Hempson, Tessa N. (2017) ***Coral reef mesopredator trophodynamics in response to reef condition.*** **PhD thesis, James Cook University.**

https://doi.org/10.4225/28/5acbfc72a2f27

CORAL REEF MESOPREDATOR TROPHODYNAMICS IN RESPONSE TO REEF CONDITION

Thesis submitted by

Tessa N. Hempson, BSc. (Hons), MSc.

In April 2017

for the degree of Doctor of Philosophy

with the ARC Centre of Excellence in Coral Reef Studies

James Cook University

Townsville, Queensland, Australia

Acknowledgements

It is difficult to even begin expressing the depth of gratitude I feel towards all the people in my life who have contributed to bringing me to this point. What a journey it has been! I was born into the magical savannas of South Africa – a great blessing. But, for many born at the same time, this meant a life without the privilege of education or even literacy. I have been privileged beyond measure in my education, much of which would not have been imaginable without the immense generosity of my ‘fairy godparents’. Thank you, Joan and Ernest Pieterse. You have given me opportunities that have changed the course of my life, and made my greatest dreams and aspirations a reality.

Few PhD students have the privilege of the support and guidance of a remarkable team of supervisors such as mine. Prof. Nick Graham, you have been the most exceptional teacher, mentor and role model I could possibly wish for, both in science and well beyond. Dr Aaron MacNeil, your passion for numbers, waves, family, and life has inspired, challenged and grounded me. Thank you both for the enormous amount of energy you have put into turning me into a scientist at last, and for all your friendship, honesty and unwavering support throughout the journey, with its many challenges and time zones. Dr Geoff Jones, it is somewhat unbelievable to think that 16 years ago I travelled halfway around the world to ask you how to get funding for undergraduate studies at JCU, and now I am submitting a PhD thesis as your student. Thank you for opening your lab and your home to me, and for all the wisdom and guidance you have shared. Dr Andy Hoey, thank you for taking me on for the final strait and being there for me whenever I have needed a sounding board. The final member of my extraordinary team was Dr Glenn Almany, a man with great passion for ecology, people, and making a positive difference in the world. Despite fighting cancer for much of my PhD, before losing the battle in 2015, he left a deep impression on me and played a pivotal role in directing my research ideas. I feel very lucky to have had his influence in my life, if all too brief.

Numerous other academics have inspired and guided me along the way. Dr Shaun Wilson, Dr Nathalie Bodin, Prof. Simon Jennings, Dr Dave Williamson, Dr Dave Wilson, and Dr Dani Ceccarelli; thank you for sharing your insight, data, and expertise, I so appreciate all the time, energy and resources you have contributed to improving my work. Thank you to Dr George and Margo Branch for 'The Living Shores of Southern Africa', which gave this bush kid her first understanding of the wonders of the ocean realm. And to Prof Charlie Griffiths, my supervisor and mentor for many years at the University of Cape Town; thank you for your remarkable belief in me, your absolute support, and for giving me my first taste of the coral reefs of east Africa, which immediately captured my heart. And to the Western Indian Ocean Marine Science Association (WIOMSA) for all the inspiration and community.

Coral reef research often relies on the support of a highly skilled team, ranging from divers and boat skippers, to lab technicians. My PhD has taken me to some beautiful field locations, where I have had the support of some exceptional people. To the Keppels team – thank you for welcoming me in with all my vials. Waking to salvage a sinking boat from icy water at dawn on day one of field work was instantly bonding! Silent-J (aka Fraser Januchowski-Hartley), thank you for the long hours of *Cephaphalopholis argus* stalking in Seychelles. Thank you to team at the Seychelles Fishing Authority (SFA) for all your support both aboard L'Amitie and in the lab – I could never have processed all those fish without you.

To everyone that played a role in my Lizard Island mega-patch-reef-caging experiment, particularly Dr Lyle Vail and Dr Anne Hoggett, thank you for the many months of field, logistical and emotional support! I don't know that I would have been able to stick it out through 2.5 cyclones and months of fighting the elements without you. And a special thank you to those that volunteered their time so generously to help me in the field; Cindy Huchery, your tenacity is inspirational; Chancey MacDonald, your love and support got me through so much; Stefano Freddi, thank you for keeping me singing and laughing to the end (and for the new fins!). Lauren Nadler, Lisa Boström Einarsson, Cassy Thompson, Steve Doo, Alexia Graba-Landry, Alex Vail, Patrick Smallhorn-West, Maria Mar Del Palacios, Chris Mirbach and all the other island family, thank you for all the support, advice, help, dinners and memories.

Throughout my thesis I have also been supported by an outstanding team of lab professionals around the world. Thank you to Sue Riley for sharing her vast experience of histology and international tissue transport, and Shannon McMahon for reading my samples. Thank you to Anna Hussey, Prof Aaron Fisk and their lab at GLIER for processing all my isotope samples, and deciphering my awful labelling – it has been such a pleasure to work with you. And to Jordan Matley for sharing the freeze-dryer shifts, and Brett Taylor and Pete Waldie for teaching me the dark art of reading otoliths.

I owe a large debt of gratitude to the exceptional team at the CoE for Coral Reef Studies for their logistical and administrative support, thank you Jenny Lappin, Olga Bazarka, Janet Swanson, Rose-Marie Vasiljuk, David Yellowlees, Vivian Doherty, and Alana Grech, and to Prof. Terry Hughes for forging the way ahead for us all. Thank you to Phil Osmond, Glenn Ewels and Jane Webb at 'Boating and Diving' for your help with all things fieldtrip and diving related. And to Andrew Norton, a very heartfelt thank you for saving my thesis from IT disaster more than once!

The 'Graham-lab has been an invaluable source of advice, honest feedback, constructive criticism and invaluable camaraderie; thank you Kirsty Nash, Karen Chong-Seng, Jan Robinson, Fraser Januchowski-Hartley, Laura Richardson, and Judith Kok. I am also so grateful to have been part of such a supportive, inspiring cohort of colleagues and friends: CY, Blanche, Christina, Pip, Tiff, Blake, Ciemon, Andy, Brock, Hugo, Justin, Tane, Katia, Grace, Katie, Georgie, and my South African PhD brothers, Jock and James – there are too many more to name, but please know I value you all.

Thank you too to some key people who either helped me find this path or keep me on it. Nigel Hussey, thank you for giving me the inspiration to finally pursue this dream; Laurence Kruger, for telling me to 'get a PhD so I can work with you!'; Josh Cinner, for your belief and giving me the push I needed to take this step; Riaan Boshoff, for loving and supporting me on the long journey that lead to this one; Jimmy White, for reminding me that anything is possible and teaching me the art of dragon-taming; and Allison Dearling and my ashtanga yoga family for keeping me sane, grounded and honest. And to my sisters; Kezza, AmyD, Linda, Chi, Rosie, Jess, Tals, Vanoushe – I cannot begin to thank you for all your love. You mean the world to me.

To my family; I feel immensely privileged to have all your unconditional love and support. Thank you all for always welcoming me home no matter how long I've been away, celebrating the wins, and keeping me brave and strong through the tough times. Ma, Pops, and Boetie – you are my rock. Thank you for being there for me every step of the way. Being a 'Hempie' is the greatest blessing imaginable. I love you all more than words can express. And, finally, I would like to dedicate this thesis to my grandmother, Grace Mary Field nee Stainer (16/03/1921 – 29/07/2015), a woman of great tenacity, energy and love, who earned a degree in physics as a woman in the 1940's. You inspire me, and it is an honour to be your granddaughter.

21 April 2017

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.

This project was funded from several sources. Tessa Hempson was funded by a Great Barrier Reef Marine Park Authority Science for Management award, and two Graduate Research Scheme (GRS) Grants from James Cook University. An International Postgraduate Research Scholarship and a six-month GRS Discretionary Fund Scholarship provided stipend and tuition support. Prof Nicholas Graham was funded by an ARC DECRA Fellowship, and the ARC Centre of Excellence for Coral Reef Studies.

Every reasonable effort has been made to gain permission and acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

Contribution of authors to publications

Publication	Author	Contribution
Marques et al. 2014*	Isabel Marques da Silva	Preparation of manuscript
	Tessa N. Hempson	Editing of manuscript
	Nigel Hussey	Editing of manuscript
Hempson et al. 2017*	Tessa N. Hempson	Data collection, analysis, interpretation, manuscript preparation
	Nicholas A. J. Graham	Advice on study design, editing of manuscript
	M. Aaron MacNeil	Advice on data analysis, editing of manuscript
	David H. Williamson	Monitoring data collection, editing of manuscript
	Geoffrey P. Jones	Advice on study design, editing of manuscript
	Glenn R. Almany	Advice on study design

**Please see Appendix F for full publications*

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 $\delta^{13}C$ 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 investigate the effects of thermally ‘vulnerable’ and ‘tolerant’ coral assemblages on the trophodynamics of reef mesopredators and their prey fish communities. Fish communities which established naturally on the low structure ‘tolerant’ patch reefs had lower diversity, abundance and biomass than ‘vulnerable’ reefs with higher structural complexity. The introduction of a mesopredator (*Cephalopholis boenak*) had a greater impact on the prey fish community composition of ‘tolerant’ reefs than ‘vulnerable’ reefs, and total lipid content of *C. boenak* indicated that those introduced to ‘tolerant’ reefs had lower energy reserves than those on ‘vulnerable’ reefs, indicating a sub-lethal 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 energy reserves. This work highlights the importance of improving our understanding of how mesopredators are affected by habitat degradation, particularly with respect to the long-term implications of sub-lethal effects for their populations. Sustainable management of these species into the future will require the explicit recognition of the potential for such costs to mesopredator condition as reefs degrade.

Table of Contents

List of Tables

List of Figures

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 (Őhman 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).

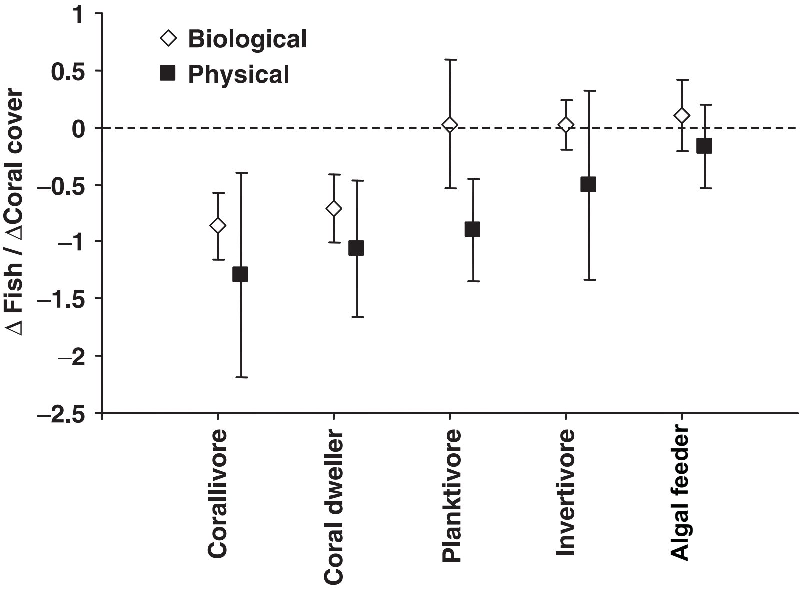


Fig. 1.1 Results of a meta-analysis illustrating mean responses of fish functional groups to biological and physical disturbance (error bars show 95% confidence intervals). The absence of data on piscivorous mesopredators highlights our lack of understanding about the effects of habitat degradation on 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, Graham et al. 2011). 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). 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.

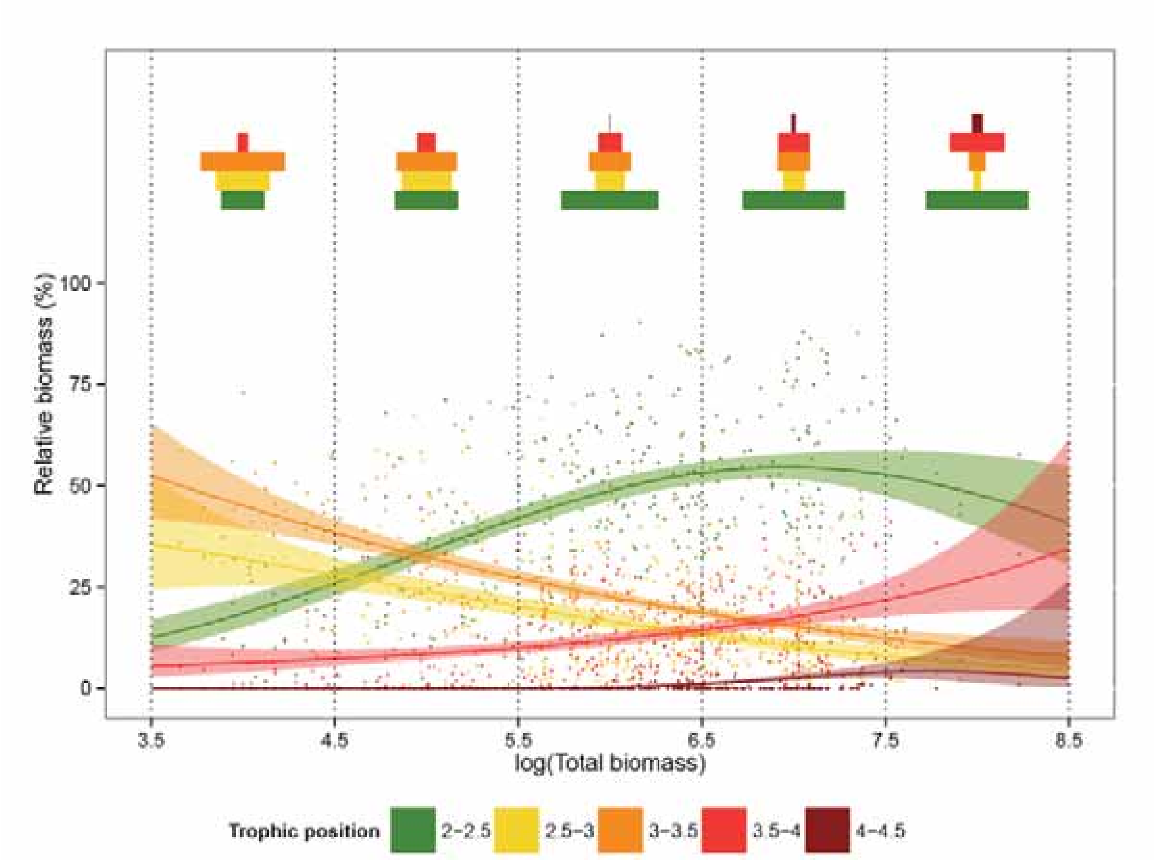


Fig. 1.2 Change in relative biomass trophic pyramid structure of coral reef fish communities across a human-driven gradient of total community biomass, based on empirical data of 253 reefs, across nine countries in the Indian Ocean. Trend lines show the modelled mean proportion and 95% confidence interval of each trophic position category (adapted from Graham et al. 2017; see Appendix E for permissions).

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

δ^{15}N 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 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[1]

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 δ^{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

---

[1] Published as: Hempson, T. N., N. A. J. Graham, M. A. MacNeil, D. H. Williamson, G. P. Jones, and G. R. Almany. 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecology and Evolution:1–10. DOI: 10.1002/ece3.2805

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’ δ^{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, δ^{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 δ^{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 m^2 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 m^2 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.

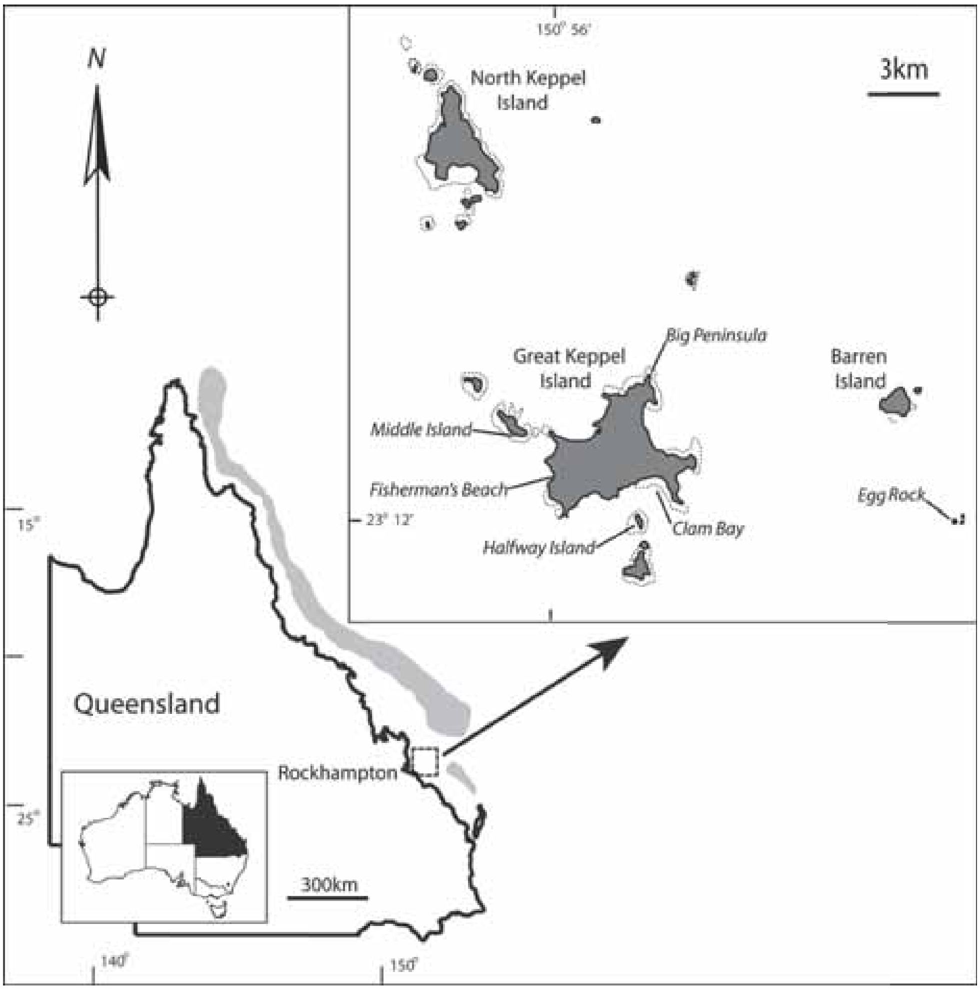


Fig. 2.1 Study area in the Keppel Island Group on the Southern Great Barrier Reef, showing the approximate location of all monitoring sites where coral grouper biopsies were collected, as well as isotope foodweb samples.

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, $\delta^{13}C$ 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 damselfishes 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 cm^3 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 400-600μg 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 (δ) values, equal to parts per thousand (‰) deviation from the standard, using the equation:

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

where X is ^{13}C and R is the ratio $^{13}C{:}^{12}C$ for $\delta^{13}C$, or X is ^{15}N and R is the ratio $^{15}N{:}^{14}N$ for $\delta^{15}N$ (Peterson 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 β_0 = 5.924 and slope β_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-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 co-variate. 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 (*Chromis nitida*) to territorial benthic-feeding damselfishes (*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.

