesopredatory species are, however, likely to feel the strongest effects of this habitat change mediated via the prey-fish community on which they feed.

Changes in the reef associated mesopredator prey fish communities, resulting from the different drivers of habitat change investigated in this thesis, showed overall trends of reduced diversity and abundance (Chapters 1 – 4). Across all studies, there
was a consistent loss of mid-trophic level species and functional groups, particularly specialists such as corallivores, or coral associated planktivores (Chapters 1 - 4), and an increase in herbivorous species. In the Keppel Islands on the GBR, the shift in the prey community associated with loss of live coral cover was most strongly characterised by a shift in the dominant species in the prey community from high abundances of schooling planktivorous damselfish (e.g. Chromis nitida), towards territorial benthic algae-feeding species (e.g. Pomacentrus wardi). Similar trends were evident in Seychelles, with prey fish communities becoming increasingly dissimilar with time since disturbance (Chapter 3 and 4). Regime-shifted reefs became increasingly dominated by herbivorous species, developing a concave trophic pyramid structure due to the loss of mid-trophic level species (e.g. corallivores, planktivores). In contrast, reefs that recovered following bleaching, regaining high live coral cover, moved towards a bottom-heavy trophic pyramid structure, with high representation of mid-trophic level species and functional groups. Prey fish communities in the Lizard Island patch reef experiment showed slightly different responses to changing benthic composition, primarily due to the fact that there was no increase in algal resources or live coral cover loss (Chapter 4). The altered, low structure coral assemblages on thermally ‘tolerant’ reefs, nonetheless showed many of the same patterns of change in the prey fish community as in previous chapters, with lower diversity and available prey biomass than on ‘vulnerable’ reef treatments.

Many mesopredator species are thought to be able to adapt their diets to exploit the most abundant available prey (Shpigel and Fishelson 1989, Kingsford 1992, Greenwood et al. 2010), thereby potentially minimising their vulnerability to these changes. Using stable isotopes, this thesis empirically demonstrated the ability of an important reef mesopredator, coral trout (Plectropomus maculatus), to shift their diets
in the Keppel Island group (Hempson et al. 2017, Chapter 1). However, despite this
trophic adaptability, this population was nonetheless in steep decline, with the strongest
driver shown to be a reduction in total available prey biomass (Hempson et al. 2017).
This decrease in the absolute biomass available to mesopredators due to habitat
degradation was a consistent trend found across all studies, and therefore an important
cause for concern given the strength of the relationship with mesopredator abundance.

6.2.3 Effects on mesopredators

Trophic downgrading, or the loss of predators from a diverse range of
ecosystems has become an issue of growing concern worldwide (Estes et al. 2011).
While top down drivers, such as fishing, are an important factor controlling abundance
of many coral reef mesopredators (e.g. Jackson et al. 2001, Pandolfi et al. 2003,
DeMartini et al. 2008), habitat has been shown in certain instances to be a stronger
driver than fishing in shaping these communities (Wilson et al. 2012a). In many
instances, trophic downgrading is a cryptic process, only becoming evident once the
high-level consumers are lost from the system. This is often attributable to the long
lifespans of many predators relative to their prey populations (Graham et al. 2007). To
understand the mechanisms controlling these long term cryptic declines in top-
consumer populations, it is necessary to examine the sub-lethal effects of habitat
degradation on these resident predators.

This thesis employed stable isotopes ($\delta^{13}$C and $\delta^{15}$N) to investigate this gap in
our knowledge of the altered trophodynamics of mesopredators in degrading systems
(Chapters 1 and 2). Carbon signatures in the Keppel Islands showed a shift from more
planktonic carbon sources, towards benthic sources, indicating that mesopredators were
adapting their diets to the changing prey availability as reefs degraded (Hempson et al.
Chapter 6: General Discussion

2017, Chapter 1), while in Seychelles mesopredators (*Cephalopholis argus*) on recovering reefs with high coral cover had a broader range of carbon sources than on regime-shifted reefs (Chapter 2). In both instances mesopredators on degraded or regime-shifted reefs had lower nitrogen signatures than those feeding on reefs with high live coral cover (Chapter 1 and 2). These results suggest that the food webs on which mesopredators are feeding are becoming simplified due to habitat degradation, resulting in shorter food chains. This pattern of reduced trophic complexity associated with altered benthic habitat is also evident in the concave structure of relative biomass pyramids on regime-shifted reefs in Seychelles (Chapter 3), and the lower diversity of fish communities on patch reefs composed of thermally tolerant coral taxa in the Lizard Island experiment (Chapter 4).

