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DEPTH AS REFUGE: DEPTH GRADIENTS IN ECOLOGICAL PATTERN, PROCESS, AND RISK MITIGATION AMONG CORAL REEF FISHES

Thesis submitted by

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STATEMENT OF CONTRIBUTION FROM OTHERS

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Declaration

This dissertation is the result of my own work and includes nothing, which is the outcome of work done in collaboration except where specifically indicated in the text. It has not been previously submitted, in part or whole, to any university of institution for any degree, diploma, or other qualification.

Signed:

Date: 26/10/2018

GENERAL ABSTRACT

The impacts of anthropogenic habitat disturbance are often asymmetric along environmental gradients and among taxa. For species that cannot successfully utilize post disturbance habitats, the ability to occupy positions on spatial gradients that fall outside of disturbance regimes may offer a key refuge. However, decreasing resource availability or quality, and changing ecological and behavioural dynamics along gradients may result in substantial physiological costs for fringe-dwelling organisms. Assessments of potential refuges therefore require nuanced spatially gradated ecological assessments that are often absent and difficult to attain.

Coral reefs are now heavily impacted by climate related disturbance, and the greatest rates of biotic attrition among reef fishes generally occur within species obligated to associate with live corals. Because key drivers of future coral loss (i.e. warm water bleaching and storm events) may attenuate with depth, deep reefs hypothetically offer a refuge to vulnerable fishes. However, because of access difficulties, most ecological studies on coral reef organisms occur in shallow waters of <15 m.

In **Chapter 2**, I investigated the natural depth distributions, depth-related variation in community structure and coral habitat associations for 123 reef fish species at 6 depths between 0m and 40m, and from inner-bay to offshore reefs. The results indicated that depth is a stronger driver of reef fish assemblages than cross shelf gradients, though complex coral habitats and some associated fish species more frequently occupy deeper depths further from shore. Total live hard coral cover did not decline with depth in Kimbe Bay, though the cover of habitat-providing complex corals declined with depth. The major break in the community assemblage of reef fishes occurred between 5 m and 10 m, and 25% of species were limited to the shallowest 5m. However, 25% of species occurred at all depths between 0m and 30m, and 12% between 0m and 40m. In addition, I show that 85% of species with strong associations with live complex coral habitats occurred at depths of 20m or below. I therefore conclude that deep reef habitats in Kimbe Bay can provide a substantial refuge potential if reef degradation does attenuate with depth and the ecological costs of occupying deep periphery habitats are not prohibitive to long-term population maintenance.

In **Chapters 3 to 6,** I utilized the Chaetodontidae family (Butterflyfishes) to further investigate how a broad suit of behaviours and ecological dynamics that influence the distribution, vulnerability and success of a wide range of taxa in multiple biomes interrelate and vary among reef fishes along a broad coral reef depth gradient, from 0 – 40 m.

Interrelationships among distribution breadth, abundance, and degree of resource specialization form the basis of many general models in ecology, as well as extinction-risk assessments in conservation biology. Species with narrow distributions, low abundance and high resource specialisation are more vulnerable to environmental change and risk increases when vulnerability traits are combined. In **Chapter 3**, I evaluate whether depth may mediate these risks in coral-specialist fishes. Contrary to expectation, the most coral-specialized species were also the most abundant and the most broadly distributed. Further, no specialist-species had combined vulnerability traits, and no specialists were wholly restricted to shallow-water. Chapter 3 demonstrates that interrelationships among vulnerability traits and occupancy depths do not necessarily follow traditional ecological expectations on coral reefs, but they do work to mediate substantial risks for species vulnerable to shallow-reef habitat declines.

Chapters 2 and 3 demonstrate that many ecologically vulnerable reef fish species may offset the risks associated with shallow-water habitat losses by utilising deep habitats. However, the refuge potential of deep peripheral habitats may be mediated by the potentially substantial costs of securing sparsely distributed resources, which can limit survival and reproductive output. Further, depth-related resource shifts are likely to be more detrimental to dietary specialists than to generalists. In **Chapter 4**, I use extensive and intensive in-situ behavioural observations in combination with physiological condition measurements to examine the costs and benefits of resource-acquisition along the depth-gradient in two obligate corallivore reef fishes with contrasting levels of dietary specialisiation. I demonstrate that the space utilised to secure coral-resources increases towards deeper depths, as expected. However, increased territory sizes result in equal or greater total resources secured within deep territories. Foraging-distance, pairing-behaviour, body condition and fecundity did not decline with depth, but competitive interactions did. Unexpectedly, therefore, coral-specialist fishes selecting high-quality coral patches in deep water access equal or greater resources than their shallow-reef counterparts, with no extra costs.