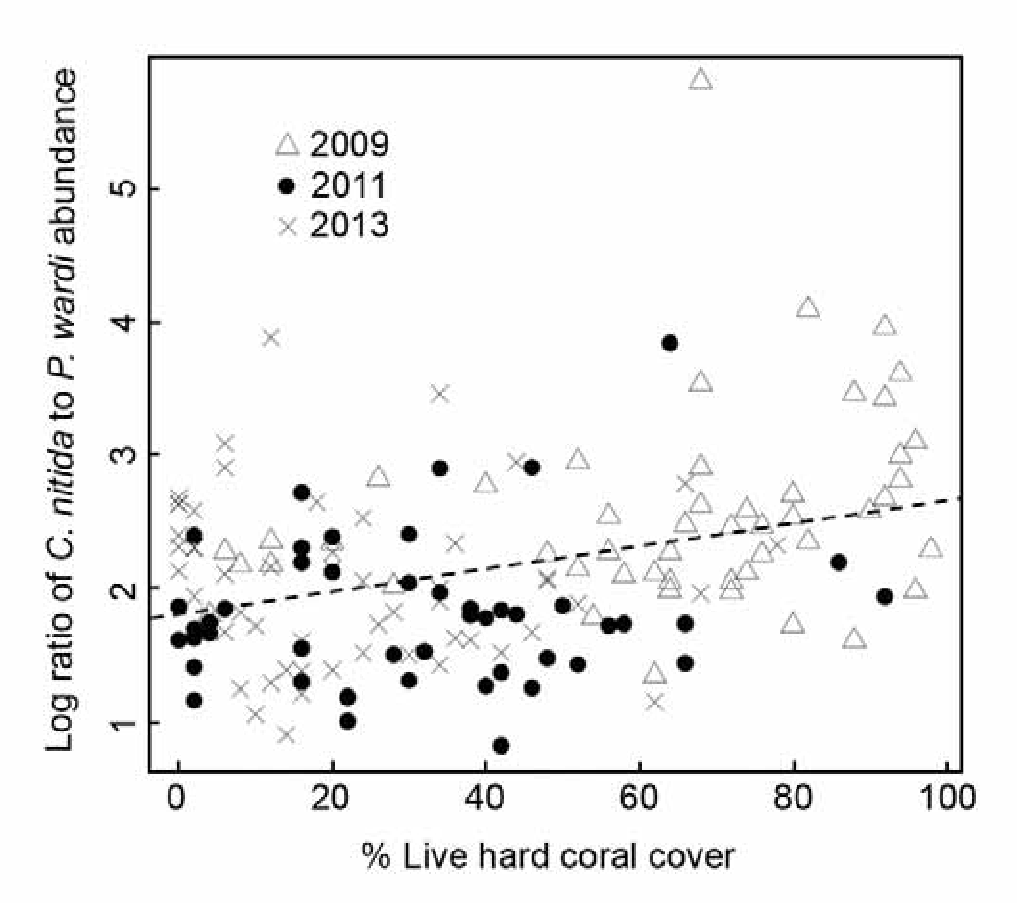


Fig. 2.2 Relationship between percent live hard coral cover and ratio of the dominant prey fish species available to mesopredators in the fish community. At higher percentage live hard coral cover, planktivorous damselfishes (*Chromis nitida*) dominate the available prey fish community, while at low 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 (δ^{13}C). Oysters, which as filter feeders, were considered to characterise the pelagic carbon signal in the system, had a mean δ^{13}C value of -18.19‰ (± 0.10 SE), a signal that was tracked by that of *Chromis nitida*, the pelagic plankton-feeding damselfish (-18.69‰ ± 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 $\delta^{13}C$ and TP (calculated from $\delta^{15}N$) 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 $\delta^{13}C$***

There was a substantial amount of variability in isotopic signals among the coral grouper sampled, with $\delta^{13}C$ 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 $\delta^{13}C$ 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) $\delta^{13}C$ signal, while fish from more degraded sites where territorial damselfishes are more dominant, had a less negative (benthic) $\delta^{13}C$ signal in their muscle tissue (Fig. 2.4a), with an overall enrichment towards a benthic signature in grouper $\delta^{13}C$ 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 $\delta^{13}C$ 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 δ^{13}C.

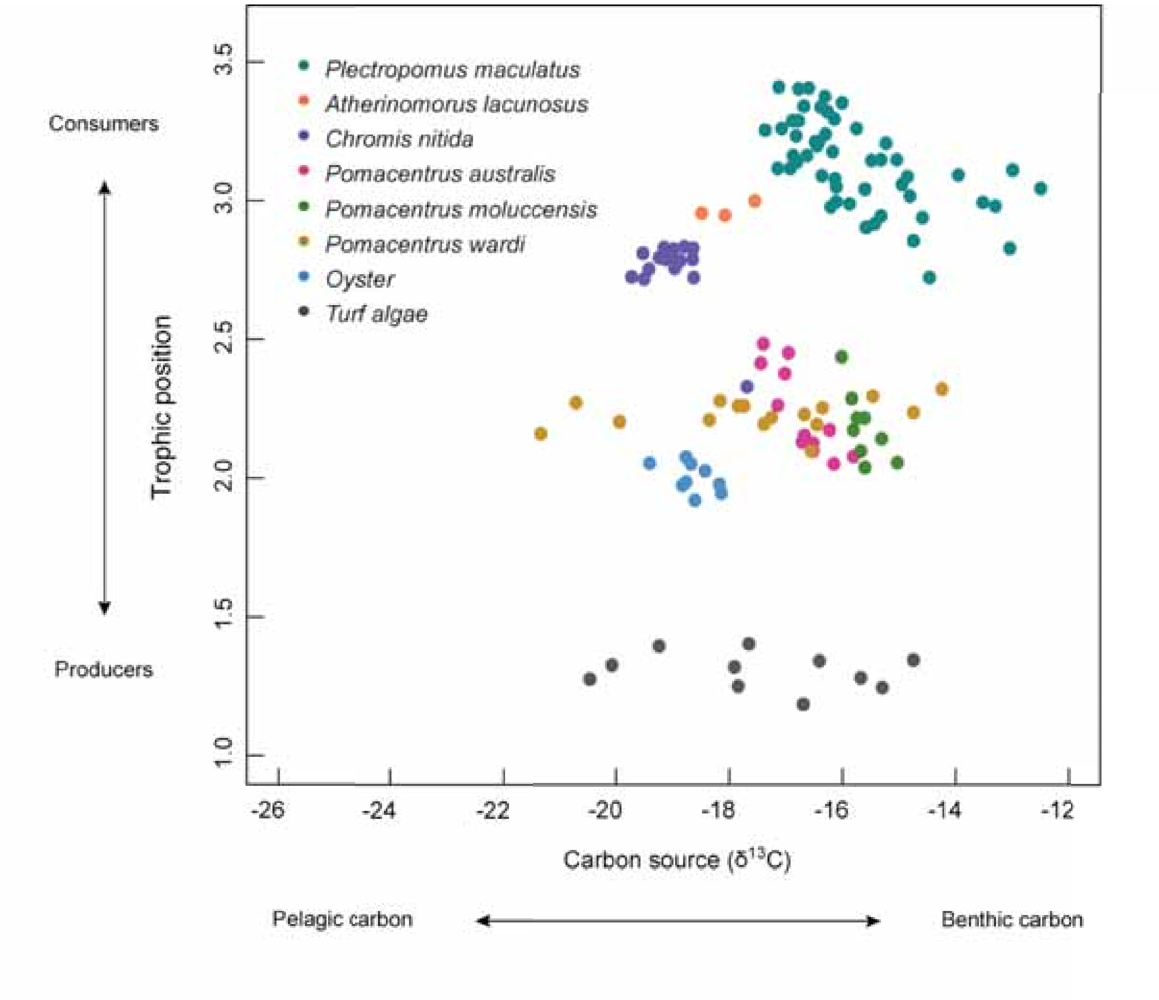


Fig. 2.3 Isotope biplot showing the trophic structuring within the Keppel Islands' coral reef foodweb in terms of carbon source (δ^{13}C) and trophic position, which is a function of δ^{15}N. Sampling sites are indicated by different shaped symbols, and species are designated by colour.

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]).

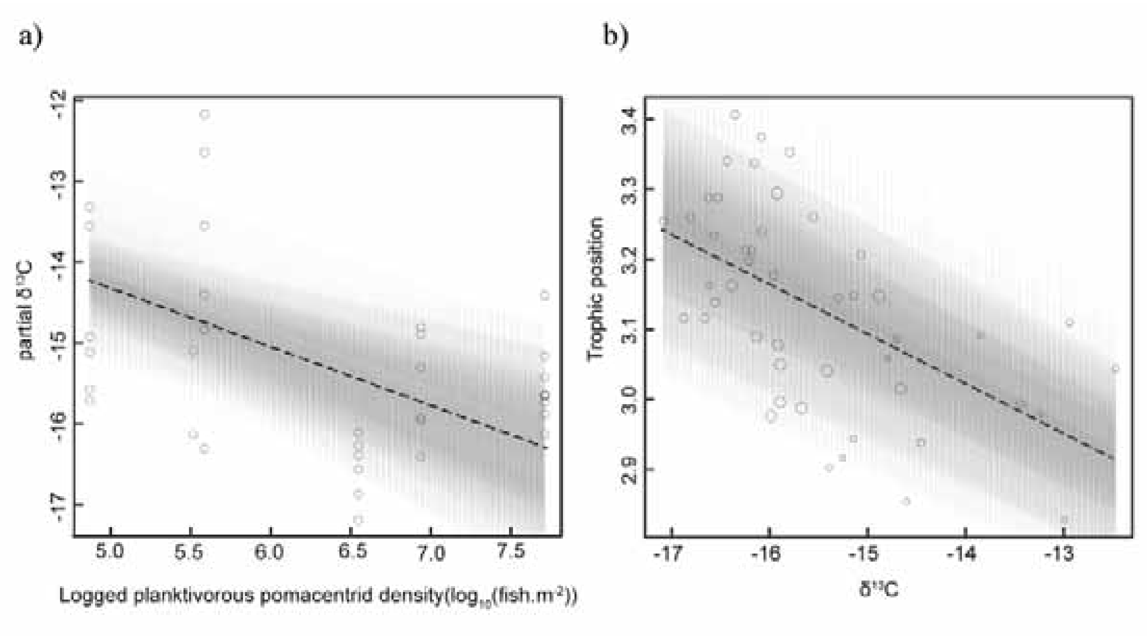


Fig. 2.4 (a) The marginal change in $\delta^{13}C$ signature of coral grouper (*P. maculatus*) sampled from the Keppel Islands between 2009 and 2013 was best explained by the decrease in planktivorous prey species in the fish community. (b) Relationship between $\delta^{13}C$ (carbon source) and trophic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

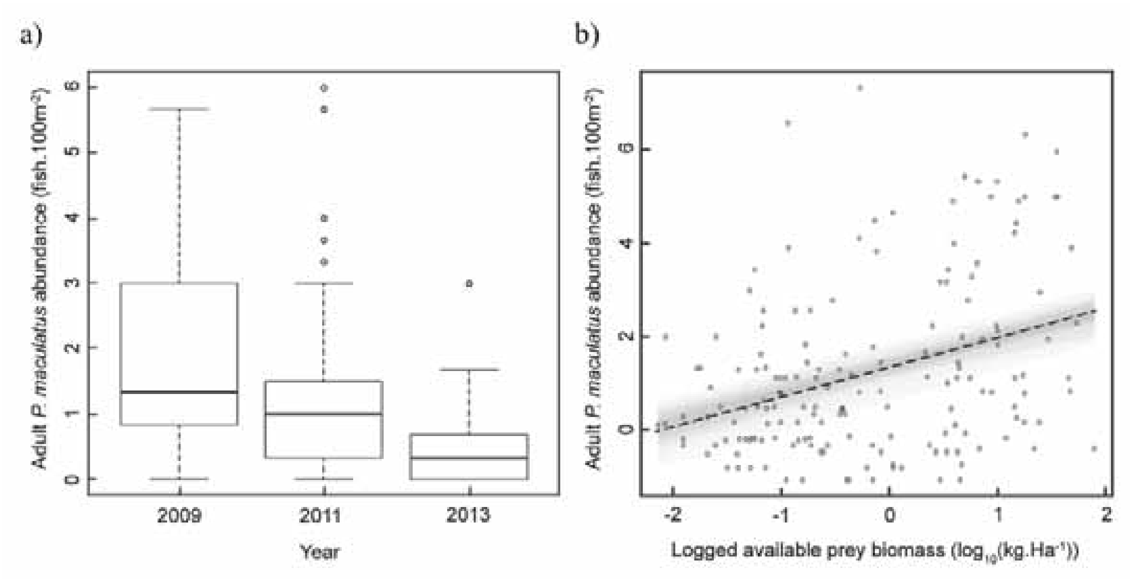


Fig. 2.5 (a) Mean abundance of adult (SL>20 cm) coral grouper (*Plectropomus maculatus*) on the reefs of the Keppel Island Group in (n=165). The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile 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 $\delta^{13}C$ 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 δ^{13}C 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.

CHAPTER 3

Sub-lethal effects of ecosystem regime shifts on mesopredators[2]

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

---

[2] Submitted for publication as: Hempson TN, Graham NAJ, MacNeil MA, Bodin N, Wilson, SK (in revision) Sub-lethal effects of ecosystem regime shifts on mesopredators. Functional Ecology

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 $\delta^{13}C$ and $\delta^{15}N$ to describe their trophic niche; (ii) morphometric, growth and hepatosomatic indices to examine body condition at a coarse scale; and (iii) histology and lipid analysis to specifically examine differences in energy reserves at a finer scale.

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 macroalgae cover, with coral cover increasing or remaining high through time. Regime-shifted reefs were identified as those where post-disturbance macroalgae cover exceeded coral cover, and was increasing or remaining high (see Graham et al. 2015 for detailed site descriptions).

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 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 cm^3) 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_∞ 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:

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

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

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.

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

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).

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

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 $\mu g.mg^{-1}$ of wet weight (ww) of sample (Parrish 1999). Total lipids ($\mu g.mg^{-1}$ 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 ≤ 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 ≤ 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:

$$M = \mathrm{lmer}(\delta^{15}N \sim \delta^{13}C * \mathrm{state} + (\,1\,|\mathrm{site}))$$

Differences in overall $\delta^{13}C$ and $\delta^{15}N$ values for *C. argus* sampled from recovering and regime-shifted reefs were assessed using notched boxplots, with non-overlapping notches providing strong evidence (95% confidence) that values differ (Zuur 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).

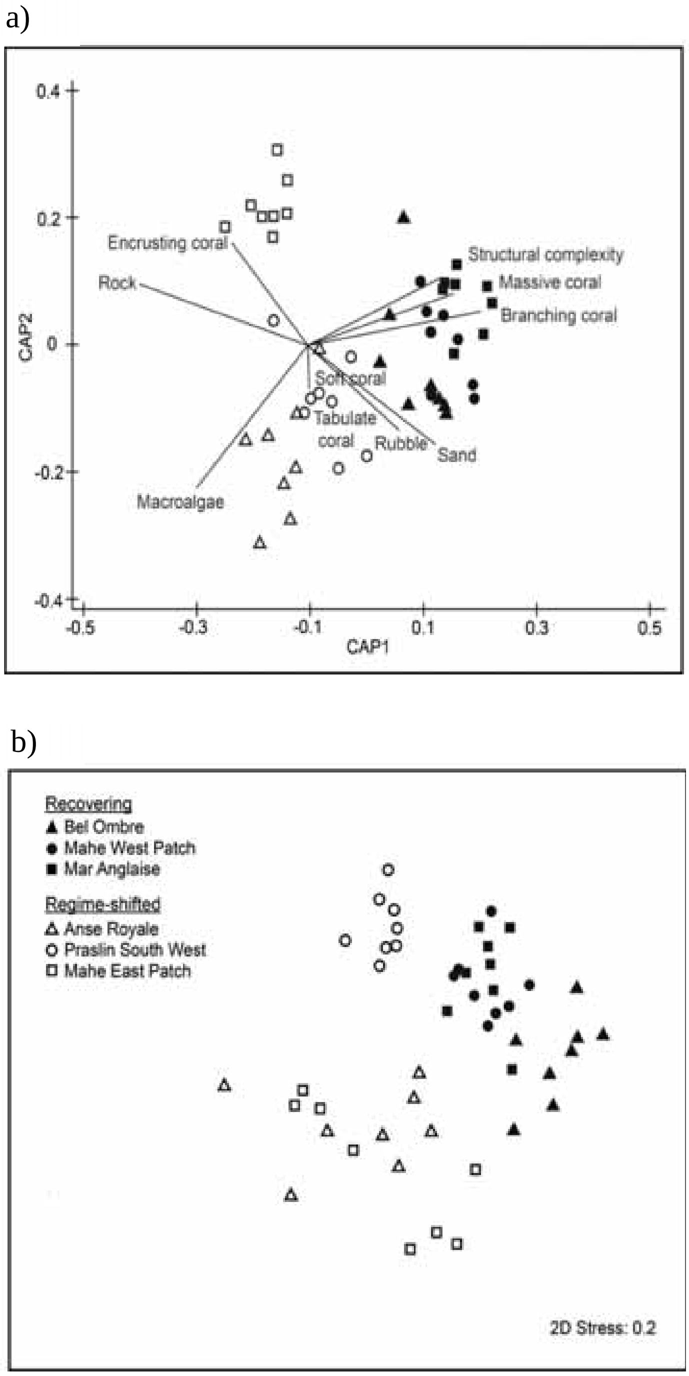


Fig. 3.1 Composition of the reef community on six sites surveyed in the Seychelles inner island group in April 2014, with sites designated by symbols, and reef state indicated by colour (Recovering = black, Regime-shifted = white). (a) Canonical analysis of principal coordinates (CAP) ordination plot 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.

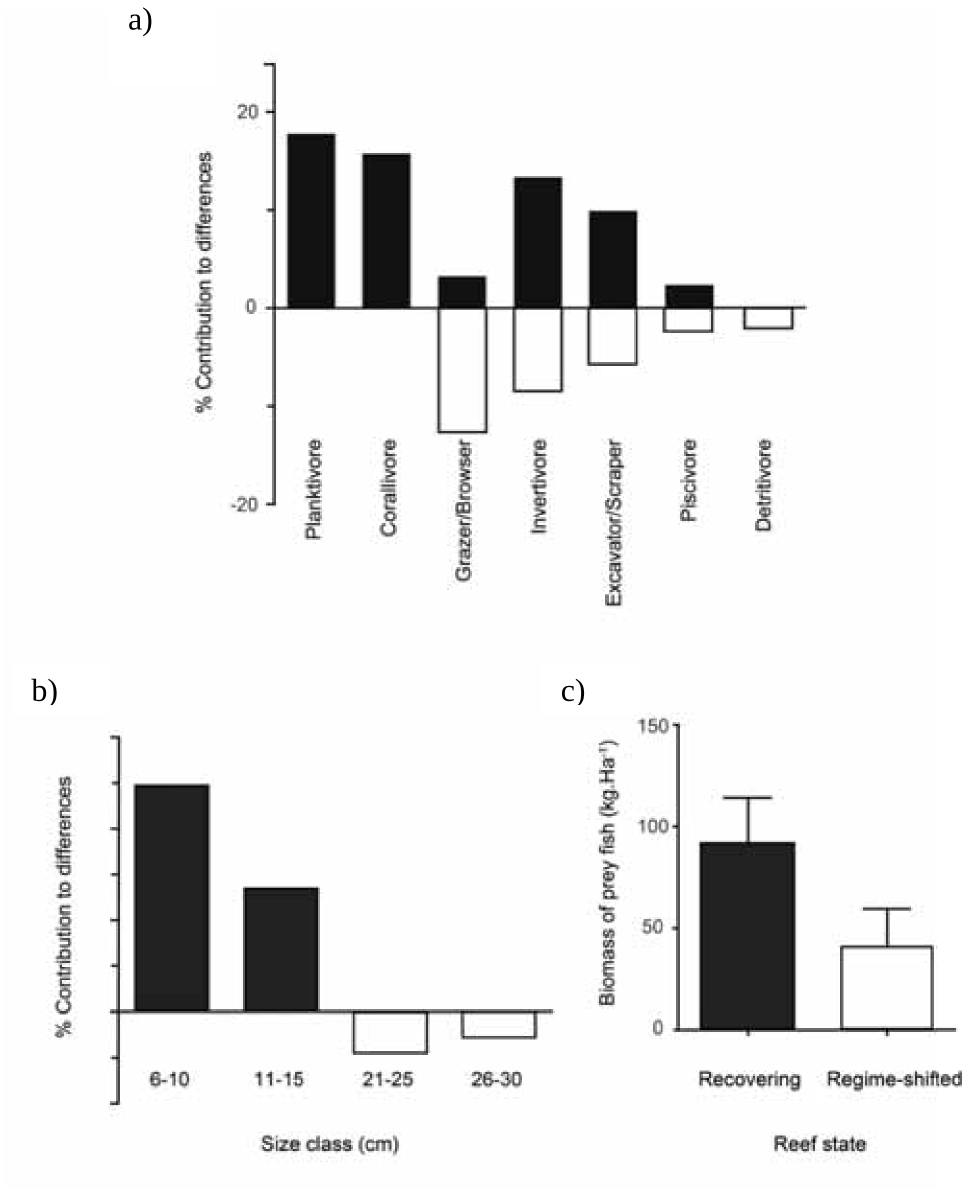


Fig. 3.2 Differences in the fish community composition between regime-shifted (white) and recovering sites (black). (a) The percentage contribution of fish functional groups to the difference between reef states in Seychelles in 2014, based on the summed percentage contribution of each functional group 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 $\leq$ 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 ± 0.27 ‰, Regime-shifted: -16.6 ± 0.24 ‰, $t_{2.664} = 2.680$, $p = 0.085$) or $\delta^{15}N$ (Recovering: 5.20 ± 0.21 ‰, Regime-shifted: 4.07 ± 0.18 ‰, $t_{2.492} = 1.309$, $p = 0.298$). Due to the potential relationship between intraspecific body size and $\delta^{15}N$ (Greenwood et al. 2010), we evaluated mean total length of *C. argus* sampled between reef states, finding it did not differ significantly (Recovering: 25.40 ± 1.14 cm, Regime-shifted: 25.80 ± 1.04 cm, $t_{66.322} = -0.260$, $p = 0.796$). This suggests that neither of these two potential sources of variation in isotopic signal 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 ± 0.160, Regime-shifted: -0.533 ± 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.