Recent isotope studies have shown that congeneric species of coral reef mesopredators with overlapping dietary niches show little overlap in space use patterns, thereby minimising competition for prey resources (Matley et al. 2016). In cases where species co-occur in space, stable isotope data suggests that their dietary niches and ecological roles differ (Matley et al. 2017). This suggests that a fine balance of resource partitioning exists between mesopredators within reef fish communities. The finding that mesopredators appear to be altering their trophic niche in response to habitat degradation, benthic assemblage shifts, and changing prey availability (Hempson et al. 2017, Chapter 1 and 2), means that competition between sympatric mesopredator species is likely to increase, as dietary and spatial niche space is lost, and niche overlap increases.

Habitat degradation thus has the potential to exact a physiological cost on piscivorous mesopredators via several indirect pathways, including changing prey bases, reducing habitat availability and structure for effective hunting (Samoilys 1997,
Kerry and Bellwood 2012, Coker et al. 2014), thereby increasing competition for resources. This thesis provides some of the first empirical evidence of these sub-lethal costs, showing that mesopredators on regime-shifted reefs in Seychelles have lower densities of hepatocyte (lipid storage) vacuoles in their livers, and reduced storage lipids in spawning female fish, than those on recovering reefs (Chapter 2). Mesopredators caged on thermally tolerant reefs in the Lizard Island experiment also had lower lipid levels than fish on the vulnerable reefs (Chapter 4). This suggests that the altered habitat on both regime-shifted reefs (Chapter 2), and transformed coral assemblages (Chapter 4), tend to be more energy depleting environments for mesopredators. Decreased energy reserves can detrimentally affect a number of important life history functions, including growth rates (Kokita and Nakazono 2001, Feary et al. 2009), age of first reproduction (Jonsson et al. 2013), fecundity and survivorship (Jones and McCormick 2002), which can lead to population declines in the long term (Graham et al. 2007). It is possible that these effects have contributed to the population declines of piscivorous mesopredators documented in the long term monitoring of the Keppel Islands (Williamson et al. 2014, 2016, Hempson et al. 2017, Chapter 1) and Seychelles reefs (Graham et al. 2007, Chapter 3). In Seychelles, the upper trophic levels of the foodweb on regime-shifted reefs have become increasingly dominated by generalist mesopredators (e.g. *Lethrinus nebulosus*) that have a broad dietary niche, including invertebrates and non-coral associated prey (Smith et al. 2003), and that scavenge over a variety of habitat types (Farmer and Wilson 2011, Chapter 3). This evidence suggest that generalists may be more successful mesopredator species in the future, as coral habitat becomes increasingly degraded or altered.

In addition to the effects of climate-driven habitat degradation mediated via the food web, mesopredators also experience direct physiological effects from increasing
ocean temperatures (Johansen et al. 2014, 2015). Recent work on the important Indo-west Pacific fisheries species, *Plectropomus leopardus*, showed that this species reduced its activity in response to increased temperatures (Johansen et al. 2014). This can directly reduce their ability to encounter and capture prey, thereby decreasing their overall energy intake. Further, as with all marine ectotherms, rising ocean temperatures increase the metabolic energy requirements of mesopredators (Pörtner and Farrell 2008), requiring that they increase their prey intake to meet these energetic demands (Johansen et al. 2015). As reef fish prey populations decline with habitat degradation, reduced activity and increased energetic demands on piscivores could result in not only a loss of condition in these consumer species, but also increased top-down pressure on prey communities as competition for diminishing resources intensifies.