As demonstrated in **Chapter 4**, the capacity for species to successfully occupy range peripheries is enhanced by their ability to mediate costs related to decreases in quantities and quality of key resources. In **Chapter 5**, I investigate the capacity to of species to employ variation in dietary strategies and energy acquisition along depth gradients. I focus on two obligate corallivores with differing levels of dietary specialization, as well as their mixotrophic coral prey. Total resource availability and total feeding effort did not decline toward deep-range peripheries in either fish species, but availability of preferred *Acropora* resources did decline. The more specialized species exhibited limited feeding plasticity along the depth gradient, and selective feeding effort on the preferred coral genus *Acropora* increased rather than decreased with depth. In contrast, the generalist's diet varied greatly with depth, reflecting changes in prey composition. Unexpectedly, the nutritional content of *Acropora* did not decline with depth, with shifts in δ^{13}C and δ^{15}N indicating increased coral heterotrophy in deeper water may offset declines in light energy. Mixed modelling of stable isotopes in amino acids of fish muscle tissue revealed a parallel increase in plankton-sourced carbon among deep-resident fish. Therefore, deep ranges appear to be supported by multiple mechanisms of dietary versatility, but for specialist species this versatility occurred at the resource level (corals), rather than among the consumers (fish). This dietary variability and trophic plasticity may act to buffer costs and bolster refuge potentials associated with dwelling at deep range peripheries, even among taxa with differential functional strategies.

In **Chapter 6**, I utilize two natural experiments to 1) demonstrate that a natural habitat disturbance event (a crown of thorns sea-star outbreak) can result in differential impacts and outcomes on shallow and deep populations of the coral obligate reef fish *Chaetodon baronessa* that favour the persistence of deep population; and 2) individual fishes are able to migrate downward, away from territories in degrading shallow-water habitats to inhabit healthy deep-reef habitats when made available via experimental competitor removal.

Overall, my thesis highlights how interrelationships among vulnerability traits, occupancy depths, and deep coral habitats, offer some risk mitigation among taxa currently thought to express high vulnerability to global-scale coral declines in shallow-water. The thesis further demonstrates how various combinations of stability and plasticity in resource specialization, space use, effort, food availability and quality, diet, feeding behaviour, and body condition, may aid the successful exploitation of deep refuges by species with contrasting functional traits. Finally, severe habitat disturbance can differentially impact fish and habitat survival between shallow and deep reefs, and individual fish are demonstrably able to utilize downward vertical migration away from declining shallow-water habitat to access higher-quality deep-water habitats where prior residence is not established.

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LIST OF ABBREVIATIONS AND ACRONYMS

AICc – Akaike's Information Criteria for small sample sizes

ANOVA – Analysis of Variance

CI – Confidence Interval

CPCe – Coral Point Count with excel extensions

FAC – Facultative coral feeding reef fish

GAM – Generalised Additive Model

GBR – Great Barrier Reef

GLM – Generalised linear model

GLMM – Generalized linear Mixed effects Model

GSI – Gonad-Somatic Index

HCC – Hard Coral Cover

HOF – hierarchical logistic regression model; named for Huisman, Olff, & Fresco

HSI – HepatoSomatic Index

K – Fulton's condition metric

LM – Linear Model

lme – linear mixed effects model

MDS – Mutli-Dimension Scaling

NON – Non coral feeding reef fish

NS – Non-Significant

OBL – Obligate coral feeding reef fish

PNG – Papua New Guinea

SD – Standard Deviation

SE – Standard Error

SIAb – Bulk Stable Isotope Analysis

SIAcs – Compound specific (amino acid) Stable Isotope Analysis

SWG – Shallow Water Geographic range study

TL – Total Length

TSRA – Total Secured Resources (Acropora corals)

TSRT – Total Secured Resources (total-corals)

W – Weight

LIST OF APPENDICES

Chapter 1 - GENERAL INTRODUCTION

Rapid climate change is causing range contractions and displacements of many species, increasing extinction risks in most taxonomic groups and degrading ecosystems in most of the earth's biomes (Parmesan and Yohe 2003, Thomas et al. 2004, Lenoir and Svenning 2015, Scheffers et al. 2016, Pecl et al. 2017). Many currently extant species radiated from organisms that survived past global-scale environmental change (e.g. Quaternary glacial cycles) in cryptic refugia at range peripheries (Stewart and Lister 2001, Provan and Bennett 2008). Successful persistence in small peripheral refuges (Scheffers et al. 2014), is likely to be important for many species' long-term resilience to asymmetric impacts from current rapid climate changes (Ashcroft 2010, Keppel et al. 2012). Therefore, investigating the functional characteristics of 1) range margins' as potential refuge locations, and 2) the species that are most likely to benefit from this potential, is an increasingly important component of ecology in the Anthropocene.