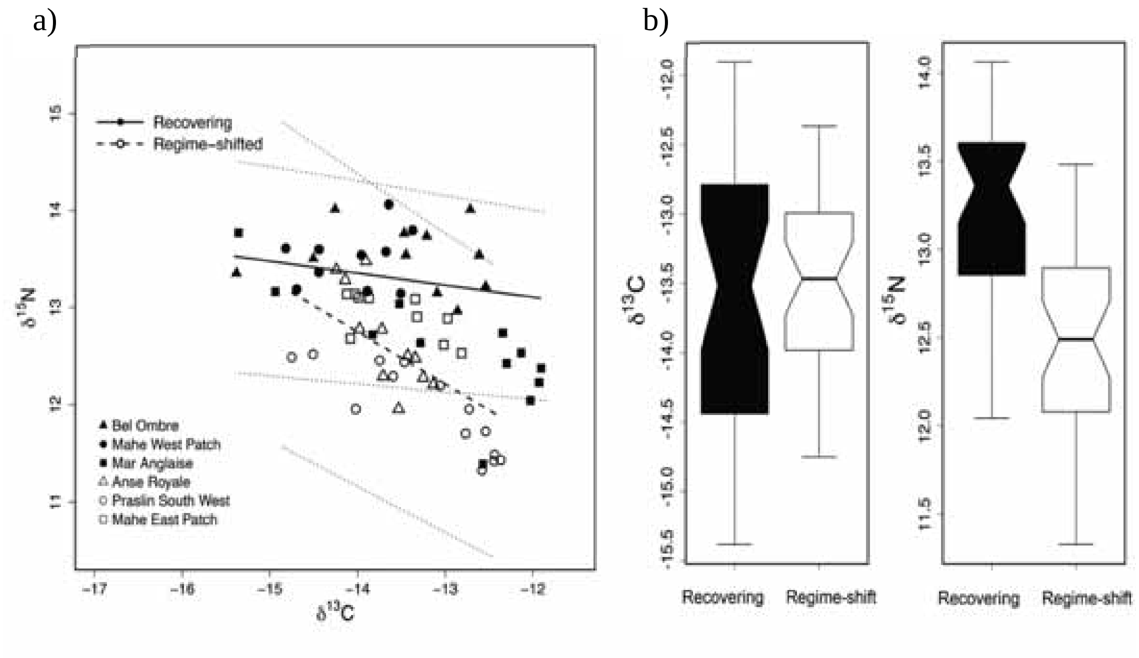


Fig. 3.3 Stable isotope signatures of *Cephalopholis argus* sampled from recovering and regime-shifted reefs in the Seychelles inner island group. (a) Biplot of δ^{13}C and δ^{15}N values from white muscle tissue, showing the differences in trophic niche of fish from different reef states in terms of their carbon food sources (δ^{13}C) and trophic level (δ^{15}N). Sampling sites are indicated by different shaped symbols, and reef states are designated by colour. Bold lines indicate the best-fit linear model for fish sampled from recovering (solid line) and regime-shifted (dashed line) reefs. Finely dashed lines indicate the 95% confidence interval around each model fit. (b) Notched boxplots of δ^{13}C and δ^{15}N for fish sampled from regime-shifted (n = 35) and recovering reefs (n = 34). Whiskers indicate maximum and minimum values, box height shows the interquartile range, the bold centre line is the median, and diagonal notches in the boxes illustrate the 95% confidence interval around the median.

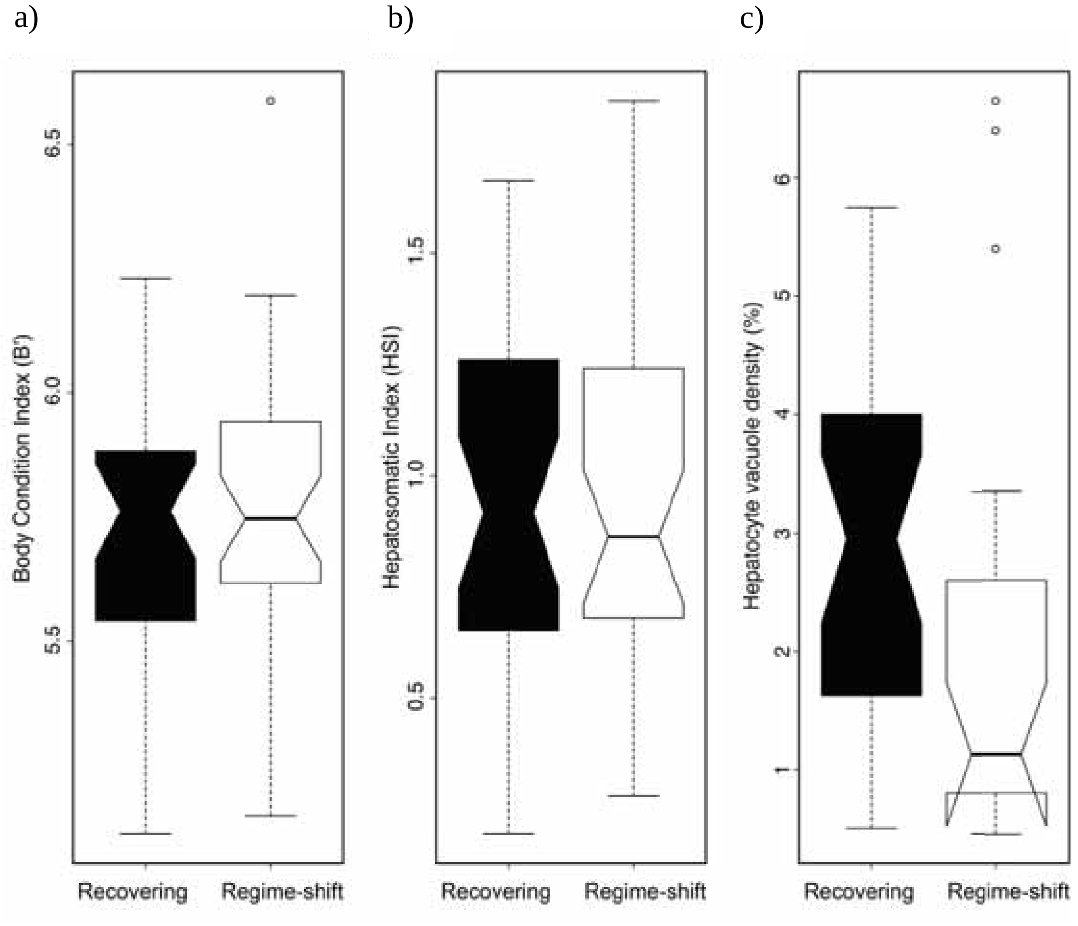


Fig. 3.4 Body condition indices of *Cephalopholis argus* sampled from regime-shifted (n = 35) and recovering (n = 34) reefs in Seychelles. Notched boxplots of (a) body condition in B', (b) hepatosomatic index (HSI), and (c) hepatocyte vacuole density from liver sections, show an increasingly fine scale 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_∞ = 41.19 cm, K = 0.19y^{-1}, t_0 = -2.02) and regime-shifted reefs (L_∞ = 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).

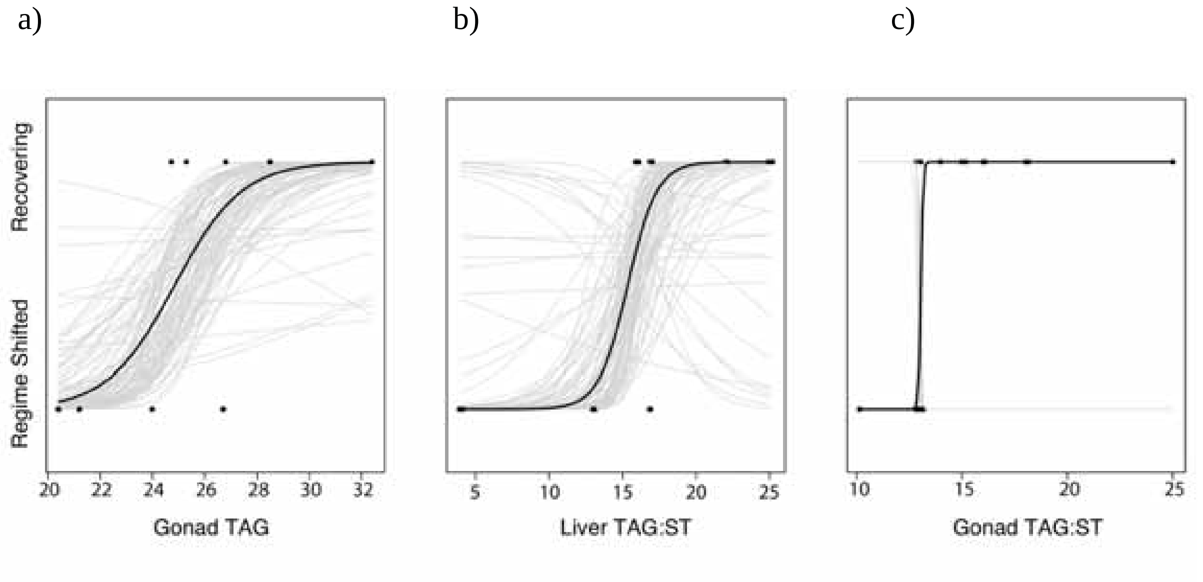


Fig. 3.5 Lipid composition and logistic regression results showing a lower concentration of (a) triacylglycerols (TAG; µg.mg^{-1} ww) in the gonads of spawning female *Cephalopholis argus* sampled from regime-shifted reefs, than for fish sampled from recovering reefs (Bootstrap parameter point estimate [95% confidence interval]: 0.741, [0.436, 1.047]). Similarly, the ratio between TAG and sterol concentrations (TAG:ST) was lower in the (b) liver (1.086, [0.659, 1.513]) and (c) gonad (18.809, [18.439, 19.178]) tissues of spawning females from regime-shifted sites. Grey lines represent variability in potential model fits.

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 δ^{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 δ^{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 δ^{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 δ^{13}C values, and a reduced δ^{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[3]

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

---

[3] Submitted for publication as: Ecosystem regime shifts disrupt trophic structure. Hempson TN, Graham NAJ, MacNeil, MA, Hoey AS, Wilson SK. Ecological Applications.

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 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.

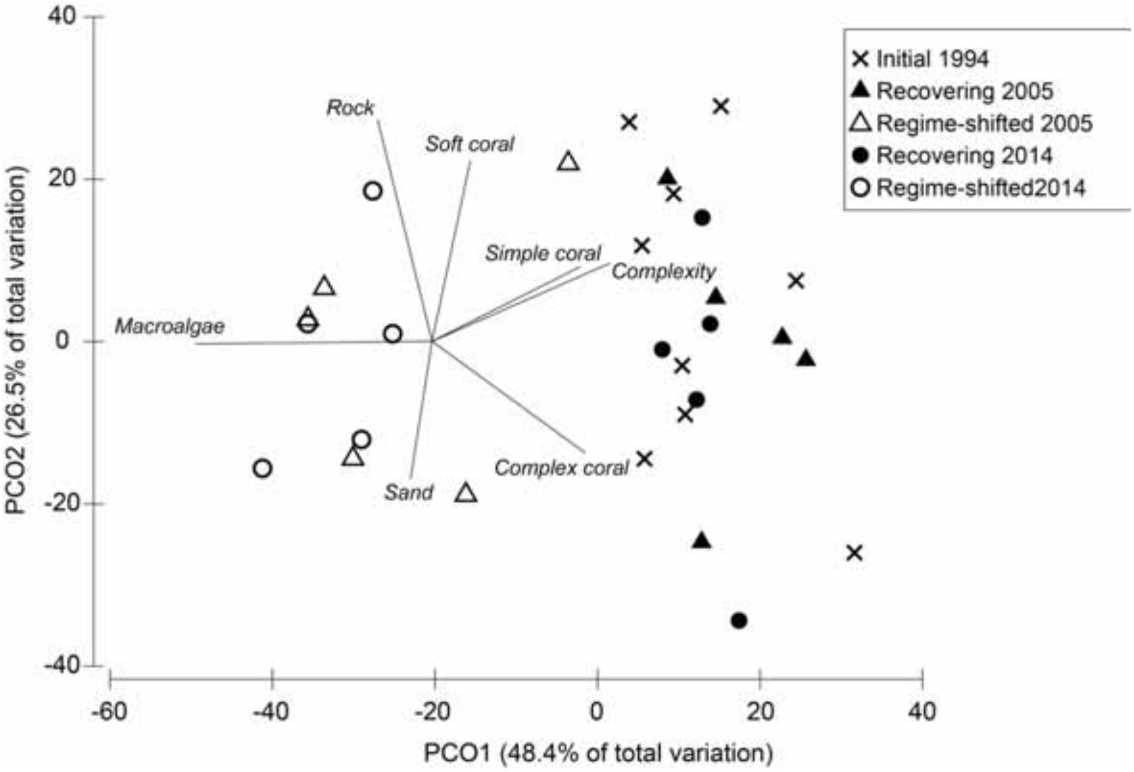


Fig. 4.1 Principal coordinates analysis of the composition of benthic cover of ten reefs surveyed in the Seychelles inner island group based on Bray-Curtis similarity (data square-root transformed). Crosses represent all reef sites surveyed in 1994, prior to the bleaching 1998 mass bleaching event. Black 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).

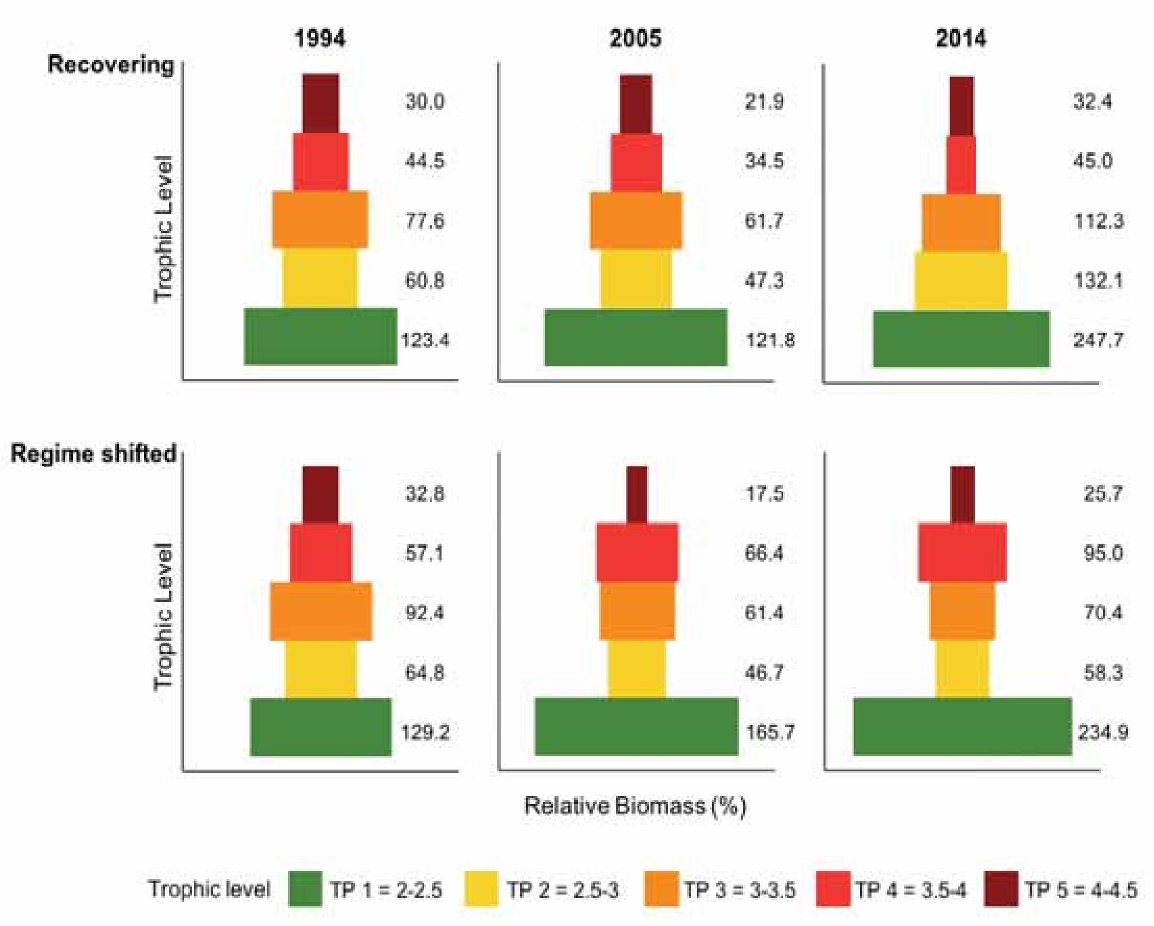


Fig. 4.2 Trophic pyramids showing the distribution of relative biomass (%) between five trophic positions in the reef fish communities on recovering (n = 5) and regime-shifted (n = 5) reefs in the Seychelles inner island group, both before the 1998 mass bleaching (1994) and after it (2005, 2014). Numbers 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.

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

Table 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.

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

Table 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.

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

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.

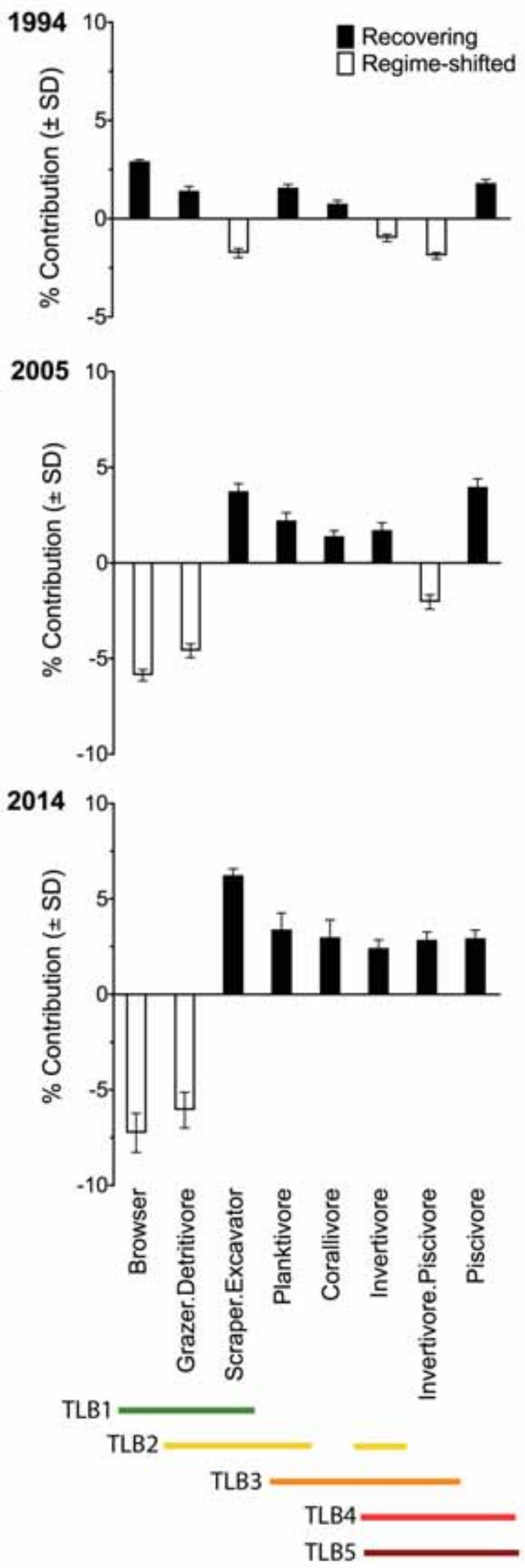


Fig. 4.3 Differences in the functional group composition between fish communities on regime-shifted (white) and recovering sites (black). The mean (± standard deviation; SD) percentage contribution of each functional group to Bray-Curtis dissimilarity between reef states in Seychelles in 1994, 2005 and 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

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.

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.

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[4]

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.

---

[4] 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.

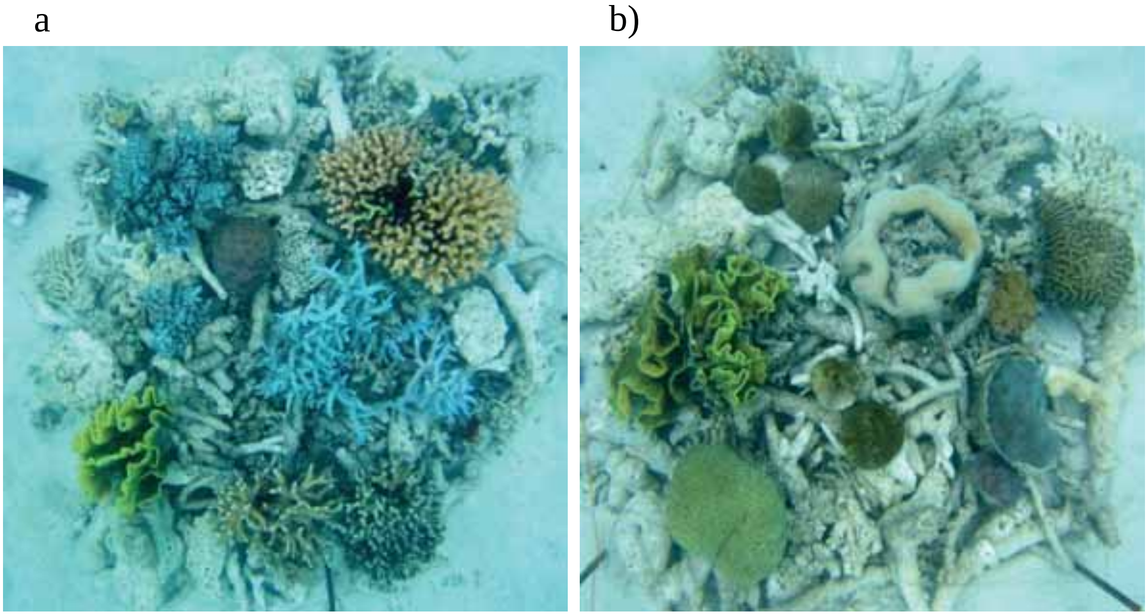


Fig. 5.1 Photos illustrating the two reef treatments in the patch reef array immediately after construction in 2013, prior to recruitment of fish communities. All reefs were constructed on a 2 m diameter base of coral rubble, with live colonies of six coral taxa each. a. Vulnerable reefs were composed 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 cm^3) 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:

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

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):

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

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.