Predator top-down control is considered to be an important driver in ecosystems (Friedlander and DeMartini 2002, Graham et al. 2003), and disruption of this trophic role can therefore result in distortion of food web trophodynamics. The mesopredator patch reef caging experiment at Lizard Island showed that the less diverse reef fish communities that established on tolerant reefs, with coral taxa of low bleaching susceptibility, experienced stronger effects of predation on community composition than the more diverse fish communities, with higher abundance and biomass on vulnerable reefs (Chapter 4). Recent work also shows that top-down effects of reef mesopredators are not limited to direct consumption of prey, but include the potential for driving behavioural trophic cascades (Vance-Chalcraft et al. 2007), whereby large bodied reef mesopredators can influence both the behaviour of smaller predators, and their interaction with their prey (Palacios et al. 2016b). This effect has also been found to extend beyond a behavioural response, to benefitting lower trophic level species physiologically, by suppressing the predation pressure of smaller predators and
allowing prey species to increase their foraging time and energy budget due to decreased predator avoidance (Palacios et al. 2016a). These findings emphasise the importance of the multiple top-down effects exerted by mesopredators in coral reef food webs, and reinforces the need for us to understand the implications of habitat degradation on this key functional group.

6.3 Management implications

This thesis highlights the importance of holistic ecological thinking for effectively managing mesopredator conservation and fisheries. Limiting the top down effects of fishing pressure on mesopredator populations using strategies such as marine protected areas (MPAs, e.g. Rizzari et al. 2015), quota systems (Little et al. 2009) or fishing gear restrictions (Cinner et al. 2009) is a relatively well established management approach. However, in the current era of climate change and widespread habitat degradation, it is becoming increasingly important to incorporate a bottom up approach. This thesis demonstrates the implications of altered habitat states and changes in the associated fish communities for the mesopredators that prey on them. Managers should plan for potential unexpected mesopredator population crashes, with the potential for sub-lethal effects of these altered trophodynamics to manifest as lag effects, reducing population growth and survivorship in the long term (Graham et al. 2007, Chapters 2 and 4). Certain mesopredator species are also reliant on live coral habitat for settlement (Jones et al. 2004) and in early life history stages (Wen et al. 2013b), with habitat rather than reserve status having a greater effect on mesopredator recruitment rates (Wen et al. 2013a).

Effectively conserving and managing mesopredator populations therefore requires an ecosystem scale approach, integrating both top-down and bottom-up
thinking. Managing the extractive impact of fisheries is essential, particularly for protecting breeding populations and source stocks (Cinner et al. 2009, Mellin et al. 2016). However, it is equally crucial that the habitats and prey populations on which mesopredators rely receive conservation focus, as without healthy coral reef habitat for settlement and recruitment of both mesopredators and their prey species, their populations will be unable to sustainably support fishing pressure. Stratification of a fishery to take into account the ecological requirements or state of particular habitats is one potential solution to maintaining a fishery, and simultaneously supporting vulnerable habitats (Mumby 2014). While MPAs are an important tool for conserving coral reef habitat, with no-take areas proving particularly effective (McCook et al. 2010), a larger scale view is indispensable in order to manage broader ecosystem threats, such as land-based sediments and nutrient runoff (Wenger et al. 2015). Integrated coastal management, based on the best available scientific knowledge, is critical to balancing social and economic objectives with ecological sustainability (The World Bank 2006). Further, it is essential that reefs are managed for resilience, by explicitly prioritising the maintenance of key functional groups and ecosystem processes (e.g. herbivory) in conservation planning and fisheries policy (Bellwood et al. 2004, Mumby and Steneck 2008). Finally, it is essential to successful conservation of coral reef ecosystems, that management strategies empower local users to take ownership of conserving their resources (Cinner et al. 2012, Ban et al. 2013, Graham et al. 2013).

6.4 Future directions

With trophic downgrading and habitat loss becoming increasingly widespread (Estes et al. 2011, McCauley et al. 2015), it is essential that we improve our
understanding of mesopredators’ vulnerability to the effects of habitat degradation and their ability to adapt to it. Important future lines of inquiry include investigating the capacity of mesopredator species to supplement their diets with invertebrate prey or source energy from outside of their normal habitat range. This knowledge would enable fisheries managers to direct fishing pressure away from trophically vulnerable species, towards those that are more robust and able to adapt their diets as ecosystems change (Chapter 1 and 3). Equally important in supporting this fisheries decision making, is to examine how the invertebrate prey base of generalist mesopredators is affected by coral reef degradation and regime shifts. Finally, this thesis also demonstrates the difficulty in detecting sub-lethal costs of habitat degradation in mesopredators without high levels of lethal sampling and costly lab analyses (Chapters 2 and 4). Research into the development of non-lethal techniques for assessing the physiological condition of mesopredators would be invaluable for sustainable fisheries management, and in preventing unexpected population crashes due to lag effects.

6.5 Concluding remarks

Habitat degradation is reaching unprecedented scales globally (Hoekstra et al. 2005), with climate change due to rising atmospheric carbon levels responsible for much of the recent acceleration (Hoegh-Guldberg et al. 2007). Coral reefs are particularly vulnerable to the effects of climate change (Hughes et al. 2003), and over the duration of this thesis, the severity, frequency and extent of coral bleaching on coral reefs has dramatically exceeded all historic baselines (Hughes et al. 2017). Over the past four years, many of the reefs located at all study sites for this thesis have undergone substantial transformation in their composition, largely due to live coral loss from

At the same time, global populations and their reliance on natural resources and ecosystem services continue to grow (Bell et al. 2013). Coral reefs directly support some of the world’s poorest populations, and therefore face intensified pressure in the immediate future both from climate and human pressure (Hicks and Cinner 2014, Graham et al. 2017).

It is thus more crucial than ever before to understand how reefs are likely to function in the future, as we move into an era of novel ecosystems and disturbance regimes (Graham et al. 2014). This thesis provides important insight into how the trophodynamics of piscivorous coral reef mesopredators and their prey communities are likely to respond to the effects of habitat degradation, providing important information on which to base decision making and guide conservation efforts and fisheries management.
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72.


Fig. S1 Shift in the $\delta^{13}C$ signal in coral grouper (*Plectropomus maculatus*) between 2009 (n=9), 2011 (n=27), and 2013 (n=12), from a more negative (i.e. planktonic) signal, to more positive (i.e. benthic) signal. The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile range past these points.
**Fig. S2** Change in logged total prey biomass available to coral grouper in the Keppel Islands between 2009 (n=9), 2011 (n=27), and 2013 (n=12). The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile range past these points.
Table S1. Composition of the benthic cover of reefs in the inner Keppel Island Group on the southern Great Barrier reef in 2009, 2011 and 2013, showing mean percentage cover (±standard error; SE) of the three dominant cover types and mean (±SE) structural complexity index (SCI; slope x rugosity).

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>n</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Live hard coral cover (%)</td>
<td>Macroalgal cover (%)</td>
<td>Dead coral &amp; rubble cover (%)</td>
<td>SCI</td>
</tr>
<tr>
<td>Big Peninsula</td>
<td>2009</td>
<td>10</td>
<td>81.60 ± 3.04</td>
<td>0.00 ± 0.00</td>
<td>10.00 ± 1.58</td>
<td>9.80 ± 0.82</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>10</td>
<td>49.40 ± 7.88</td>
<td>0.00 ± 0.00</td>
<td>31.00 ± 6.42</td>
<td>7.36 ± 0.65</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>10</td>
<td>32.20 ± 5.62</td>
<td>0.20 ± 0.20</td>
<td>27.20 ± 5.58</td>
<td>5.92 ± 0.41</td>
</tr>
<tr>
<td>Clam Bay</td>
<td>2009</td>
<td>15</td>
<td>46.67 ± 8.37</td>
<td>40.53 ± 10.19</td>
<td>7.20 ± 1.55</td>
<td>5.73 ± 0.14</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>15</td>
<td>33.60 ± 7.34</td>
<td>0.27 ± 0.18</td>
<td>60.93 ± 7.85</td>
<td>4.54 ± 0.31</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>15</td>
<td>20.80 ± 6.51</td>
<td>17.87 ± 3.59</td>
<td>51.87 ± 4.39</td>
<td>4.48 ± 0.25</td>
</tr>
<tr>
<td>Halfway Island</td>
<td>2009</td>
<td>15</td>
<td>68.00 ± 6.11</td>
<td>18.67 ± 7.08</td>
<td>8.40 ± 2.34</td>
<td>6.29 ± 0.39</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>15</td>
<td>36.27 ± 4.14</td>
<td>0.00 ± 0.00</td>
<td>51.73 ± 5.28</td>
<td>7.13 ± 0.41</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>15</td>
<td>21.87 ± 3.57</td>
<td>3.60 ± 1.05</td>
<td>62.53 ± 4.57</td>
<td>4.37 ± 0.17</td>
</tr>
<tr>
<td>Middle Island</td>
<td>2009</td>
<td>15</td>
<td>67.60 ± 4.73</td>
<td>15.73 ± 4.76</td>
<td>15.07 ± 2.77</td>
<td>7.50 ± 0.19</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>15</td>
<td>26.67 ± 5.17</td>
<td>0.00 ± 0.00</td>
<td>66.53 ± 7.08</td>
<td>4.73 ± 0.23</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>15</td>
<td>17.33 ± 5.11</td>
<td>24.80 ± 5.51</td>
<td>52.13 ± 6.61</td>
<td>4.39 ± 0.32</td>
</tr>
</tbody>
</table>
Table S2. Number (n) of coral grouper (*Plectropomus maculatus*) samples collected at five sites, during three sampling periods in the Keppel Island Group on the Great Barrier Reef, showing mean total length (TL, cm) ± standard error (SE) for each site and year sampled.