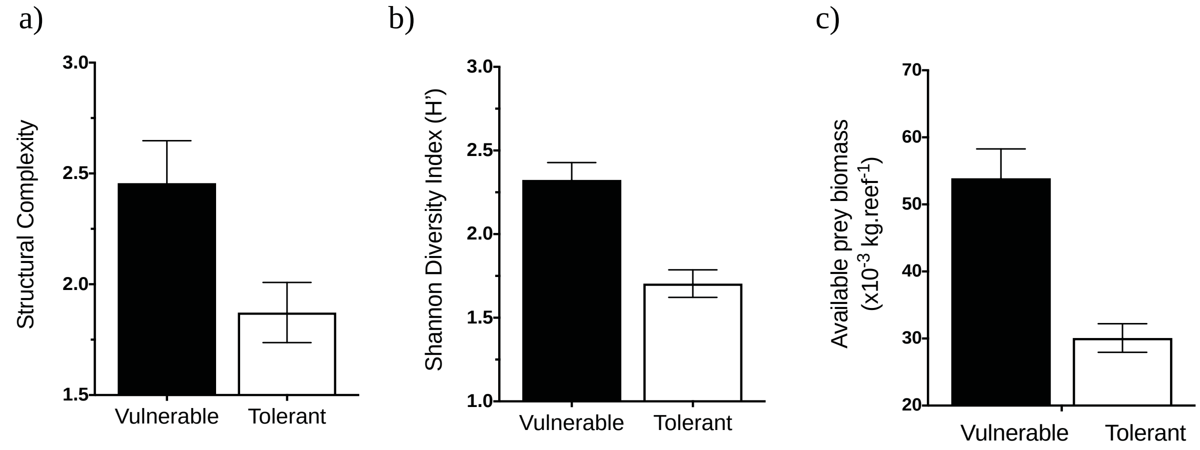


Fig. 5.2 Comparison of mean (± standard error) (a) benthic structural complexity, (b) Shannon Diversity (H') of fish communities, and **c** prey fish biomass available to *C. boenak* between vulnerable and tolerant reef treatments at the start of the mesopredator caging experiment in March 2015.

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).

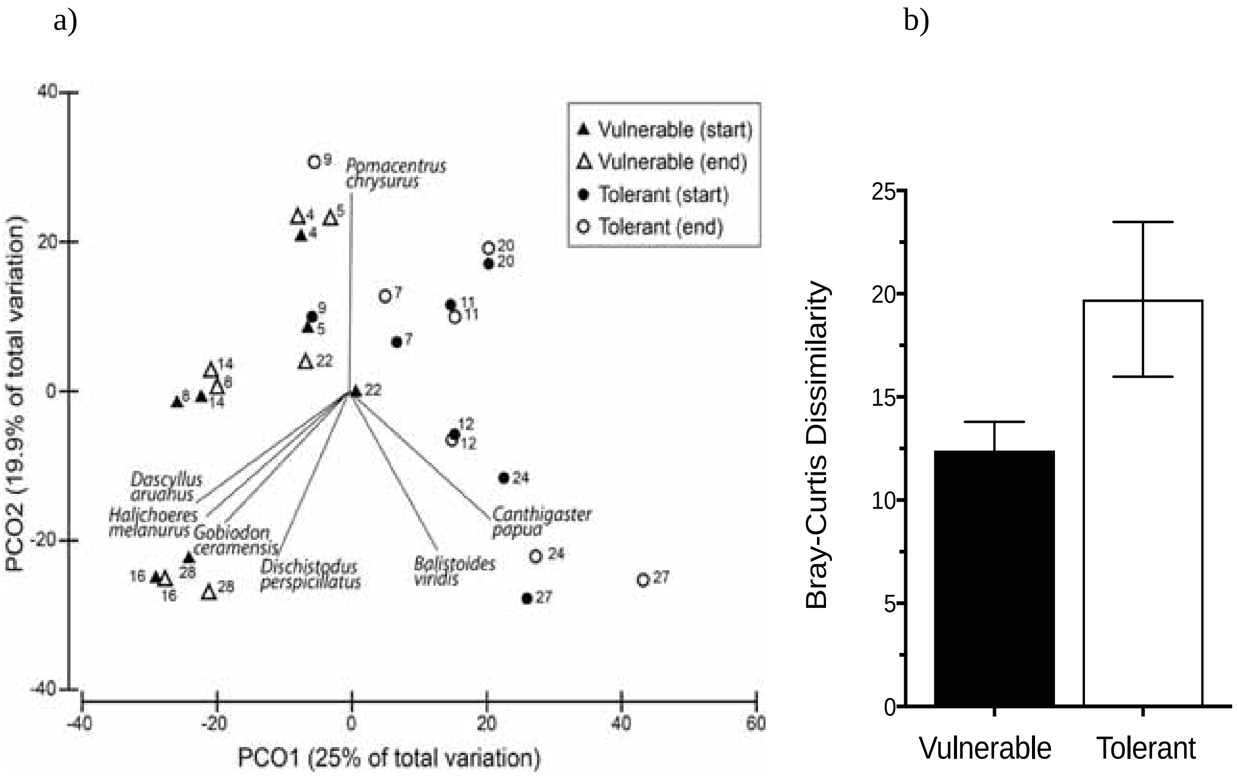


Fig. 5.3 (a) Principal Co-Ordinates Analysis of fish communities on patch reefs prior to Mesopredator introduction and after 6 weeks. (b) Bray-Curtis similarity between fish communities at the start and end of mesopredator caging experiment (mean ± standard error).

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, $t_{10.89} = -0.988$, $p = 0.344$). 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, $t_{9.81} = -0.555$, $p = 0.591$).

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).

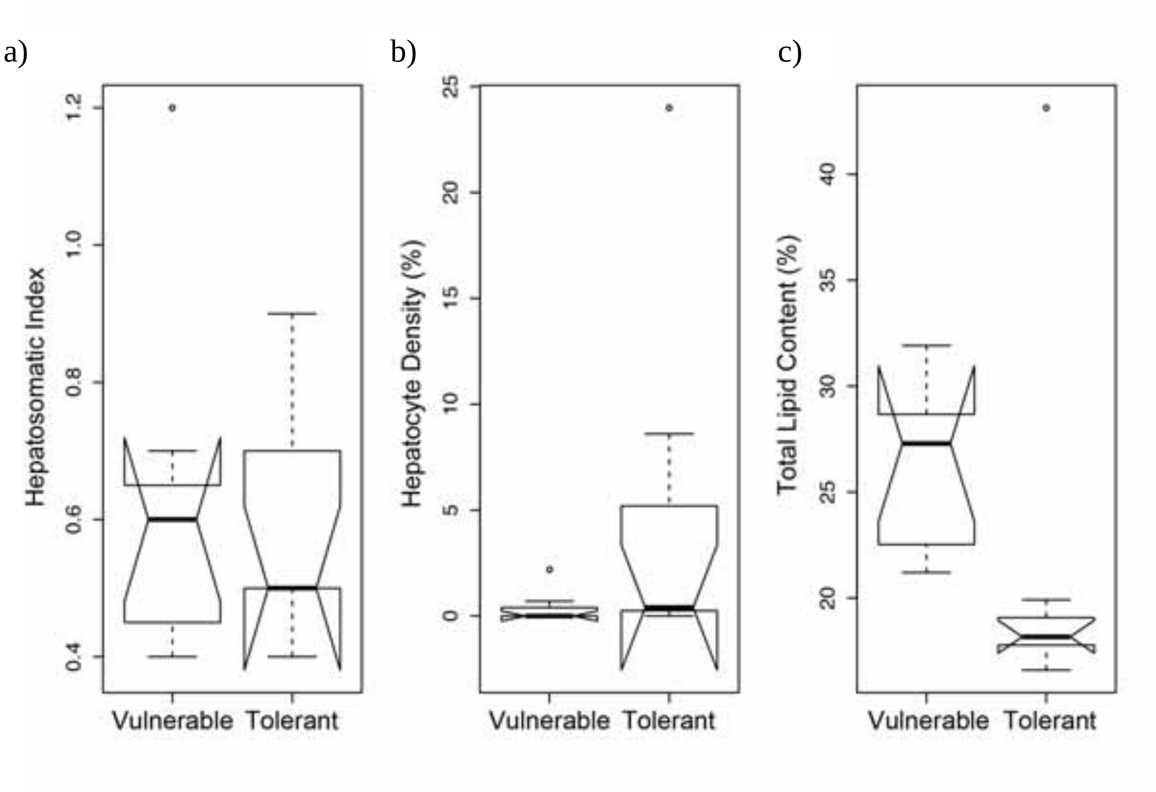


Fig. 5.4 Notched boxplots of (a) hepatosomatic index (HSI), (b) hepatocyte densities from liver tissue sections, and c. percentage total lipid content in white muscle tissue of *C. boenak* after removal from mesopredator caging experiment on vulnerable and tolerant patch reef treatments. Bold centre 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.

CHAPTER 6

General Discussion

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.

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 bleaching and cyclone damage (personal observation, Ceccarelli et al. 2016, Williamson et al. 2016).

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.

REFERENCES

Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G. Bernardi. 2011. Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. PLoS ONE 6:e23717.

Allen, G. R. 1991. Damselfishes of the world. Mergus Publishers, Melle, Germany.

Alvarez-Filip, L., J. P. Carricart-Ganivet, G. Horta-Puga, and R. Iglesias-Prieto. 2013. Shifts in coral-assemblage composition do not ensure persistence of reef functionality. Scientific Reports 3:3486.

Alvarez-Filip, L., J. A. Gill, and N. K. Dulvy. 2011. Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. Ecosphere 2:1–17.

Amara, R., T. Meziane, C. Gilliers, G. Hermel, and P. Laffargue. 2007. Growth and condition indices in juvenile sole Solea solea measured to assess the quality of essential fish habitat. Marine Ecology Progress Series 351:201–208.

Anderson, M. J., and T. J. Willis. 2003. Canonical analysis of principal coordinates : a useful method of constrained ordination for ecology. Ecology 84:511–525.

Baker, R., A. Buckland, and M. Sheaves. 2014. Fish gut content analysis: robust measures of diet composition. Fish and Fisheries 15:170–177.

Ban, N. C., M. Mills, J. Tam, C. C. Hicks, S. Klain, N. Stoeckl, M. C. Bottrill, J. Levine, R. L. Pressey, T. Satterfield, and K. M. A. Chan. 2013. A social-ecological approach to conservation planning: Embedding social considerations. Frontiers in Ecology and the Environment 11:194–202.

Ban, S. S., N. A. J. Graham, and S. R. Connolly. 2014. Evidence for multiple stressor interactions and effects on coral reefs. Global Change Biology 20:681–697.

Bell, J. D., C. Reid, M. J. Batty, P. Lehodey, L. Rodwell, A. J. Hobday, J. E. Johnson, and A. Demmke. 2013. Effects of climate change on oceanic fisheries in the tropical Pacific: Implications for economic development and food security. Climatic Change 119:199–212.

Bellwood, D. R., A. S. Hoey, J. L. Ackerman, and M. Depczynski. 2006. Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. Global Change Biology 12:1587–1594.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. Nature 429:827–833.

Berkelmans, R., A. M. Jones, and B. Schaffelke. 2012. Salinity thresholds of *Acropora* spp. on the Great Barrier Reef. Coral Reefs 31:1103–1110.

Berumen, M. L., and M. S. Pratchett. 2006. Recovery without resilience: Persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs 25:647–653.

Berumen, M. L., M. S. Pratchett, and M. I. McCormick. 2005. Within-reef differences in diet and body condition of coral-feeding butterflyfishes (Chaetodontidae). Marine Ecology Progress Series 287:217–227.

Beukers-Stewart, B. D., and G. P. Jones. 2004. The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. Journal of Experimental Marine Biology and Ecology 299:155–184.

Beukers, J. S., and G. P. Jones. 1997. Habitat complexity modifes the impact of piscivores on a coral reef fish population. Oecologia 114:50–59.

Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Page Fishery Investigations Series 2, Vol. 19. UK Ministry of Agriculture. Fisheries.

Bligh, E. G., and W. J. Dyer. 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37:911–917.

Bodin, N., H. Budzinski, K. Le Ménach, and N. Tapie. 2009. ASE extraction method for simultaneous carbon and nitrogen stable isotope analysis in soft tissues of aquatic organisms. Analytica Chimica Acta 643:54–60.

Boecklen, W. J., C. T. Yarnes, B. A. Cook, and A. C. James. 2011. On the use of stable isotopes in trophic ecology. Annual Review of Ecology, Evolution, and Systematics 42:411–440.

Bonin, M. C., L. Boström-Einarsson, P. L. Munday, and G. P. Jones. 2015. The Prevalence and Importance of Competition Among Coral Reef Fishes. Annual Review of Ecology, Evolution, and Systematics 46:169–190.

Booth, D. J., and G. A. Beretta. 2002. Changes in a fish assemblage after a coral bleaching event. Marine Ecology Progress Series 245:205–212.

Boström-Einarsson, L., M. C. Bonin, P. L. Munday, and G. P. Jones. 2014. Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. Ecology 95:3056–3067.

Brandt, J. S., M. A. Haynes, T. Kuemmerle, D. M. Waller, and V. C. Radeloff. 2013. Regime shift on the roof of the world: Alpine meadows converting to shrublands in the southern Himalayas. Biological Conservation 158:116–127.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: >50 years of data suggests CO_2 as a driver. Global Change Biology 18:675–684.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed). Page Ecological Modelling. Springer-Verlag New York, inc.

Byrnes, J. E., D. C. Reed, B. J. Cardinale, K. C. Cavanaugh, S. J. Holbrook, and R. J. Schmitt. 2011. Climate-driven increases in storm frequency simplify kelp forest food webs. Global Change Biology 17:2513–2524.

Carabel, S., E. Godínez-Domínguez, P. Verísimo, L. Fernández, and J. Freire. 2006. An assessment of sample processing methods for stable isotope analyses of marine food webs. Journal of Experimental Marine Biology and Ecology 336:254–261.

Carassou, L., M. Kulbicki, T. J. R. Nicola, and N. V. C. Polunin. 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquatic Living Resources 21:1–12.

Carpenter, K. E., and G. R. Allen. 1989. Emperor fishes and large-eye breams of the world (family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date. FAO Fish. Synop. 125(9):118 p. Rome: FAO. Page FAO Species Catalogue. Rome.

Carpenter, S. R., J. J. Cole, M. L. Pace, R. D. Batt, W. A. Brock, T. J. Cline, J. Coloso, J. R. Hodgson, J. F. Kitchell, D. A. Seekell, L. Smith, and B. C. Weidel. 2011. Early warnings of regime shifts: a whole- ecosystem experiment. Science 332:1079–1082.

Ceccarelli, D. M., M. J. Emslie, and Z. T. Richards. 2016. Post-disturbance stability of fish assemblages measured at coarse taxonomic resolution masks change at finer scales. PLoS ONE 11:1–22.

Chan, T. T. C., and Y. Sadovy. 2002. Reproductive biology, age and growth in the chocolate hind, *Cephalopholis boenak* (Bloch, 1790), in Hong Kong. Marine And Freshwater Research 53:791–803.

Chong-Seng, K. M., T. D. Mannering, M. S. Pratchett, D. R. Bellwood, and N. A. J. Graham. 2012. The influence of coral reef benthic condition on associated fish assemblages. PLoS ONE 7:e42167.

Cinner, J. E., C. Huchery, E. S. Darling, A. T. Humphries, N. A. J. Graham, C. C. Hicks, N. Marshall, and T. R. McClanahan. 2013a. Evaluating social and ecological vulnerability of coral reef fisheries to climate change. PLoS ONE 8:e74321–e74321.

Cinner, J. E., T. R. McClanahan, N. A. J. Graham, M. S. Pratchett, S. K. Wilson, and J. B. Raina. 2009. Gear-based fisheries management as a potential adaptive response to climate change and coral mortality. Journal of Applied Ecology 46:724–732.

Cinner, J. E., T. R. McClanahan, M. A. MacNeil, N. A. J. Graham, T. M. Daw, A. Mukminin, D. A. Feary, A. L. Rabearisoa, A. Wamukota, N. Jiddawi, S. J. Campbell, A. H. Baird, F. A. Januchowski-Hartley, S. Hamed, R. Lahari, T. Morove, and J. Kuange. 2012. Comanagement of coral reef social-ecological systems. Proceedings of the National Academy of Sciences 109:5219–5222.

Cinner, J. E., T. R. McClanahan, A. Wamukota, E. S. Darling, A. T. Humphries, C. C. Hicks, C. Huchery, N. Marshall, T. N. Hempson, N. A. J. Graham, O. Bodin, T. M. Daw, and E. H. Allison. 2013b. The vulnerability of fishing-dependent economies to climatic shocks. FAO Fisheries and Aquaculture, 1082, pp 63. Rome.

Clarke, K., and R. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E. Plymouth.

Cohen, L. A., L. Pichegru, D. Grémillet, J. Coetzee, L. Upfold, and P. G. Ryan. 2014. Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade. Marine Ecology Progress Series 505:281–293.

Coker, D. J., S. K. Wilson, and M. S. Pratchett. 2014. Importance of live coral habitat for reef fishes. Reviews in Fish Biology and Fisheries 24:89–126.

Cooney, R. T., and R. D. Brodeur. 1998. Carrying capacity and north pacific salmon production : stock-enhancement implications. Bulletin of Marine Science 62:443–464.

Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Canadian Journal of Fisheries and Aquatic Sciences 54:726–738.

Darling, E. S., N. A. J. Graham, F. A. Januchowski-Hartley, K. L. Nash, M. S. Pratchett, and S. K. Wilson. 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561–575.

Darling, E. S., T. R. McClanahan, and I. M. Côté. 2013. Life histories predict coral community disassembly under multiple stressors. Global Change Biology 19:1930–1940.

DeMartini, E. E., A. M. Friedlander, S. A. Sandin, and E. Sala. 2008. Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. Marine Ecology Progress Series 365:199–215.

DeNiro, M. J., and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42:495–506.

Diaz-Pulido, G., L. J. McCook, S. Dove, R. Berkelmans, G. Roff, D. I. Kline, S. Weeks, R. D. Evans, D. H. Williamson, and O. Hoegh-Guldberg. 2009. Doom and boom on a resilient reef: Climate change, algal overgrowth and coral recovery. PLoS ONE 4:e5239.

Dierking, J., I. D. Williams, and W. J. Walsh. 2009. Diet composition and prey selection of the introduced grouper species peacock hind (*Cephalopholis argus*) in Hawaii. Fishery Bulletin:464–476.

Dobson, A., D. Lodge, J. Alder, G. S. Cumming, J. Keymer, J. Mcglade, H. Mooney, J. A. Rusak, O. Sala, V. Wolters, D. Wall, R. Winfree, and M. A. Xenopoulos. 2011. Habitat loss , trophic collapse , and the decline of ecosystem services. Ecology 87:1915–1924.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters 6:680–687.

Duffy, J. E., J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, and G. J. Edgar. 2016. Biodiversity enhances reef fish biomass and resistance to climate change. Proceedings of the National Academy of Sciences of the United States of America 113:6230–6235.

Dulvy, N. K., N. V. C. Polunin, A. C. Mill, and N. A. J. Graham. 2004. Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. Canadian Journal of Fisheries and Aquatic Sciences 61:466–475.

Elvidge, C. D., J. B. Dietz, R. Berkelmans, S. Andréfouët, W. Skirving, A. E. Strong, and B. T. Tuttle. 2004. Satellite observation of Keppel Islands (Great Barrier Reef) 2002 coral bleaching using IKONOS data. Coral Reefs 23:461–462.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Evans, R. D., S. K. Wilson, S. N. Field, and J. A. Y. Moore. 2014. Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Marine Biology 161:599–607.

Fabina, N. S., M. L. Baskett, and K. Gross. 2015. The differential effects of increasing frequency and magnitude of extreme events on coral populations. Ecological Applications 25:1534–1545.

Farmer, B. M., and S. K. Wilson. 2011. Diet of finfish targeted by fishers in North West Australia and the implications for trophic cascades. Environmental Biology of Fishes 91:71–85.

Feary, D. A., M. I. McCormick, and G. P. Jones. 2009. Growth of reef fishes in response to live coral cover. Journal of Experimental Marine Biology and Ecology 373:45–49.

Ferreira, B. P., and G. R. Russ. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces, Serranidae) from the Central Great Barrier Reef, Australia. Australian Journal of Marine and Freshwater Research 43:1301–1312.