<table>
<thead>
<tr>
<th>Year</th>
<th>Big Peninsula Mean TL (cm)</th>
<th>± SE</th>
<th>n</th>
<th>Clam Bay Mean TL (cm)</th>
<th>± SE</th>
<th>n</th>
<th>Egg Rock Mean TL (cm)</th>
<th>± SE</th>
<th>n</th>
<th>Halfway Island Mean TL (cm)</th>
<th>± SE</th>
<th>n</th>
<th>Middle Island Mean TL (cm)</th>
<th>± SE</th>
<th>n</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>60.5</td>
<td>4.5</td>
<td>2</td>
<td>41.7</td>
<td>1.2</td>
<td>9</td>
<td>59.3</td>
<td>3.2</td>
<td>5</td>
<td>52.5</td>
<td>4.4</td>
<td>6</td>
<td>45.0</td>
<td>1.2</td>
<td>6</td>
<td>9</td>
</tr>
<tr>
<td>2012</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>53.2</td>
<td>3.0</td>
<td>7</td>
<td>60.3</td>
<td>3.1</td>
<td>6</td>
<td>52.5</td>
<td>4.4</td>
<td>6</td>
<td>45.0</td>
<td>1.2</td>
<td>6</td>
<td>27</td>
</tr>
<tr>
<td>2013</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>51.7</td>
<td>4.6</td>
<td>6</td>
<td>75.1</td>
<td>0.6</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>16</td>
<td>12</td>
<td>12</td>
<td>6</td>
<td>6</td>
<td>48</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table S3. Prey fish species functional group allocations

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Functional Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pomacentridae</td>
<td><em>Chromis amboinensis</em></td>
<td>Planktivorous pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Chromis atripectoralis</em></td>
<td>Planktivorous pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Chromis nitida</em></td>
<td>Planktivorous pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Chromis ternatensis</em></td>
<td>Planktivorous pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Pomacentrus lepidogenis</em></td>
<td>Planktivorous pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Hemiglyphidodon plagiometapon</em></td>
<td>Territorial pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Neoglyphidodon melas</em></td>
<td>Territorial pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Pomacentrus bankanensis</em></td>
<td>Territorial pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Pomacentrus wardi</em></td>
<td>Territorial pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Stegastes apicalis</em></td>
<td>Territorial pomacentrid</td>
</tr>
<tr>
<td></td>
<td><em>Stegastes fasciolatus</em></td>
<td>Territorial pomacentrid</td>
</tr>
</tbody>
</table>
Table S4. Standardised AIC-weighted model-averaged parameter estimates with 95% confidence intervals for models of stable isotope ($\delta^{13}$C and $\delta^{15}$N) signatures in coral grouper (*Plectropomus maculatus*).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Model parameter</th>
<th>Estimate</th>
<th>lower 95% limit</th>
<th>upper 95% limit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta^{13}$C</td>
<td>Distance from shore</td>
<td>-0.38</td>
<td>-0.98</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Total length</td>
<td>0.02</td>
<td>-0.66</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>Planktivorous pomacentrid abundance</td>
<td>-1.30</td>
<td>-2.01</td>
<td>-0.59</td>
</tr>
<tr>
<td>$\delta^{15}$N</td>
<td>Total length</td>
<td>0.60</td>
<td>0.35</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>Territorial pomacentrid abundance</td>
<td>0.57</td>
<td>0.38</td>
<td>0.75</td>
</tr>
</tbody>
</table>

**METHODS**

Methods of ethanol storage experiment

In November 2014, 20 clean white muscle tissue samples of 0.5 cm$^3$ were taken from a single fresh adult specimen of *Plectropomus leopardus*. Tissue samples were thoroughly rinsed with distilled water to remove any salt or other contaminants. Ten samples were stored in 100% ethanol, while the other 10 samples were frozen in sealed vials. After 9 months of storage, the samples stored in ethanol were again rinsed in distilled water to remove the preservative, and all samples were freeze-dried, lipid extracted and analysed for $\delta^{13}$C bulk stable isotope content.
METHODS

Sexual maturity categorisation

Female fish were categorised according to their reproductive status through gonad appearance based on conventional macroscopic criteria (West 1990): “developing” females were characterised with slightly coloured ovaries, and non-visible oocytes; “spawning” females had very large ovaries occupying the entire abdominal cavity and ovulated oocytes that can be fully expelled from the oviduct with gentle pressure; finally “regressing” females includes recently spawned and post-spawning fish with flaccid, red-brown or blood coloured ovaries and few remaining large oocytes.

Stable isotope sample preparation

Muscle tissue samples were freeze-dried and ground to a fine homogeneous powder with a MM200 mixer mill (Retsch®, Eragny sur Oise, France). A subsample (0.35 ± 0.1 g) of each sample was weighed out and all lipids extracted with 8 mL of dichloromethane at 100°C under 1900 psi for 10 min using an ASE 200 Accelerated Solvent Extractor (Dionex, Voisins De Bretonneux, France) (Bodin et al. 2009). The lipid-free samples were dried under an extractor fan and stored in a desiccator until sent for bulk stable isotope analysis of carbon and nitrogen at the Great Lakes Institute for Environmental Research (GLIER) laboratory at the University of Windsor, Canada. Isotope ratios were calculated for 400 - 600 μg of each sample, added to tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (Finnigan MAT Deltaplus, Thermo Finnigan, San Jose, California, USA).
**Lipid analysis**

Tissue samples were cryogenically ground to a homogenised powder using a MM400 mixer mill (Retsch®, Verder, France), and then a subsample (0.1 ± 0.001 g) weighed out under a nitrogen atmosphere. Total lipids were extracted using the Folch method (Folch et al. 1957) and dotted onto S-III Chromarods (Iatron Laboratories Inc., Tokyo, Japan), which were scanned with a Iatrosan MK-VI (Iatron Laboratories) thin-layer chromatography-flame-ionization detector analyser. Lipid classes were quantified using lipid standards (Cholesteryl palmitate, glyceryl tripalmitate, cholesterol, oleic acid, DL-palmitine and phosphatidil choline, Sigma-Aldrich) with PeakSimple 3.93 Software.
Fig. S1 Map of the study site in the Seychelles Inner Island Group showing the location of the 6 study sites. Recovering sites (Bel Ombre, Mahe West Patch, Mar Anglaise), are indicated by black squares, and regime-shifted sites (Anse Royale, Praslin South West, Mahe East Patch) by black triangles.
Fig. S2 Size-at-age of *Cephalopholis argus* sampled from reefs recovering from bleaching and regime-shifted reefs in Seychelles. Growth rate curves were fitted using the Von Bertalanffy Growth Model for fish from recovering (solid line) and regime-shifted (dashed lines).
### Table S1. Mean (± standard error) piscivorous mesopredator species abundance (fish.500m$^{-2}$) and biomass (kg. ha$^{-1}$) on regime-shifted (algae-dominated) and recovering (coral-dominated) reefs in Seychelles.