Folch, J., M. Lees, and G. H. S. Stanley. 1957. A simple method for the isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry 226:497–509.

Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. Marine Ecology Progress Series 230:253–264.

Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1–30.

Froese, R., and D. Pauly. 2016. FishBase, www.fishbase.org, version (10/2016). http://www.fishbase.org.

Fry, B. 2006. Stable isotope ecology. Springer, New York.

Fry, B., and E. B. Sherr. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27:13–47.

GBRMPA. 2014. Great Barrier Reef Outlook Report 2014: In brief. Townsville, Townsville.

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

Goreau, T., T. McClanahan, R. Hayes, and A. Strong. 2000. Conservation of coral reefs after the 1998 global bleaching event. Conservation Biology 14:5–15.

Graham, N. A. J. 2007. Ecological versatility and the decline of coral feeding fishes following climate driven coral mortality. Marine Biology 153:119–127.

Graham, N. A. J. 2014. Habitat complexity: Coral structural loss leads to fisheries declines. Current Biology 24:R359–R361.

Graham, N. A. J., D. R. Bellwood, J. E. Cinner, T. P. Hughes, A. V. Norström, and M. Nyström. 2013. Managing resilience to reverse phase shifts in coral reefs. Frontiers in Ecology and the Environment 11:541–548.

Graham, N. A. J., P. Chabanet, R. D. Evans, S. Jennings, Y. Letourneur, M. A. MacNeil, T. R. McClanahan, M. C. Öhman, N. V. C. Polunin, and S. K. Wilson. 2011. Extinction vulnerability of coral reef fishes. Ecology Letters 14:341–348.

Graham, N. A. J., J. E. Cinner, A. V. Norström, and M. Nyström. 2014. Coral reefs as novel ecosystems: embracing new futures. Current Opinion in Environmental Sustainability 7:9–14.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation 30:200–208.

Graham, N. A. J., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97.

Graham, N. A. J., T. R. McClanahan, M. A. MacNeil, S. K. Wilson, J. E. Cinner, C. Huchery, and T. H. Holmes. 2017. Human disruption of coral reef trophic structure. Current Biology 27:231–236.

Graham, N. A. J., T. R. McClanahan, M. A. MacNeil, S. K. Wilson, N. V. C. Polunin, S. Jennings, P. Chabanet, S. Clark, M. D. Spalding, Y. Letourneur, L. Bigot, R. Galzin, M. C. Öhman, K. C. Garpe, A. J. Edwards, and C. R. C. Sheppard. 2008. Climate warming, marine protected areas and the ocean-scale integrity of coral reef ecosystems. PLoS ONE 3:e3039.

Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326.

Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. P. Bijoux, and J. Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Sciences of the United States of America 103:8425–8429.

Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. Robinson, J. P. Bijoux, and T. M. Daw. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conservation Biology 21:1291–1300.

Grandcourt, E. M. 1999. The population biology of a selection of exploited reef fish from the Seychelles and Great Barrier Reef. M.Sc. thesis, James Cook University. James Cook University.

Greenwood, N. D. W., C. J. Sweeting, and N. V. C. Polunin. 2010. Elucidating the trophodynamics of four coral reef fishes of the Solomon Islands using δ^{15}N and δ^{13}C. Coral Reefs 29:785–792.

Gross, K., B. J. Cardinale, J. W. Fox, A. Gonzalez, M. Loreau, H. W. Polley, P. B. Reich, J. van Ruijven, H. Wayne Polley, P. B. Reich, and J. van Ruijven. 2014. Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. American Naturalist 183:1–12.

Gross, T., L. Rudolf, S. A. Levin, and U. Dieckmann. 2009. Generalized models reveal stabilizing factors in food webs. Science 325:747–750.

Grottoli, A. G., L. J. Rodrigues, and J. E. Palardy. 2006. Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189.

Harrison, H. B., D. H. Williamson, R. D. Evans, G. R. Almany, S. R. Thorrold, G. R. Russ, K. a. Feldheim, L. Van Herwerden, S. Planes, M. Srinivasan, M. L. Berumen, and G. P. Jones. 2012. Larval export from marine reserves and the recruitment benefit for fish and fisheries. Current Biology 22:1023–1028.

Hatton, I. A., K. S. McCann, J. M. Fryxell, T. J. Davies, M. Smerlak, A. R. E. Sinclair, and M. Loreau. 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. Science 349:aac6284.

Hempson, T. N., N. A. J. Graham, M. A. MacNeil, D. H. Williamson, G. P. Jones, and G. R. Almany. 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecology and Evolution:1–10.

Hicks, C. C., and J. E. Cinner. 2014. Social, institutional, and knowledge mechanisms mediate diverse ecosystem service benefits from coral reefs. Proceedings of the National Academy of Sciences 111:17791–17796.

Hicks, C. C., L. B. Crowder, N. A. J. Graham, J. N. Kittinger, and E. Le Cornu. 2016. Social drivers forewarn of marine regime shifts. Frontiers in Ecology and the Environment 14:252–260.

Hixon, M. A., and J. P. Beets. 1993. Predation , prey refuges , and the structure of coral-reef fish assemblages. Ecological Monographs 63:77–101.

Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology 86:2847–2859.

Hobson, K. A., J. F. Piatt, and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786–798.

Hoegh-Guldberg, O., and J. F. Bruno. 2010. The impact of climate change on the world’s marine ecosystems. Science 328:1523–1528.

Hoegh-Guldberg, O., P. J. Mumby, A. J. Hooten, R. S. Steneck, P. Greenfield, E. Gomez, C. D. Harvell, P. F. Sale, A. J. Edwards, K. Caldeira, N. Knowlton, C. M. Eakin, R. Iglesias-Prieto, N. Muthiga, R. H. Bradbury, A. Dubi, and M. E. Hatziolos. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742.

Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecology Letters 8:23–29.

Hoey, A., E. Howells, J. Johansen, J.-P. Hobbs, V. Messmer, D. McCowan, S. Wilson, and M. Pratchett. 2016. Recent advances in understanding the effects of climate change on coral reefs. Diversity 8:12.

Hoey, A. S., and D. R. Bellwood. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37–47.

Holbrook, S. J., and R. J. Schmitt. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 83:2855–2868.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a caribbean coral reef. Science 265:1547–1551.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003.

Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Hughes, T. P., S. Carpenter, J. Rockström, M. Scheffer, and B. Walker. 2013. Multiscale regime shifts and planetary boundaries. Trends in Ecology and Evolution 28:389–395.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J.-P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C.-Y. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. McCulloch, H. A. Malcolm, M. J. McWilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, and S. K. Wilson. 2017. Global warming and mass bleaching of corals. Nature 543:373–377.

Hughes, T. P., M. J. Rodrigues, D. R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschaniwskyj, M. S. Pratchett, R. S. Steneck, and B. Willis. 2007. Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Current Biology 17:360–365.

Hussey, N. E., M. A. MacNeil, B. C. McMeans, J. A. Olin, S. F. J. Dudley, G. Cliff, S. P. Wintner, S. T. Fennessy, and A. T. Fisk. 2014. Rescaling the trophic structure of marine food webs. Ecology Letters 17:239–250.

Isnard, E., J. Tournois, D. J. McKenzie, F. Ferraton, N. Bodin, C. Aliaume, and A. M. Darnaude. 2015. Getting a good start in life? A comparative analysis of the quality of lagoons as juvenile habitats for the gilthead seabream *Sparus aurata* in the Gulf of Lions. Estuaries and Coasts 38:1937–1950.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637.

Jennings, S., and S. Mackinson. 2003. Abundance-body mass relationships in size-structured food webs. Ecology Letters 6:971–974.

Jennings, S., J. K. Pinnegar, N. V. C. Polunin, and T. W. Boon. 2001. Weak crossspecies relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology 70:934–944.

Johansen, J. L., V. Messmer, D. J. Coker, A. S. Hoey, and M. S. Pratchett. 2014. Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. Global Change Biology 20:1067–74.

Johansen, J. L., M. S. Pratchett, V. Messmer, D. J. Coker, A. J. Tobin, and A. S. Hoey. 2015. Large predatory coral trout species unlikely to meet increasing energetic demands in a warming ocean. Scientific Reports 5:13830.

Jones, G. P., and M. I. McCormick. 2002. Numerical and energetic processes in the ecology of coral reef fishes. Pages 221–238*in* P. F. Sale, editor.Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego.

Jones, G. P., M. I. McCormick, M. Srinivasan, and J. V Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences of the United States of America 101:8251–8253.

Jonsson, B., N. Jonsson, and A. G. Finstad. 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: An experimental test with Atlantic salmon. Journal of Animal Ecology 82:201–210.

Kelly, B., J. B. Dempson, and M. Power. 2006. The effects of preservation on fish tissue stable isotope signatures. Journal of Fish Biology 69:1595–1611.

Kerry, J. T., and D. R. Bellwood. 2012. The effect of coral morphology on shelter selection by coral reef fishes. Coral Reefs 31:415–424.

Kingsford, M. J. 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 11:193–198.

Kok, J. E., N. A. J. Graham, and M. O. Hoogenboom. 2016. Climate-driven coral reorganisation influences aggressive behaviour in juvenile coral-reef fishes. Coral Reefs 35:473–483.

Kokita, T., and A. Nakazono. 2001. Rapid response of an obligately corallivorous filefish *Oxymonacanthus longirostris* (Monacanthidae) to a mass coral bleaching event. Coral Reefs 20:155–158.

van de Koppel, J., M. Rietkerk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology & Evolution 12:352–356.

Kosten, S., M. Vernooij, E. H. Van Nes, M. de los Á. G. Sagrario, J. G. P. W. Clevers, and M. Scheffer. 2012. Bimodal transparency as an indicator for alternative states in South American lakes. Freshwater Biology 57:1191–1201.

Layman, C. A., D. A. Arrington, C. G. Montaña, and D. M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:42–48.

Lédée, E. J. I., S. G. Sutton, R. C. Tobin, and D. M. De Freitas. 2012. Responses and adaptation strategies of commercial and charter fishers to zoning changes in the Great Barrier Reef Marine Park. Marine Policy 36:226–234.

Legović, T. 1989. Predation in food webs. Ecological Modelling 48:267–276.

Letourneur, Y., T. Lison de Loma, P. Richard, M. Harmelin-Vivien, P. Cresson, D. Banaru, M.-F. Fontaine, T. Gref, and S. Planes. 2013. Identifying carbon sources and trophic position of coral reef fishes using diet and stable isotope (∂^{15}N and ∂^{13}C) analyses in two contrasted bays in Moorea , French Polynesia. Coral Reefs 32:1091–1102.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

Lindén, O., D. Souter, D. Wilhelmsson, and D. Obura. 2002. Status of Coral Reefs in East Africa. Page (O. Lindén, D. Souter, D. Wilhelmsson, and D. Obura, Eds.) Coral Reef Degradation in the Indian Ocean. Status Report 2002. CORDIO.

Little, L. R., G. A. Begg, B. Goldman, A. Williams, B. D. Mapstone, A. E. Punt, M. Russell, B. Kerrigan, R. Officer, S. Slade, G. Muldoon, and A. Penny. 2009. Modelling individual transferable quotas as a management tool in the queensland coral reef fin fish fishery. Page Technical Report (James Cook University. Fishing and Fisheries Research Centre; no. 3.

Loeuille, N. 2010. Consequences of adaptive foraging in diverse communities. Functional Ecology 24:18–27.

Loya, Sakai, Yamazato, Nakano, Sambali, and W. Van. 2001. Coral bleaching: the winners and the losers. Ecology Letters 4:122–131.

Luckhurst, B. E., and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. Marine Biology 49:317–323.

MacNeil, M. A., K. G. Drouillard, and A. T. Fisk. 2006. Variable uptake and elimination of stable nitrogen isotopes between tissues in fish. Canadian Journal of Fisheries and Aquatic Sciences 63:345–353.

Marshall, P. A., and A. H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. Coral Reefs 19:155–163.

Matley, J. K., M. R. Heupel, A. T. Fisk, C. A. Simpfendorfer, and A. J. Tobin. 2016.

Measuring niche overlap between co-occurring *Plectropomus* spp. using acoustic telemetry and stable isotopes. Marine and Freshwater Research 68:1468–1478.

Matley, J., A. Tobin, C. Simpfendorfer, A. Fisk, and M. Heupel. 2017. Trophic niche and spatio-temporal changes in the feeding ecology of two sympatric species of coral trout (*Plectropomus leopardus* and *P. laevis*). Marine Ecology Progress Series 563:197–210.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

McCann, K. S. 2000. The diversity-stability debate. Nature 405:228–233.

McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. Ecology Letters 8:513–523.

McCauley, D. J., F. Micheli, H. S. Young, D. P. Tittensor, D. R. Brumbaugh, E. M. P. Madin, K. E. Holmes, J. E. Smith, H. K. Lotze, P. a. DeSalles, S. N. Arnold, and B. Worm. 2010. Acute effects of removing large fish from a near-pristine coral reef. Marine Biology 157:2739–2750.

McCauley, D. J., M. L. Pinsky, S. R. Palumbi, J. A. Estes, F. H. Joyce, and R. R. Warner. 2015. Marine defaunation: Animal loss in the global ocean. Science 347.

McClanahan, T. R., and R. Arthur. 2001. the Effect of Marine Reserves and Habitat on Populations of East African Coral Reef Fishes. Ecological Applications 11:559–569.

McClanahan, T. R., M. Ateweberhan, N. A. J. Graham, S. K. Wilson, C. Ruiz Sebastiàn, M. M. M. Guillaume, and J. H. Bruggemann. 2007. Western Indian Ocean coral communities:bleaching responses and susceptibility to extinction. Marine Ecology Progress Series 337:1–13.

McClanahan, T. R., A. H. Baird, P. A. Marshall, and M. A. Toscano. 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. Marine Pollution Bulletin 48:327–335.

McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann, and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. Proceedings of the National Academy of Sciences 108:17230–17233.

McClanahan, T. R., and N. A. Muthiga. 2016. Geographic extent and variation of a coral reef trophic cascade. Ecology 97:1862–1872.

McCook, L. J., T. Ayling, M. Cappo, J. H. Choat, R. D. Evans, D. M. De Freitas, M.

Heupel, T. P. Hughes, G. P. Jones, B. Mapstone, H. Marsh, M. Mills, F. J. Molloy, C. R. Pitcher, R. L. Pressey, G. R. Russ, S. Sutton, H. Sweatman, R. Tobin, D. R. Wachenfeld, and D. H. Williamson. 2010. Adaptive management of the Great Barrier Reef: a globally significant demonstration of the benefits of networks of marine reserves. Proceedings of the National Academy of Sciences of the United States of America 107:18278–85.

McMahon, K. W., S. R. Thorrold, L. A. Houghton, and M. L. Berumen. 2016. Tracing carbon flow through coral reef food webs using a compound-specific stable isotope approach. Oecologia 180:809–821.

McNamara, M. E., and D. J. Lonsdale. 2014. Interannual differences in microplankton drive changes in the feeding and fecundity of *Mnemiopsis leidyi* in a Long Island estuary. Estuarine, Coastal and Shelf Science 144:1–7.

Mellin, C., M. A. MacNeil, A. J. Cheal, M. J. Emslie, and M. J. Caley. 2016. Marine protected areas increase resilience among coral reef communities. Ecology Letters 19:629–637.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: Variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist 130:730–757.

Milicich, M. J., and P. J. Doherty. 1994. Larval supply of coral reef fish populations - Magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. Marine Ecology Progress Series 110:121–134.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of δ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48:1135–1140.

Mora, C., O. Aburto-Oropeza, A. Ayala-Bocos, P. M. Ayotte, S. Banks, A. G. Bauman, M. Beger, S. Bessudo, D. J. Booth, E. Brokovich, A. Brooks, P. Chabanet, J. E. Cinner, J. Cortés, J. J. Cruz-Motta, A. Cupul-Magaña, E. E. DeMartini, G. J. Edgar, D. A. Feary, S. C. A. Ferse, A. M. Friedlander, K. J. Gaston, C. Gough, N. A. J. Graham, A. Green, H. Guzman, M. Hardt, M. Kulbicki, Y. Letourneur, A. Ĺpez-Pérez, M. Loreau, Y. Loya, C. Martinez, I. Mascareñas-Osorio, T. Morove, M. O. Nadon, Y. Nakamura, G. Paredes, N. V. C. Polunin, M. S. Pratchett, H. Reyes Bonilla, F. Rivera, E. Sala, S. A. Sandin, G. Soler, R. Stuart-Smith, E. Tessier, D. P. Tittensor, M. Tupper, P. Usseglio, L. Vigliola, L. Wantiez, I. Williams, S. K. Wilson, and F. A. Zapata. 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biology 9:e1000606.

Mourier, J., J. Maynard, V. Parravicini, L. Ballesta, E. Clua, M. L. Domeier, and S. Planes. 2016. Extreme inverted trophic pyramid of seef sharks supported by spawning groupers. Current Biology 26:2011–2016.

Mumby, P. J. 2014. Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. Fish and Fisheries:1–13.

Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101.

Mumby, P. J., A. R. Harborne, J. Williams, C. V Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America 104:8362–8367.

Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends in Ecology and Evolution 23:555–563.

Mumby, P. J., R. S. Steneck, A. J. Edwards, R. Ferrari, R. Coleman, A. R. Harborne, and J. P. Gibson. 2012. Fishing down a Caribbean food web relaxes trophic cascades. Marine Ecology Progress Series 445:13–24.

Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology 10:1642–1647.

Munday, P. L., and G. P. Jones. 1998. The ecological implications of small body size among coral reef fishes. Oceanography and Marine Biology: An Annual Review 36:373–411.

Munday, P. L., G. P. Jones, M. S. Pratchett, and A. J. Williams. 2008. Climate change and the future for coral reef fishes. Fish and Fisheries 9:261–285.

Munday, P. L., G. P. Jones, M. Sheaves, A. J. Williams, and G. Goby. 2007. Vulnerability of fishes of the Great Barrier Reef to climate change. Pages 357–391*in* J. Johnson and P. Marshall, editors.Climate Change and the Great Barrier Reef. Great Barrier Reef Marine Park Authority, Townsville, Australia.

Nash, K. L., N. A. J. Graham, S. Jennings, S. K. Wilson, D. R. Bellwood, and D. Angeler. 2016. Herbivore cross-scale redundancy supports response diversity and promotes coral reef resilience. Journal of Applied Ecology 53:646–655.

Nash, K. L., N. A. J. Graham, S. K. Wilson, and D. R. Bellwood. 2013. Cross-scale habitat structure drives fish body size distributions on coral reefs. Ecosystems 16:478–490.

Nelson, G. A. 2015. Fishery Science Methods and Models in R. Version 1.9-0.

Nyström, M., N. A. J. Graham, J. Lokrantz, and A. V. Norström. 2008. Capturing the cornerstones of coral reef resilience: Linking theory to practice. Coral Reefs 27:795–809.

Őhman, M. C., A. Rajasuriya, and S. Svensson. 1998. The use of butterflyfishes (Chaetodontidae) as bio-indicators of habitat structure and human disturbance. Ambio 27:708–716.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. The American Naturalist 155:703–723.

Ostaszewska, T., K. Dabrowski, K. Czumińska, W. Olech, and M. Olejniczak. 2005. Rearing of pike-perch larvae using formulated diets - First success with starter feeds. Aquaculture Research 36:1167–1176.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Palacios, M. M., S. S. Killen, L. E. Nadler, J. R. White, and M. I. McCormick. 2016a. Top predators negate the effect of mesopredators on prey physiology. Journal of Animal Ecology 85:1078–1086.

Palacios, M. M., D. T. Warren, and M. I. Mccormick. 2016b. Sensory cues of a top-predator indirectly control a reef fish mesopredator. Oikos 125:201–209.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958.

Pandolfi, J. M., S. R. Connolly, D. J. Marshall, and A. L. Cohen. 2011. Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422.

Parrish, C. C. 1999. Determination of total lipid, lipid classes, and fatty acids in aquatic samples. Pages 4–20. Lipids in freshwater ecosystems. Springer New York, New York, NY.

Peers, M. J. L., M. Wehtje, D. H. Thornton, and D. L. Murray. 2014. Prey switching as a means of enhancing persistence in predators at the trailing southern edge. Global

Change Biology 20:1126–1135.

Persson, L. 1999. Trophic Cascades: Abiding heterogeneity and the trophic level concept at the end of the road. Oikos 85:385–397.

Peterson, B. J. 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. Acta Oecologica 20:479–487.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Phillips, D. L., and J. W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–9.

Pinnegar, J. K., and N. V. C. Polunin. 1999. Differential fractionation of δ^{13}C and δ^{15}N among fish tissues: implications for the study of trophic interactions. Functional Ecology 13:225–231.

Pinnegar, J. K., and N. V. C. Polunin. 2000. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399–409.

Polovina, J. J. 1984. Model of a coral reef ecosystem. Coral Reefs 3:1–11.

Pörtner, H. O., and A. P. Farrell. 2008. Physiology and climate change. Science 322:690–692.

Post, D. M. 2002a. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–718.

Post, D. M. 2002b. The long and short of food chain length. Trends in Ecology & Evolution 17:269–277.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña. 2007. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179–189.