<table>
<thead>
<tr>
<th>Mesopredator species</th>
<th>Abundance</th>
<th>Biomass</th>
<th>Diversity (H)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>±s.e.</td>
<td>mean</td>
</tr>
<tr>
<td><strong>Regime-shifted (n = 32)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aprion virescens</em></td>
<td>0.30</td>
<td>0.20</td>
<td>4.73</td>
</tr>
<tr>
<td><em>Cephalopholis argus</em></td>
<td>0.20</td>
<td>0.23</td>
<td>1.57</td>
</tr>
<tr>
<td><em>Oxycheilinus digramma</em></td>
<td>0.71</td>
<td>0.33</td>
<td>1.08</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>0.20</td>
<td>0.16</td>
<td>1.23</td>
</tr>
<tr>
<td><strong>Recovering (n = 24)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anyperodon leucogrammicus</em></td>
<td>0.27</td>
<td>0.19</td>
<td>1.34</td>
</tr>
<tr>
<td><em>Cephalopholis argus</em></td>
<td>0.81</td>
<td>0.35</td>
<td>5.56</td>
</tr>
<tr>
<td><em>Cephalopholis miniata</em></td>
<td>0.14</td>
<td>0.14</td>
<td>0.13</td>
</tr>
<tr>
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### Table S2. Coefficient of variation (CV) and 95% confidence interval for isotopic signatures of *Sargassum* sp. sampled from regime-shifted and recovering reefs in Seychelles.

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<tr>
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Table S3. Mean (± standard error) lipid concentrations (µg .mg\(^{-1}\)) calculated for *Cephalopholis argus* sampled from recovering and regime-shifted reefs in Seychelles.

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<td>(n)</td>
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Appendix C: Supplemental information for Chapter 4

FIGURES

Fig. S2 Map of the study site in the Seychelles Inner Island Group showing the location of the ten study sites. The five recovering sites are indicated by black circles, and the five regime-shifted sites by black triangles.
Fig. S2 Heat map showing the number of species from each functional group within each level (trophic position; TP) of the trophic pyramids.
**Fig. S3** Trophic pyramids showing the distribution of absolute biomass (kg. ha⁻¹) 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).
Table S1. List of species presence and absence within in trophic level (1 – 5), reef state (recovering and regime-shifted) and year (pre-bleaching: 1994, post-bleaching: 2005, 2014), showing functional group allocation. Trophic levels relate to the five levels within the trophic pyramids; level 1 (green): trophic positions 2 – 2.5, level 2 (yellow): trophic positions 2.5 – 3, level 3 (orange): trophic positions 3 - 3.5, level 4 (bright red): trophic positions 3.5 – 4, level 5 (dark red): trophic positions 4 – 4.5.

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<th>TP</th>
<th>Species name</th>
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<th>Recovering '05</th>
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Table S2. Species responsible for 50% dissimilarity (SIMPER, Bray-Curtis) between pre-bleaching fish communities (1994) and post-bleaching (2014), within each trophic position (TP) and each reef state (recovering vs regime-shifted reefs).

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Fig. S 1 Notched boxplots of Bray-Curtis dissimilarity between fish communities on patch reefs prior to the introduction of a mesopredator (Cephalopholis boenak) to each reef, and six weeks later when the C. boenak were removed. Within each coral assemblage treatment (vulnerable vs tolerant, n = 10), C. boenak were introduced to seven caged reefs, while three control reefs were caged, but no mesopredators were introduced. 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.
Figure 1.1
Journal: Global Change Biology
Publication title: Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient?
Publication authors: Shaun K. Wilson, Nicholas A. J. Graham, Morgan S. Pratchett, Geoffrey P. Jones, Nicholas V. C. Polunin
Publication date: 18 September 2006
Content publisher: John Wiley and Sons
Licence date: 20 April 2017
License number: 4092441388852

Figure 1.2
Journal: Current Biology
Publication title: Human Disruption of Coral Reef Trophic Structure
Publication authors: Nicholas A.J. Graham, Tim R. McClanahan, M. Aaron MacNeil, Shaun K. Wilson, Joshua E. Cinner, Cindy Huchery, Thomas H. Holmes
Publication date: 23 January 2017
Content publisher: Elsevier
Licence date: 20 April 2017
License number: 4092440594536
Appendix D: Publications arising during candidature

Publications derived from thesis chapters


Other peer-reviewed articles published during PhD candidature