Post, D. M., M. L. Pace, and N. G. Hairston. 2000. Ecosystem size determines food-chain length in lakes. Nature 405:1047–9.

Pratchett, M. S., N. Gust, G. Goby, and S. O. Klanten. 2001. Consumption of coral propagules represents a significant trophic link between corals and reef fish. Coral Reefs 20:13–17.

Pratchett, M. S., A. S. Hoey, and S. K. Wilson. 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Current Opinion in Environmental Sustainability 7:37–43.

Pratchett, M. S., A. S. Hoey, S. K. Wilson, V. Messmer, and N. A. J. Graham. 2011.

Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity 3:424–452.

Pratchett, M. S., P. L. Munday, S. K. Wilson, N. A. J. Graham, J. E. Cinner, D. R. Bellwood, G. P. Jones, N. V. C. Polunin, and T. R. McClanahan. 2008. Effects of climate-induced coral bleaching on coral-reef fishes—ecological and economic consequences. Oceanography and Marine Biology: An Annual Review 46:251–296.

Pratchett, M. S., S. K. Wilson, and A. H. Baird. 2006. Declines in the abundance of Chaetodon butterflyfishes following extensive coral depletion. Journal of Fish Biology 69:1269–1280.

Pratchett, M. S., S. K. Wilson, M. L. Berumen, and M. I. McCormick. 2004. Sublethal effects of coral bleaching on an obligate coral feeding butterflyfish. Coral Reefs 23:352–356.

Rasher, D. B., A. S. Hoey, and M. E. Hay. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function. Ecology 94:1347–1358.

Richter, H., C. Lückstädt, U. L. Focken, and K. Becker. 2000. An improved procedure to assess fish condition on the basis of length-weight relationships. Archive of Fishery and Marine Research 48:226–235.

Riegl, B., A. Bruckner, S. L. Coles, P. Renaud, and R. E. Dodge. 2009. Coral reefs: Threats and conservation in an era of global change. Annals of the New York Academy of Sciences 1162:136–186.

Riegl, B. M., A. W. Bruckner, G. P. Rowlands, S. J. Purkis, and P. Renaud. 2012. Red Sea coral reef trajectories over 2 decades suggest increasing community homogenization and decline in coral size. PLoS ONE 7:5–11.

Rizzari, J. R., B. J. Bergseth, and A. J. Frisch. 2015. Impact of conservation areas on trophic interactions between apex predators and herbivores on coral reefs. Conservation Biology 29:418–429.

Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of coral reef fisheries to a loss of structural complexity. Current Biology 24:1000–1005.

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265–269.

Ruiz-Cooley, R. I., K. Y. Garcia, and E. D. Hetherington. 2011. Effects of lipid removal and preservatives on carbon and nitrogen stable isotope ratios of squid tissues: Implications for ecological studies. Journal of Experimental Marine Biology and

Ecology 407:101–107.

Sadovy de Mitcheson, Y., M. T. Craig, A. A. Bertoncini, K. E. Carpenter, W. W. L. Cheung, J. H. Choat, A. S. Cornish, S. T. Fennessy, B. P. Ferreira, P. C. Heemstra, M. Liu, R. F. Myers, D. A. Pollard, K. L. Rhodes, L. A. Rocha, B. C. Russell, M. A. Samoilys, and J. Sanciangco. 2013. Fishing groupers towards extinction: A global assessment of threats and extinction risks in a billion dollar fishery. Fish and Fisheries 14:119–136.

Samoilys, M. A. 1997. Movement in a large predatory fish: coral trout, *Plectropomus leaopardus* (Pisces: Serranidae), on Heron Reef, Australia. Coral Reefs 16:151–158.

Sandin, S. A., J. E. Smith, E. E. DeMartini, E. A. Dinsdale, S. D. Donner, A. M. Friedlander, T. Konotchick, M. Malay, J. E. Maragos, D. Obura, O. Pantos, G. Paulay, M. Richie, F. Rohwer, R. E. Schroeder, S. Walsh, J. B. C. Jackson, N. Knowlton, and E. Sala. 2008. Baselines and degradation of coral reefs in the Northern Line Islands. PLoS ONE 3:e1548.

Sano, M., M. Shimizu, and Y. Nose. 1987. Long-term effects of destruction of hermatypic corals by *Acanthaster plana* infestation on reef fish communities at Iriomote Island, Japan . Marine Ecology Progress Series 37:191–199.

Sarakinos, H. C., M. L. Johnson, and M. J. Vander Zanden. 2002. A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. Canadian Journal of Zoology 80:381–387.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–6.

Schriever, T. A. 2015. Food webs in relation to variation in the environment and species assemblage: A multivariate approach. PloS ONE 10:e0122719.

Sheppard, C. R. C. 2003. Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425:294–297.

Sheppard, C. R. C., M. Spalding, C. Bradshaw, and S. Wilson. 2002. Erosion El Nino: Recovery vs . Reefs , Chagos of Coral Indian Reefs Ocean after. Coral Reefs 31:40–48.

Shpigel, M., and L. Fishelson. 1989. Food habits and prey selection of three species of groupers from the genus *Cephalopholis* (Serranidae: Teleostei). Environmental Biology of Fishes 24:67–73.

Smith, J. L. B., M. M. Smith, and P. C. Heemstra. 2003. Smith’s Sea Fishes. Struik.

St John, J. 1995. Feeding ecology of the coral trout, *Plectropomus leopardus* (Serranidae), on the Great Barrier Reef, Australia.

St John, J. 1999. Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): Patterns in taxa, size and habitat of prey. Marine Ecology Progress Series 180:233–246.

Stallings, C. D., F. C. Coleman, C. C. Koenig, and D. A. Markiewicz. 2010. Energy allocation in juveniles of a warm-temperate reef fish. Environmental Biology of Fishes 88:389–398.

Staver, A. C., S. Archibald, and S. Levin. 2016. Tree cover in sub-Saharan Africa: Rainfall and fire constrain forest and savanna as alternative stable states. Ecology 92:1063–1072.

Stevenson, R. D., and W. A. Woods. 2006. Condition indices for conservation: New uses for evolving tools. Integrative and Comparative Biology 46:1169–1190.

Sweeting, C. J., N. V. C. Polunin, and S. Jennings. 2004. Tissue and fixative dependent shifts of δ^{13}C and δ^{15}N in preserved ecological material. Rapid Communications in Mass Spectrometry 18:2587–2592.

Syms, C., and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral- reef fish community. Ecology 81:2714–2729.

Team, R. C. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

The World Bank. 2006. Scaling up marine management - The role of marine protected areas.

Theilacker, G. H. 1978. Effect of starvation on the histological and morphological characteristics of jack mackerel, *Trachurus symmetricus*, larvae. Fishery Bulletin 76:403–414.

Trebilco, R., J. K. Baum, A. K. Salomon, and N. K. Dulvy. 2013. Ecosystem ecology: Size-based constraints on the pyramids of life. Trends in Ecology and Evolution 28:423–431.

Vance-Chalcraft, H. D., J. A. Rosenheim, J. R. Vonesh, C. W. Osenberg, and A. Sih. 2007. The influence of intraguild predation on prey suppression and prey release: A meta-analysis. Ecology 88:2689–2696.

Varkey, D., C. H. Ainsworth, and T. J. Pitcher. 2012. Modelling reef fish population responses to fisheries restrictions in marine protected areas in the Coral Triangle. Journal of Marine Biology 2012:1–18.

Wada, E., H. Mizutani, and M. Minagawa. 1991. The use of stable isotopes for food web analysis. Critical Reviews in Food Science and Nutrition 30:361–371.

Walters, C., D. Pauly, and V. Christensen. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554.

Warner, R. R., and T. P. Hughes. 1988. The population dynamics of reef fishes. Pages 149–155. Proceedings of the 6th International Coral Reef Symposium, Australia.

Watson, J., and J. A. Estes. 2011. Stability, resilience, and phase shifts in rocky subtidal communities along the west coast of Vancouver Island, Canada. Ecological Monographs 81:215–239.

Welch, B. L. 1947. The generalization of `Student's' problem when several different population variances are involved. Biometrika 34:28–35.

Wen, C. K. C., G. R. Almany, D. H. Williamson, M. S. Pratchett, and G. P. Jones. 2012. Evaluating the effects of marine reserves on diet, prey availability and prey selection by juvenile predatory fishes. Marine Ecology Progress Series 469:133–144.

Wen, C. K. C., G. R. Almany, D. H. Williamson, M. S. Pratchett, T. D. Mannering, R. D. Evans, J. M. Leis, M. Srinivasan, and G. P. Jones. 2013a. Recruitment hotspots boost the effectiveness of no-take marine reserves. Biological Conservation 166:124–131.

Wen, C. K. C., M. S. Pratchett, G. R. Almany, and G. P. Jones. 2013b. Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the southern Great Barrier Reef, Australia. Coral Reefs 32:389–398.

Wenger, A. S., D. H. Williamson, E. T. Silva, D. M. Ceccarelli, N. K. Browne, C. Petus, and M. J. Devlin. 2015. Effects of reduced water quality on coral reefs in and out of no-take marine reserves. Conservation Biology 30:142–153.

Wernberg, T., S. Bennett, R. C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, J. Fromont, C. J. Fulton, R. K. Hovey, E. S. Harvey, T. H. Holmes, G. A. Kendrick, B. Radford, J. Santana-Garcon, B. J. Saunders, D. A. Smale, M. S. Thomsen, C. A. Tuckett, F. Tuya, M. A. Vanderklift, and S. Wilson. 2016. Climate-driven regime shift of a temperate marine ecosystem. Science 353:169–

72.

West, G. 1990. Methods of assessing ovarian development in fishes: a review. Marine and Freshwater Research 41:199.

Williamson, D., D. Ceccarelli, G. Rossetti, G. Russ, and G. Jones. 2016. Assessing the cumulative impacts of climatic disturbances on coral reefs in the Keppel Islands, Great Barrier Reef Marine Park Assessing the cumulative impacts of climatic disturbances on coral reefs in the Keppel Islands , Great Barrier Reef Marine Park. Report to the National Environmental Science Programme. Reef and Rainforest Research Centre Limited, Cairns.

Williamson, D. H., D. M. Ceccarelli, R. D. Evans, G. P. Jones, and G. R. Russ. 2014. Habitat dynamics, marine reserve status, and the decline and recovery of coral reef fish communities. Ecology and Evolution 4:337–354.

Wilson, S. K., M. Adjeroud, D. R. Bellwood, M. L. Berumen, D. Booth, Y.-M. Bozec, P. Chabanet, A. Cheal, J. Cinner, M. Depczynski, D. A. Feary, M. Gagliano, N. A. J. Graham, A. R. Halford, B. S. Halpern, A. R. Harborne, A. S. Hoey, S. J. Holbrook, G. P. Jones, M. Kulbiki, Y. Letourneur, T. L. De Loma, T. McClanahan, M. I. McCormick, M. G. Meekan, P. J. Mumby, P. L. Munday, M. C. Ohman, M. S. Pratchett, B. Riegl, M. Sano, R. J. Schmitt, and C. Syms. 2010a. Crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes. The Journal of Experimental Biology 213:894–900.

Wilson, S. K., R. C. Babcock, R. Fisher, T. H. Holmes, J. A. Y. Moore, and D. P. Thomson. 2012a. Relative and combined effects of habitat and fishing on reef fish communities across a limited fishing gradient at Ningaloo. Marine Environmental Research 81:1–11.

Wilson, S. K., M. Depczynski, R. Fisher, T. H. Holmes, R. A. O’Leary, and P. Tinkler. 2010b. Habitat associations of juvenile fish at Ningaloo Reef, Western Australia: The importance of coral and algae. PLoS ONE 5:e15185.

Wilson, S. K., M. Depczynski, T. H. Holmes, M. M. Noble, B. T. Radford, P. Tinkler, and C. J. Fulton. 2017. Climatic conditions and nursery habitat quality provide indicators of reef fish recruitment strength. Limnology and Oceanography. doi 10.1002/lno.10540

Wilson, S. K., R. Fisher, M. S. Pratchett, N. A. J. Graham, N. K. Dulvy, R. A. Turner, A. Cakacaka, and N. V. C. Polunin. 2010c. Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecological Applications

20:442–451.

Wilson, S. K., R. Fisher, M. S. Pratchett, N. A. J. Graham, N. K. Dulvy, R. A. Turner, A. Cakacaka, N. V. C. Polunin, and S. P. Rushton. 2008. Exploitation and habitat degradation as agents of change within coral reef fish communities. Global Change Biology 14:2796–2809.

Wilson, S. K., N. A. J. Graham, R. Fisher, J. Robinson, K. Nash, K. Chong-Seng, N. V. C. Polunin, R. Aumeeruddy, and R. Quatre. 2012b. Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. Conservation Biology 26:995–1004.

Wilson, S. K., N. A. J. Graham, and N. V. C. Polunin. 2007. Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151:1069–1076.

Wilson, S. K., N. A. J. Graham, M. S. Pratchett, G. P. Jones, and N. V. C. Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? Global Change Biology 12:2220–2234.

Van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. Marine Ecology Progress Series 434:67–76.

World Bank. 2012. Hidden harvest : the global contribution of capture fisheries. Washington DC.

Zudaire, I., H. Murua, M. Grande, F. Pernet, and N. Bodin. 2014. Accumulation and mobilization of lipids in relation to reproduction of yellowfin tuna (*Thunnus albacares*) in the Western Indian Ocean. Fisheries Research.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

Zuur, A., E. N. Ieno, and G. M. Smith. 2007. Analysing Ecological Data. Springer Science and Business Media.

Appendix A: Supplemental information for Chapter 2

FIGURES

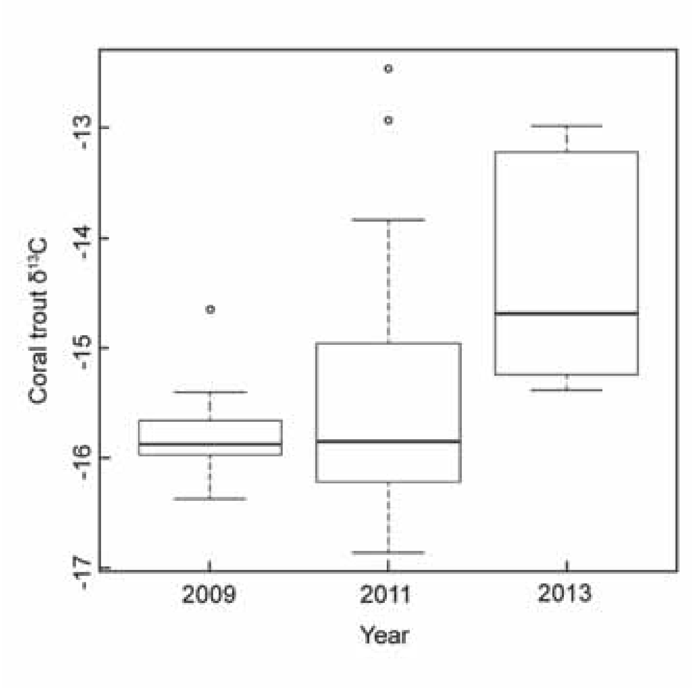


Fig. S1 Shift in the δ^{13}C signal in coral grouper (*Plectropomus maculatus)* between 2009 (n=9), 2011 (n=27), and 2013 (n=12), from a more negative (i.e. planktonic) signal, to more positive (i.e. benthic) signal. The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile range past these points.

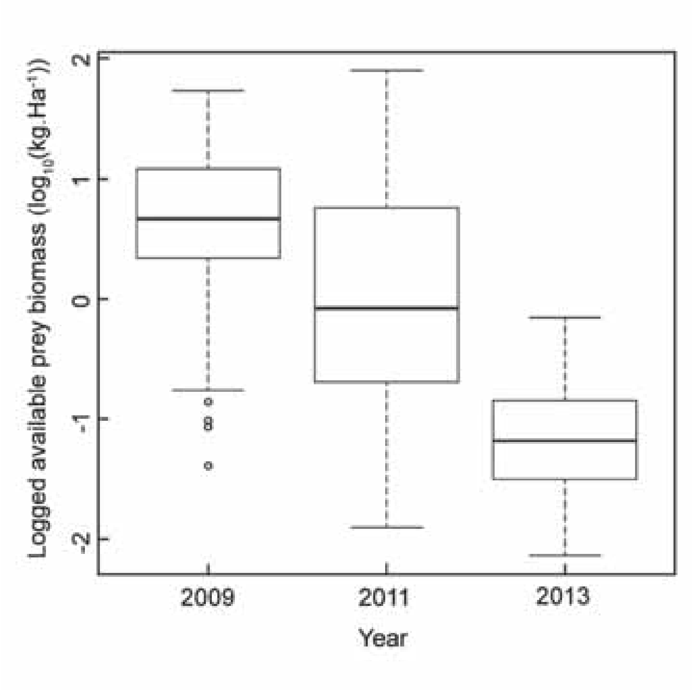


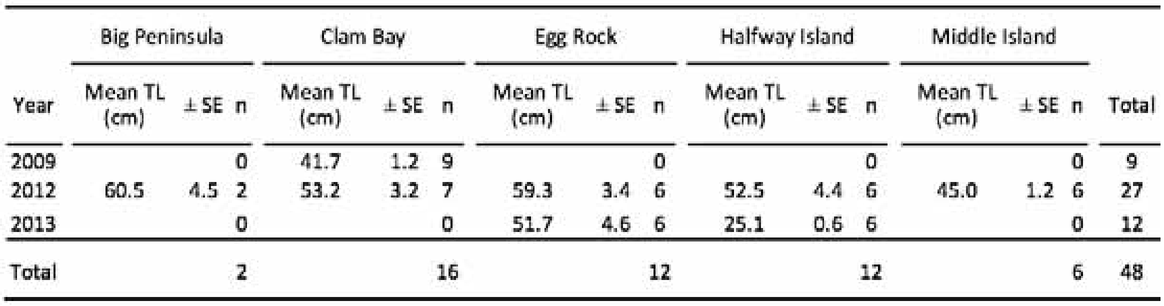
Fig. S2 Change in logged total prey biomass available to coral grouper in the Keppel Islands between 2009 (n=9), 2011 (n=27), and 2013 (n=12). The dark line indicates the median of the data, boxes represent the bounds of the first and third quartile, with whiskers extending to 1.5 times the interquartile range past these points.

TABLES

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).

			Live hard coral cover (%)		Macroalgae cover (%)		Dead coral & rubble cover (%)		SCI	
Site	Year	n	Mean	± SE	Mean	± SE	Mean	± SE	Mean	± SE
Big Peninsula	2009	10	81.60	3.04	0.00	0.00	10.00	1.58	9.80	0.82
	2011	10	49.40	7.88	0.00	0.00	31.00	6.42	7.36	0.65
	2013	10	32.20	5.62	0.20	0.20	27.20	5.58	5.92	0.41
Clam Bay	2009	15	46.67	8.37	40.53	10.19	7.20	1.55	5.73	0.14
	2011	15	33.60	7.34	0.27	0.18	60.93	7.85	4.54	0.31
	2013	15	20.80	6.51	17.87	3.59	51.87	4.39	4.48	0.25
Halfway Island	2009	15	68.00	6.11	18.67	7.08	8.40	2.34	6.29	0.39
	2011	15	36.27	4.14	0.00	0.00	51.73	5.28	7.13	0.41
	2013	15	21.87	3.57	3.60	1.05	62.53	4.57	4.37	0.17
Middle Island	2009	15	67.60	4.73	15.73	4.76	15.07	2.77	7.50	0.19
	2011	15	26.67	5.17	0.00	0.00	66.53	7.08	4.73	0.23
	2013	15	17.33	5.11	24.80	5.51	52.13	6.61	4.39	0.32

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.

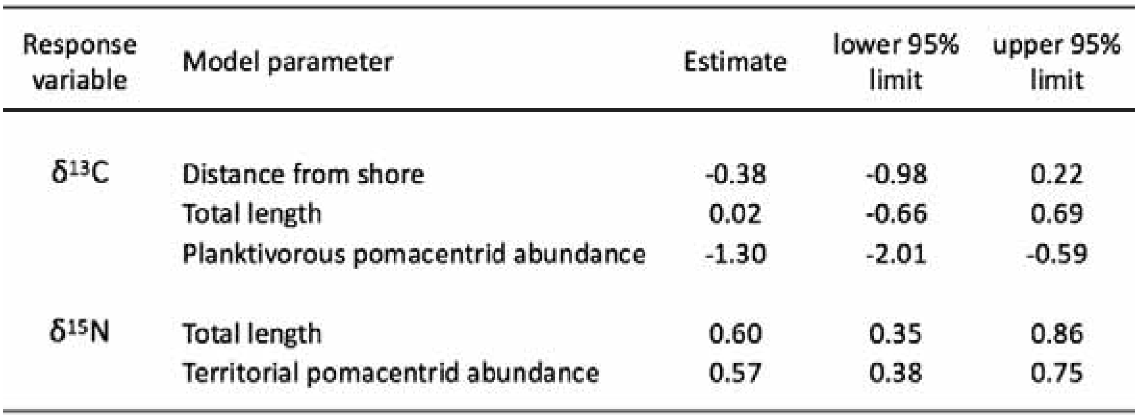


	Big Peninsula			Clam Bay			Egg Rock			Halfway Island			Middle Island			
Year	Mean TL (cm)	± SE	n	Mean TL (cm)	± SE	n	Mean TL (cm)	± SE	n	Mean TL (cm)	± SE	n	Mean TL (cm)	± SE	n	Total
2009			0	41.7	1.2	9			0			0			0	9
2012	60.5	4.5	2	53.2	3.2	7	59.3	3.4	6	52.5	4.4	6	45.0	1.2	6	27
2013			0			0	51.7	4.6	6	25.1	0.6	6			0	12
Total			2			16			12			12			6	48

Table S3. Prey fish species functional group allocations

Family	Species	Functional Group
Pomacentridae	*Chromis amboinensis*	Planktivorous pomacentrid
	Chromis atripectoralis	Planktivorous pomacentrid
	Chromis nitida	Planktivorous pomacentrid
	Chromis ternatensis	Planktivorous pomacentrid
	Pomacentrus lepidogenis	Planktivorous pomacentrid
	Hemiglyphidodon plagiometapon	Territorial pomacentrid
	Neoglyphidodon melas	Territorial pomacentrid
	Pomacentrus bankanensis	Territorial pomacentrid
	Pomacentrus wardi	Territorial pomacentrid
	Stegastes apicalis	Territorial pomacentrid
	Stegastes fasciolatus	Territorial pomacentrid

Table S4. Standardised AIC-weighted model-averaged parameter estimates with 95% confidence intervals for models of stable isotope (δ^{13}C and δ^{15}N) signatures in coral grouper (*Plectropomus maculatus*).



Response variable	Model parameter	Estimate	lower 95% limit	upper 95% limit
δ^{13}C	Distance from shore	-0.38	-0.98	0.22
	Total length	0.02	-0.66	0.69
	Planktivorous pomacentrid abundance	-1.30	-2.01	-0.59
δ^{15}N	Total length	0.60	0.35	0.86
	Territorial pomacentrid abundance	0.57	0.38	0.75

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 δ^{13}C bulk stable isotope content.

Appendix B: Supplemental information for Chapter 3

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 Iatroscan 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.

FIGURES

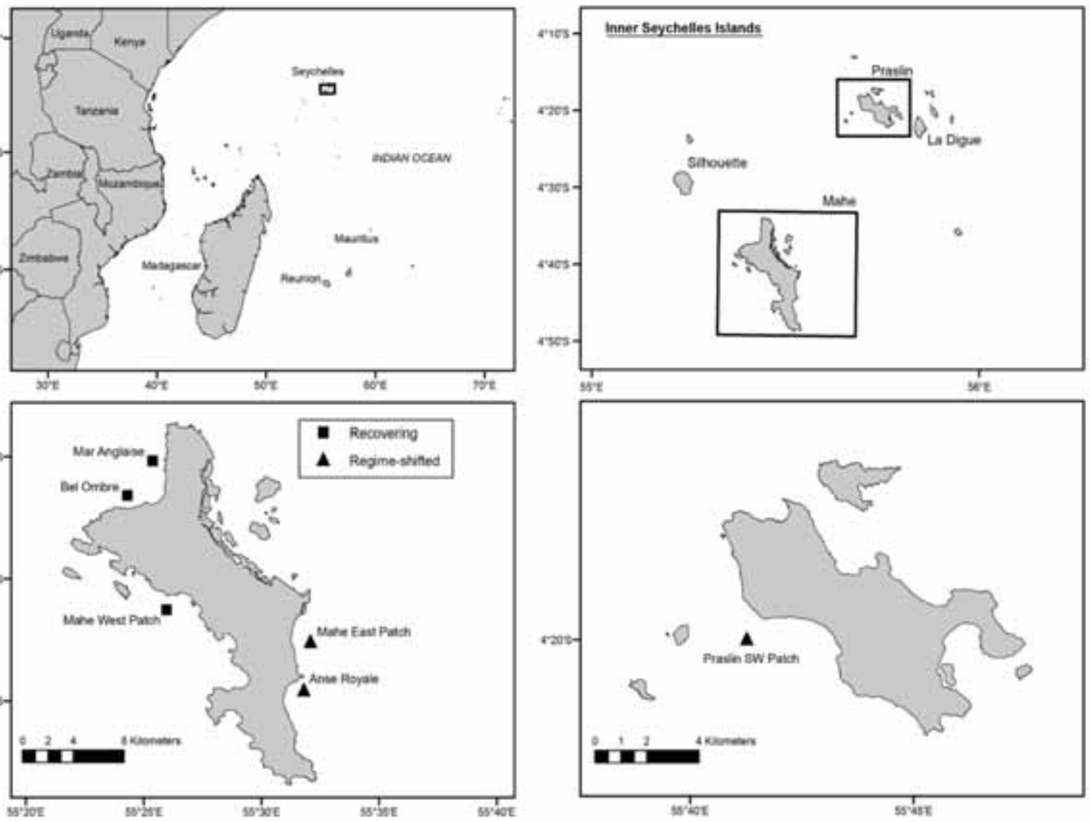


Fig. S1 Map of the study site in the Seychelles Inner Island Group showing the location of the 6 study sites. Recovering sites (Bel Ombre, Mahe West Patch, Mar Anglaise), are indicated by black squares, and regime-shifted sites (Anse Royale, Praslin South West, Mahe East Patch) by black triangles.

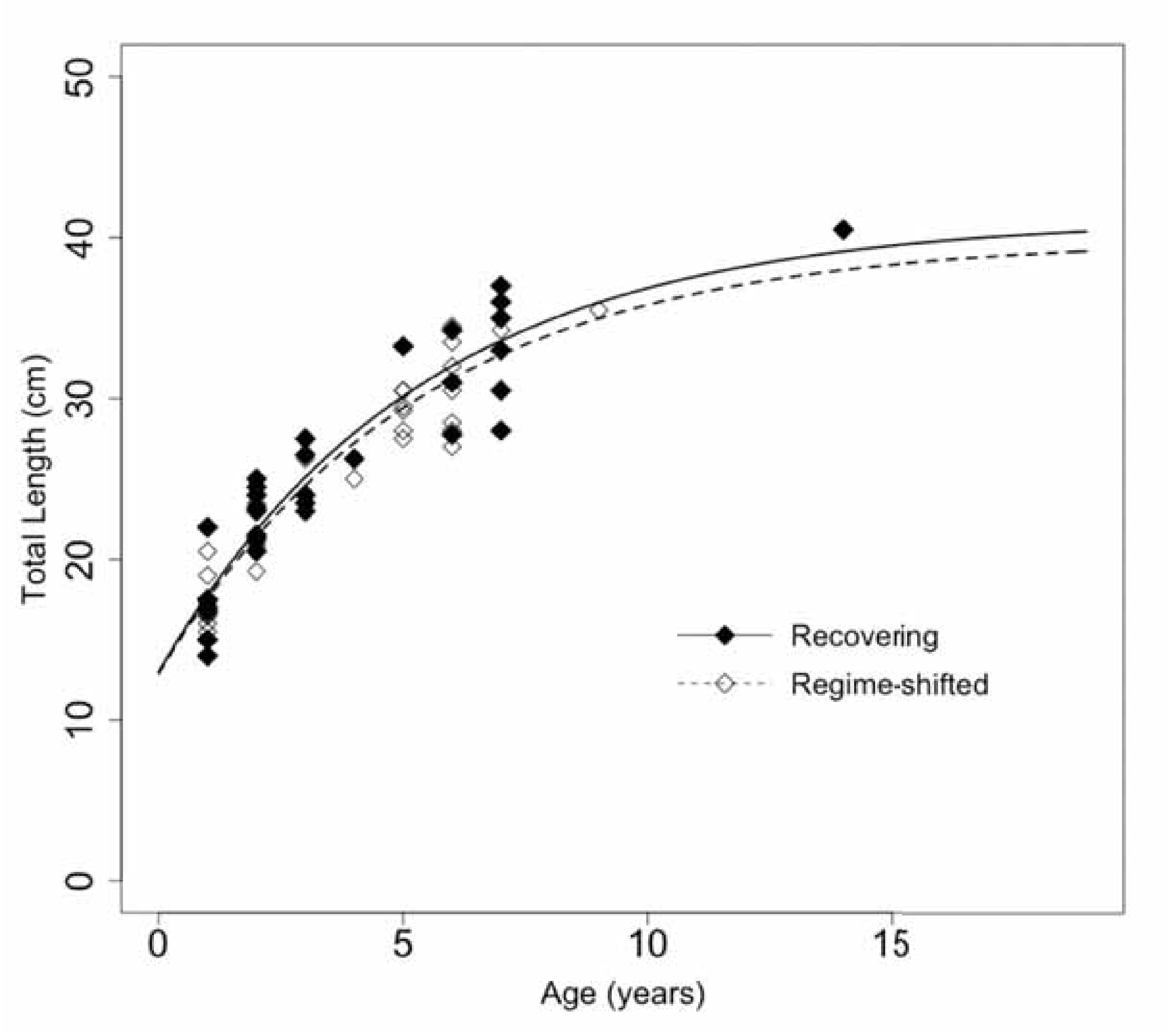


Fig. S2 Size-at-age of *Cephalopholis argus* sampled from reefs recovering from bleaching and regime-shifted reefs in Seychelles. Growth rate curves were fitted using the Von Bertalanffy Growth Model for fish from recovering (solid line) and regime-shifted (dashed lines).

TABLES

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.

Mesopredator species	Abundance		Biomass		Diversity (H)	
	mean	±s.e.	mean	±s.e.	mean	±s.e.
Regime-shifted (n = 32)						
Aprion virescens	0.30	0.20	4.73	2.82		
Cephalopholis argus	0.20	0.23	1.57	1.57		
Oxycheilinus digramma	0.71	0.33	1.08	0.54		
Total	0.20	0.16	1.23	1.35	0.02	0.02
Recovering (n = 24)						
Anyperodon leucogrammicus	0.27	0.19	1.34	1.10		
Cephalopholis argus	0.81	0.35	5.56	3.25		
Cephalopholis miniata	0.14	0.14	0.13	0.13		
Lutjanus bohar	0.68	0.28	5.19	2.51		
Oxycheilinus digramma	3.52	0.70	8.19	2.10		
Total	0.90	0.42	3.40	2.00	0.28	0.07

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.

	$\delta^{13}C$		$\delta^{15}N$	
	CV	[95% interval]	CV	[95% interval]
Recovering (n=10)	-8.681	-6.591, -12.726	14.004	10.605, 20.651
Regime-shifted (n=10)	-8.837	-7.229, -11.373	28.533	23.059, 37.553

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

			Phosopholipid (PL)		Sterols (ST)		Triacylglycerols (TAG)		TAG:ST		Total Lipids	
		(n)	mean ± se		mean ± se		mean ± se		mean ± se		mean ± se	
MUSCLE	**REGIME-SHIFTED**											
	Female											
	Developing	(4)	3.25	0.18	0.20	0.00	0.88	0.41	4.50	1.94	4.88	0.35
	Regressing	(8)	2.55	0.36	0.19	0.03	1.81	0.80	7.75	3.00	5.08	1.01
	Spawning	(5)	3.22	0.18	0.22	0.02	1.16	0.43	6.40	2.77	5.06	0.41
	Male											
	Developing	(1)	2.80		0.20		1.90		8.00		5.10	
	Regressing	(2)	2.35	0.25	0.20	0.00	0.90	0.80	4.00	4.00	3.95	0.55
	Immature											
	Indeterminate	(13)	3.73	0.25	0.29	0.03	1.22	0.21	4.31	0.80	5.97	0.43
	RECOVERING											
	Female											
	Developing	(5)	3.40	0.29	0.26	0.05	2.08	0.64	7.00	2.12	5.76	0.94
	Spawning	(6)	3.83	0.75	0.23	0.02	1.43	0.38	6.17	1.51	6.00	0.59
	Male											
	Developing	(1)	4.00		0.40		3.10		8.00		8.80	
	Regressing	(2)	3.70	0.40	0.15	0.05	2.90	1.20	20.50	6.50	7.35	1.65
	Immature											
	Indeterminate	(20)	3.06	0.18	0.27	0.03	0.70	0.15	3.59	1.08	4.51	0.31
LIVER	**REGIME SHIFTED**											
	Female											
	Developing	(4)	8.60	0.27	1.30	0.29	27.05	6.33	21.50	3.30	40.15	6.82
	Regressing	(8)	11.63	0.87	1.26	0.18	29.81	5.03	31.13	8.37	46.05	4.59
	Spawning	(4)	10.43	0.70	1.30	0.06	15.70	3.81	11.75	2.75	24.78	7.08
	Male											
	Developing	(1)	12.90		1.80		35.50		20.00		53.50	
	Regressing	(2)	8.75	2.05	1.15	0.45	8.80	4.20	11.00	8.00	23.55	3.25
	Immature											
	Indeterminate	(9)	10.48	1.43	1.18	0.19	34.38	7.64	35.56	9.38	50.66	9.12
	RECOVERING											
	Female											
	Developing	(5)	13.44	1.25	1.20	0.17	26.04	3.58	22.80	2.82	43.62	4.28
	Spawning	(6)	10.37	1.14	0.82	0.07	15.13	1.12	18.83	1.54	28.85	2.45
	Male											
	Developing	(1)	8.80		2.80		39.80		14.00		53.90	
	Regressing	(2)	11.60	3.20	2.00	0.30	29.25	4.35	15.50	4.50	49.75	1.25
	Immature											
	Indeterminate	(11)	9.38	1.52	1.38	0.22	24.36	5.17	20.91	4.97	38.11	5.52
GONAD	**REGIME-SHIFTED**											
	Female											
	Developing	(4)	20.35	6.09	1.70	0.29	36.63	9.22	25.25	10.60	66.10	3.48
	Regressing	(8)	15.24	1.47	1.48	0.13	18.65	2.18	12.50	0.87	45.00	5.43
	Spawning	(4)	19.65	0.83	1.85	0.10	23.08	1.43	12.25	0.75	57.30	2.01
	Male											
	Developing	(1)	8.90		1.10		1.80		2.00		15.00	
	Regressing	(2)	6.15	1.45	1.10	0.10	1.00	0.10	1.00	0.00	10.95	0.15
	RECOVERING											
	Female											
	Developing	(4)	20.23	1.65	2.15	0.12	29.35	1.41	13.50	0.29	67.48	4.03
	Spawning	(6)	19.27	1.14	1.70	0.17	27.70	1.14	16.83	1.78	60.58	3.82
	Male											
	Developing	(1)	4.40		1.00		1.00		1.00		7.70	
	Regressing	(2)	9.65	3.95	1.90	0.80	0.55	0.25	0.50	0.50	13.35	4.35

Appendix C: Supplemental information for Chapter 4

FIGURES

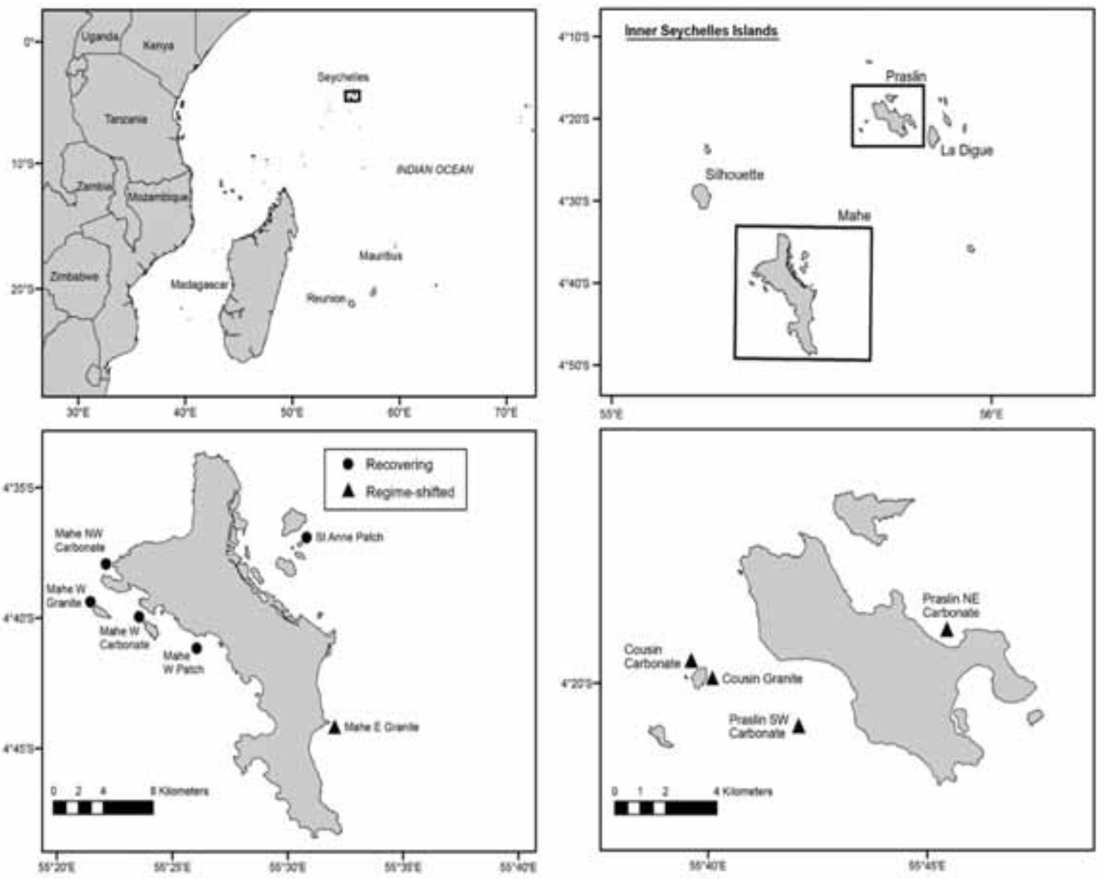


Fig. S2 Map of the study site in the Seychelles Inner Island Group showing the location of the ten study sites. The five recovering sites are indicated by black circles, and the five regime-shifted sites by black triangles.

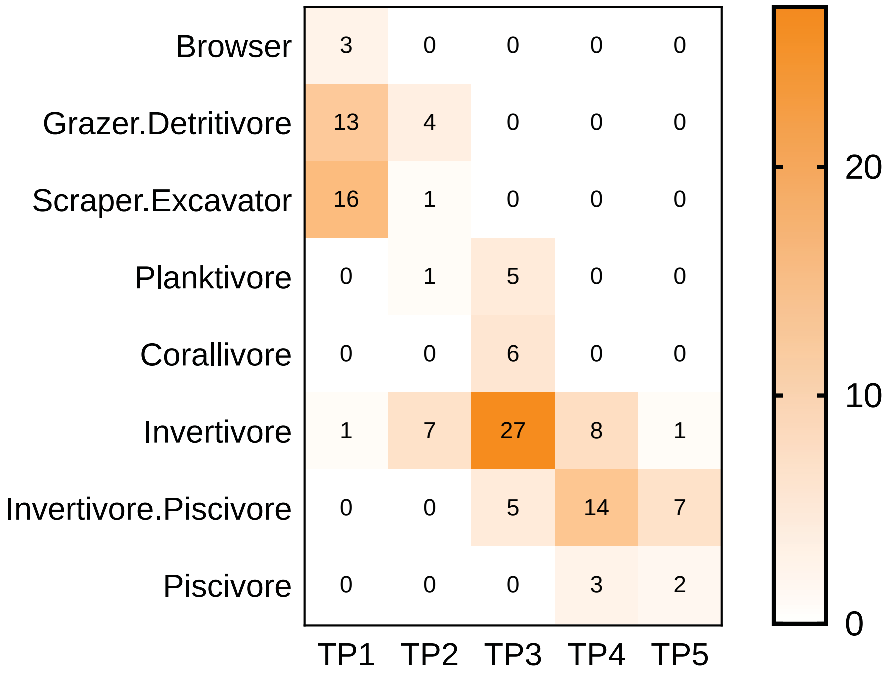


Fig. S2 Heat map showing the number of species from each functional group within each level (trophic position; TP) of the trophic pyramids.

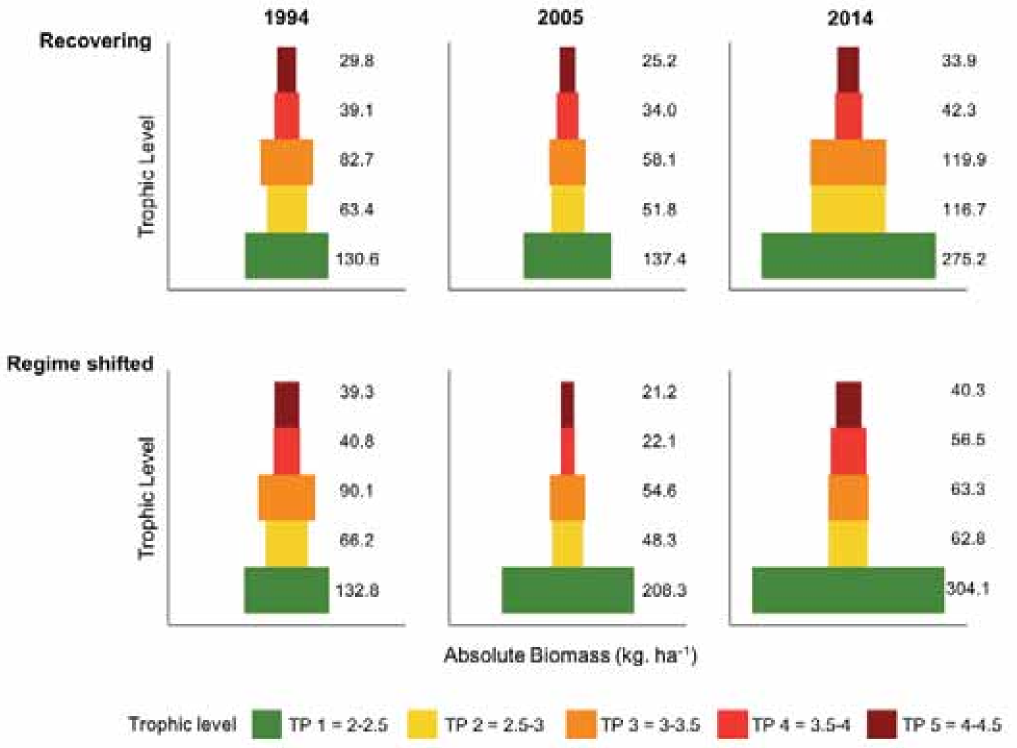


Fig. S3 Trophic pyramids showing the distribution of absolute biomass (kg. ha^{-1}) between five trophic positions in the reef fish communities on recovering (n = 5) and regime-shifted (n = 5) reefs in the Seychelles inner island group, both before the 1998 mass bleaching (1994) and after it (2005, 2014).

TABLES

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.

TP	**Species name**	**Functional Group**	**Recovering**			**Regime-Shift**		
			'94	**'05**	**'14**	**'94**	**'05**	**'14**
1	*Acanthurus leucosternon*	Grazer.Detritivore	x	x	x	x	x	x
1	*Acanthurus lineatus*	Grazer.Detritivore	x	x		x		
1	*Acanthurus nigrofuscus*	Grazer.Detritivore	x	x	x	x	x	x
1	*Acanthurus tennentii*	Grazer.Detritivore	x	x	x	x	x	x
1	*Calotomus carolinus*	Browser				x	x	x
1	*Cetoscarus bicolor*	Scraper.Excavator	x		x	x		
1	*Chlorurus atrilunula*	Scraper.Excavator	x	x	x	x	x	x
1	*Chlorurus strongylocephalus*	Scraper.Excavator	x	x	x	x		x
1	*Ctenochaetus binotatus*	Grazer.Detritivore	x	x	x			
1	*Ctenochaetus striatus*	Grazer.Detritivore	x	x	x	x	x	x
1	*Ctenochaetus truncatus*	Grazer.Detritivore	x	x	x	x	x	x
1	*Hipposcarus harid*	Scraper.Excavator	x	x	x	x	x	x
1	*Leptoscarus vaigiensis*	Browser					x	x
1	*Naso elegans*	Browser	x	x			x	x
1	*Plectroglyphidodon lacrymatus*	Grazer.Detritivore	x	x	x	x	x	x
1	*Scarus caudofasciatus*	Scraper.Excavator	x	x	x		x	x
1	*Scarus falcipinnis*	Scraper.Excavator	x	x	x	x	x	
1	*Scarus frenatus*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus ghobban*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus globiceps*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus niger*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus prasiognathos*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus psittacus*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus rubroviolaceus*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus scaber*	Scraper.Excavator	x	x	x	x	x	
1	*Scarus tricolor*	Scraper.Excavator	x	x	x	x	x	x
1	*Scarus viridifucatus*	Scraper.Excavator	x	x	x	x		
1	*Siganus argenteus*	Grazer.Detritivore	x	x	x	x	x	x

Table S1. continued

TP	**Species name**	**Functional Group**	**Recovering**			**Regime-Shift**		
			'94	**'05**	**'14**	**'94**	**'05**	**'14**
1	*Siganus sutor*	Grazer.Detritivore				x		x
1	*Stegastes nigricans*	Grazer.Detritivore			x			
1	*Zanclus cornutus*	Invertivore	x	x	x	x	x	x
1	*Zebrasoma desjardinii*	Grazer.Detritivore	x	x	x	x	x	
1	*Zebrasoma scopas*	Grazer.Detritivore	x	x	x	x		x
2	*Acanthurus triostegus*	Grazer.Detritivore			x	x	x	x
2	*Apolemichthys trimaculatus*	Invertivore	x	x	x	x		
2	*Centropyge multispinis*	Invertivore	x	x	x	x	x	
2	*Chaetodon lunula*	Invertivore	x	x	x	x	x	
2	*Chaetodon xanthocephalus*	Invertivore	x	x		x	x	
2	*Chlorurus sordidus*	Scraper.Excavator	x	x	x	x	x	x
2	*Dascyllus trimaculatus*	Planktivore	x	x	x			
2	*Neoglyphidodon melas*	Invertivore	x	x		x		
2	*Pomacanthus imperator*	Invertivore	x	x	x	x		x
2	*Pomacanthus semicirculatus*	Invertivore	x	x	x	x	x	x
2	*Pomacentrus trilineatus*	Grazer.Detritivore	x	x	x	x	x	x
2	*Siganus puelloides*	Grazer.Detritivore	x	x	x	x	x	x
2	*Siganus stellatus*	Grazer.Detritivore	x	x	x	x	x	x
3	*Amblyglyphidodon leucogaster*	Planktivore	x	x	x	x		
3	*Anampses meleagrides*	Invertivore	x	x	x	x	x	x
3	*Bodianus axillaris*	Invertivore	x	x	x	x	x	x
3	*Cantherhines pardalis*	Invertivore	x	x	x	x	x	
3	*Chaetodon auriga*	Invertivore	x	x	x	x	x	x
3	*Chaetodon guttatissimus*	Invertivore	x	x	x	x	x	
3	*Chaetodon kleinii*	Invertivore	x	x	x	x	x	
3	*Chaetodon lineolatus*	Invertivore				x		
3	*Chaetodon melannotus*	Invertivore	x	x		x		
3	*Chaetodon meyeri*	Corallivore				x		
3	*Chaetodon trifascialis*	Corallivore	x		x	x		
3	*Chaetodon trifasciatus*	Corallivore	x	x	x	x	x	x
3	*Chaetodon zanzibarensis*	Corallivore	x	x	x	x		
3	*Cheilinus fasciatus*	Invertivore	x	x	x	x		
3	*Chromis atripectoralis*	Planktivore	x	x	x	x		
3	*Chromis ternatensis*	Planktivore	x	x	x	x	x	
3	*Chromis weberi*	Planktivore	x	x	x	x	x	
3	*Coris formosa*	Invertivore	x	x	x	x	x	x
3	*Gomphosus caeruleus*	Invertivore	x	x	x	x	x	x
3	*Halichoeres hortulanus*	Invertivore	x	x	x	x	x	x
3	*Halichoeres scapularis*	Invertivore	x	x	x			

Table S1. continued

TP	**Species name**	**Functional Group**	**Recovering**			**Regime-Shift**		
			'94	**'05**	**'14**	**'94**	**'05**	**'14**
3	*Hemigymnus fasciatus*	Invertivore	x	x	x	X	x	x
3	*Labrichthys unilineatus*	Corallivore	x		x	x		x
3	*Lethrinus harak*	Invertivore.Piscivore	x	x	x	x	x	x
3	*Lethrinus mahsena*	Invertivore.Piscivore			x	x	x	x
3	*Lethrinus obsoletus*	Invertivore.Piscivore	x	x	x	x	x	x
3	*Macropharyngodon bipartitus*	Invertivore	x	x	x	x	x	
3	*Monotaxis grandoculis*	Invertivore	x	x	x	x		
3	*Mulloidichthys flavolineatus*	Invertivore.Piscivore	x	x	x	x		x
3	*Novaculichthys taeniourus*	Invertivore	x	x	x	x	x	x
3	*Oxymonacanthus longirostris*	Corallivore	x	x	x	x		x
3	*Paracanthurus hepatus*	Planktivore						
3	*Parupeneus barberinus*	Invertivore	x	x	x	x	x	x
3	*Parupeneus ciliatus*	Invertivore.Piscivore	x	x	x	x		x
3	*Parupeneus macronemus*	Invertivore	x	x	x	x	x	x
3	*Parupeneus rubescens*	Invertivore				x		
3	*Plectroglyphidodon dickii*	Invertivore	x	x	x	x		x
3	*P. johnstonianus*	Invertivore	x	x	x	x		
3	*Scolopsis frenatus*	Invertivore	x	x	x	x	x	x
3	*Sufflamen chrysopterum*	Invertivore	x	x	x	x	x	x
3	*Thalassoma hardwicke*	Invertivore	x		x	x		x
3	*Thalassoma hebraicum*	Invertivore	x	x	x	x	x	x
3	*Thalassoma lunare*	Invertivore	x	x	x			
4	*Anyperodon leucogrammicus*	Piscivore	x	x	x	x		
4	*Cephalopholis leopardus*	Invertivore.Piscivore	x	x				
4	*Cephalopholis urodeta*	Invertivore.Piscivore	x		x			
4	*Cheilinus trilobatus*	Invertivore	x	x	x	x	x	x
4	*Epinephelus coeruleopunctatus*	Invertivore.Piscivore	x	x				
4	*Epinephelus fasciatus*	Invertivore.Piscivore	x	x	x	x	x	
4	*Epinephelus hexagonatus*	Invertivore.Piscivore						
4	*Epinephelus merra*	Invertivore.Piscivore	x	x		x	x	x
4	*Epinephelus spilotoceps*	Invertivore.Piscivore	x			x		
4	*Halichoeres cosmetus*	Invertivore	x	x		x	x	x
4	*Halichoeres marginatus*	Invertivore	x	x	x	x	x	x
4	*Hemigymnus melapterus*	Invertivore	x	x	x	x	x	
4	*Lethrinus enigmaticus*	Invertivore.Piscivore	x		x		x	x
4	*Lethrinus lentjan*	Invertivore.Piscivore		x	x	x	x	x
4	*Lethrinus nebulosus*	Invertivore.Piscivore	x	x			x	x
4	*Lethrinus rubrioperculatus*	Invertivore.Piscivore		x			x	

Table S1. continued

TP	Species name	Functional Group	Recovering			Regime-Shift		
			'94	'05	'14	'94	'05	'14
4	*Lutjanus bohar*	Piscivore	x	x	x	x	x	
4	*Lutjanus fulviflamma*	Invertivore.Piscivore	x	x	x	x		x
4	*Lutjanus gibbus*	Invertivore.Piscivore		x		x	x	x
4	*Lutjanus kasmira*	Invertivore.Piscivore	x		x	x		
4	*Oxycheilinus digramma*	Piscivore.Invertivore	x	x	x	x		
4	*Parupeneus trifasciatus*	Invertivore		x			x	x
4	*Plectorhinchus orientalis*	Invertivore			x	x		x
4	*Plectorhinchus schotaf*	Invertivore		x		x		x
4	*Stethojulis albovittata*	Invertivore	x	x	x	x	x	x
5	*Aethaloperca rogaa*	Invertivore.Piscivore	x	x	x		x	
5	*Cephalopholis argus*	Piscivore	x	x	x	x	x	x
5	*Cephalopholis miniata*	Piscivore	x	x	x	x	x	
5	*Epibulus insidiator*	Invertivore.Piscivore	x	x	x	x	x	x
5	*Labroides bicolor*	Invertivore	x	x	x	x	x	x
5	*Lethrinus olivaceus*	Invertivore.Piscivore					x	
5	*Lutjanus monostigma*	Invertivore.Piscivore		x		x		
5	*Macolor niger*	Invertivore.Piscivore	x	x	x	x	x	
5	*Parupeneus cyclostomus*	Invertivore.Piscivore	x	x	x	x	x	x
5	*Plectorhinchus gibbosus*	Invertivore.Piscivore						x

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).

	RECOVERING								**REGIME-SHIFTED**							
TP	**Avg.Diss**	**Species**	**Av. Abun'94**	**Av. Abun'14**	**Av. Diss**	**Diss /SD**	**Contrib %**	**Cum. %**	**Avg.Diss**	**Species**	**Av. Abun'94**	**Av. Abun'14**	**Av. Diss**	**Diss /SD**	**Contrib %**	**Cum. %**
1	**41.13**	*Scarus falcipinnis*	0.72	1.99	2.86	0.74	6.95	6.95	**59.82**	*Siganus sutor*	0.59	6.24	7.13	2.04	11.91	11.91
		Plectroglyphidodon lacrymatus	3.19	4.37	2.72	1.16	6.61	13.56		*Plectroglyphidodon lacrymatus*	5.16	0.72	5.92	1.26	9.9	21.81
		Hipposcarus harid	1.54	0.95	2.58	1.13	6.27	19.83		*Siganus argenteus*	2.75	3.49	5.11	1.15	8.54	30.35
		Acanthurus nigrofuscus	2.26	2.78	1.96	1.51	4.77	24.6		*Scarus prasiognathos*	4.79	2.19	4.13	1.63	6.9	37.25
		Scarus psittacus	1.47	2.81	1.86	1.17	4.52	29.12		*Chlorurus atrilunula*	1.08	2.74	2.77	1.36	4.63	41.89
		Scarus prasiognathos	3.72	3.07	1.83	1.42	4.46	33.58		*Zebrasoma desjardinii*	1.95	0	2.65	4.47	4.43	46.31
		Siganus argenteus	1.2	0.8	1.8	1.06	4.37	37.94		*Leptoscarus vaigiensis*	0	1.84	2.53	1.47	4.23	50.55
		Scarus rubroviolaceus	1.11	1.49	1.73	1.25	4.22	42.16								
		Ctenochaetus truncatus	1.82	1.41	1.72	1.14	4.18	46.34								
		Scarus frenatus	1.47	0.36	1.7	1.42	4.14	50.48								
2	**47.75**	*Pomacentrus trilineatus*	1.42	3.13	8.12	1.37	17.01	17.01	**49.54**	*Centropyge multispinis*	2.59	0	10.59	3.86	21.38	21.38
		Siganus puelloides	2.22	0.62	6.03	3.02	12.64	29.65		*Acanthurus triostegus*	1.41	1.26	5.05	1.12	10.19	31.56
		Siganus stellatus	1.69	0.36	4.79	1.26	10.03	39.68		*Pomacanthus semicirculatus*	1.7	1.29	4.82	1.08	9.72	41.29
		Chaetodon lunula	1.52	0.36	4.28	1.05	8.97	48.65		*Siganus puelloides*	2.41	1.24	4.73	1.06	9.55	50.84
		Dascyllus trimaculatus	1.31	0.51	3.97	1.15	8.32	56.96								
3	**38.21**	*Chromis atripectoralis*	5.57	4.82	3.45	1.31	9.02	9.02	**55.18**	*Chromis atripectoralis*	3.6	0	3.95	1.26	7.16	7.16
		Chromis ternatensis	4.07	0.79	2.89	1.14	7.56	16.57		*Chromis ternatensis*	2.69	0	2.98	0.92	5.41	12.57
		Oxymonacanthus longirostris	2.69	5.54	2.21	1.88	5.79	22.37		*Anampses meleagrides*	2.84	0.36	2.87	2.63	5.2	17.77
		Amblyglyphidodon leucogaster	3.02	1.8	2.03	1.33	5.32	27.69		*Chromis weberi*	2.43	0	2.82	0.94	5.12	22.88
		Lethrinus obsoletus	1.14	1.98	1.4	0.9	3.65	31.34		*Labrichthys unilineatus*	2.38	0.36	2.41	1.7	4.37	27.26
		Mulloidichthys flavolineatus	1.49	0.81	1.35	1.26	3.54	34.88		*Oxymonacanthus longirostris*	2.96	1.23	2.37	1.55	4.3	31.56
		Labrichthys unilineatus	1.65	2.62	1.29	1.45	3.37	38.26		*Cantherhines pardalis*	1.99	0	2.32	4.98	4.21	35.77
		Chromis weberi	3.7	2.76	1.19	1.33	3.12	41.37		*Plectroglyphidodon dickii*	2.25	0.36	2.27	1.48	4.12	39.89
		Chaetodon auriga	1.66	0.51	1.19	1.63	3.12	44.49		*Amblyglyphidodon leucogaster*	1.88	0	2.08	1.18	3.77	43.66
		Macropharyngodon bipartitus	0.42	1.7	1.16	1.54	3.05	47.54		*Chaetodon melannotus*	1.65	0	1.8	1.86	3.26	46.93
		Plectroglyphidodon dickii	1.59	1.44	1.06	1.13	2.76	50.31		*Gomphosus caeruleus*	1.99	1.59	1.52	1.51	2.75	49.68
										Lethrinus obsoletus	1.33	0.36	1.4	1.15	2.54	52.22
4	**42**	*Lutjanus fulviflamma*	1.69	0.36	4.6	1.14	10.96	10.96	**57.09**	*Lethrinus nebulosus*	0	2.26	5.95	1.02	10.42	10.42
		Hemigymnus melapterus	0.36	1.92	4.48	2	10.66	21.62		*Plectorhinchus schotaf*	1.31	1.95	5.52	0.97	9.67	20.09
		Cephalopholis urodeta	0.84	1.48	3.25	1.32	7.75	29.37		*Lutjanus bohar*	1.83	0	4.89	5.13	8.57	28.66
		Lutjanus bohar	0.36	1.08	2.8	1.1	6.67	36.04		*Oxycheilinus digramma*	1.48	0	3.88	1.69	6.8	35.46
		Epinephelus fasciatus	0.76	0.72	2.54	0.96	6.05	42.09		*Lutjanus gibbus*	1.7	0.72	3.87	1.24	6.77	42.23
		Lethrinus enigmaticus	0.36	0.72	2.43	0.68	5.78	47.87		*Lutjanus fulviflamma*	1.09	1.35	3.67	1.17	6.43	48.66
		Lethrinus lentjan	0	0.93	2.35	0.49	5.59	53.46		*Halichoeres cosmetus*	0.72	1.71	3.44	1.26	6.03	54.68
5	**39.98**	*Labroides bicolor*	1.88	0.72	8.4	1.23	21.02	21.02	**71.97**	*Parupeneus cyclostomus*	1.35	0.36	18.13	0.66	25.19	25.19
		Epibulus insidiator	1.84	1.29	6.49	1.06	16.24	37.26		*Epibulus insidiator*	1.46	1.17	16.11	0.59	22.39	47.58
		Aethaloperca rogaa	1.14	1.08	6.35	0.97	15.89	53.15		*Cephalopholis argus*	1.17	1.14	11.82	0.92	16.42	64

Appendix D: Supplemental information for Chapter 5

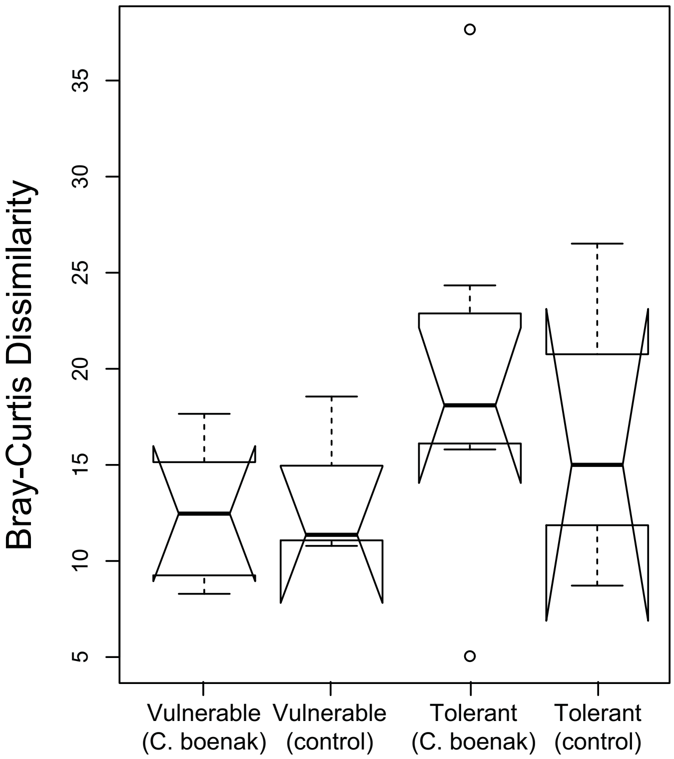


Fig. S 1 Notched boxplots of Bray-Curtis dissimilarity between fish communities on patch reefs prior to the introduction of a mesopredator (*Cephalopholis boenak*) to each reef, and six weeks later when the *C. boenak* were removed. Within each coral assemblage treatment (vulnerable vs tolerant, n = 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.

Appendix E: Copyright permissions

Fig. 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

Fig. 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

Hempson, T. N., N. A. J. Graham, M. A. MacNeil, D. H. Williamson, G. P. Jones, and G. R. Almany. 2017. Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecology and Evolution:1–10.

Other peer-reviewed articles published during PhD candidature

Marques da Silva, I., T. Hempson, and N. E. Hussey. 2014. Giant trevally spawning aggregation highlights importance of community fisheries management no-take zone. Marine Biodiversity. DOI 10.1007/s12526-014-0235-2