Understanding patterns in species distributions is fundamental to assessing exposure risks and resilience potentials in response to environmental change. Most species have distributions that follow environmental gradients such as latitude, altitude and depth (Schall and Pianka 1978, Gaston 2000, Connolly et al. 2003). These distributions are linked to changes in the physical environment (e.g. temperature, rainfall, light and nutrient availability), gradients in biotic habitat structure (e.g. vegetation type or canopy height) (Gaston 2000, Hawkins et al. 2003), and the interrelationships among these gradients and species' functional strategies (Cogbill and White 1991, Poorter 1999, Lavorel and Garnier 2002, McGill et al. 2006). A full understanding of species' distributions and distribution drivers therefore requires investigations of trait-specific responses to gradients in several environmental dimensions. For example, hypothetical frog populations living in mountainous environments may express greater resilience to warming temperatures than low-land populations. This is because they have the possibility of occupying a broader elevational range. Moreover, certain functional traits such as particular habitat associations will predispose some species groups to better express this resilience capacity than others.

Vulnerability assessments in conservation biology are often formed around commonly recurring ecological interrelationships among distribution breadth, abundance and degree of resource specialisation (Rabinowitz 1981, Gaston et al. 1997, Gaston et al. 2000, Julliard et al. 2004, Graham et al. 2011). Species with small distributional ranges, low local abundance or high levels of resource specialization, are particularly susceptible to localized disturbances (McKinney 1997), the risks of small population size (Williams et al. 2008), and declining resources (Gaston et al. 1997). Most often, narrow species ranges are related to lower overall abundances (Hanski 1982, Brown 1984, Swain and Wade 1993, Gaston 1996, Gaston et al. 1997, Lawton 1999, Frisk et al. 2011), and resource specialists often have low abundances and narrow ranges, due to the limited distribution and abundance of their prey (Gaston et al. 1997, Lawton 1999, Harcourt et al. 2002). Where these generalizations hold and interact, extinction risk can compound to form a 'double jeopardy' or 'triple jeopardy' (e.g. Harcourt et al. 2002, Munday 2004, Swartz et al. 2006, Hughes et al. 2014). However, where they do not (e.g. Roberts and Hawkins 1999, Hawkins et al. 2000, Munday 2004, Graham et al. 2011), species may mitigate some of the risks associated with rapid and drastic environmental change. This potential may be particularly strong where otherwise vulnerable species have peripheral populations whose distributions do not overlap with the most disturbed habitats in their range.

Species presence at marginal positions along environmental gradients does not always relate to individual success or long-term population viability (Booth et al. 2007, Figueira and Booth 2010, Booth et al. 2011, Feary et al. 2014). The potential for peripheral habitats to act as refuges depends not only on a species' capacity to survive in or disperse to those environments, but also on habitat quality and individual performance at these ecological extremes. While species' realized-niches are ideally centred on regions of optimal performance along gradients (e.g. González-Guzmán and Mehlman 2001, McGill et al. 2006), source-sink dynamics, density-dependence, and intra-trophic competition cause species to extend beyond ideal niches (Terborgh 1977, Lawton 1993, Pulliam 2000). At range margins, habitats and populations often become more fragmented (Brown 1984, Thomas and Kunin 1999), occupancy decreases (Kawecki 2008), and there are natural reductions in the quantity and or quality of resources (Brown 1984, Thomas and Kunin 1999). These changes often result in costs to consumers, including both lethal (lower life expectancy) and sublethal (reduced reproductive potential, lower condition) responses (Zammuto and Millar 1985, Badyaev and Ghalambor 2001, Smallhorn-West et al. 2017). Understanding key processes at range margins, including the ecological factors that limit individual fitness and population viability, the capacity for flexible behavioural responses and potential compensatory mechanisms of energy acquisition, will be vital to predicting future trajectories for many species vulnerable to extirpation and extinction.

For "energy maximizing" species (Hixon 1982), the ability to persist in marginal habitats, such as range peripheries, is likely to be reliant on flexible diets or feeding rates (Flesch and Steidl 2010, Yeager et al. 2014). Consequently, shifts in resource availability in response to disturbances and environmental gradients, tend to result in shifts in consumer communities that favour resource generalists over specialists (Clavel et al. 2011). Comparisons of dietary strategies and trade-offs at range peripheries among species with differential specialization is, therefore, a promising way of studying the ecological mechanisms that drive broad distributions and refuge potential at range margins.

Coral reefs offer an ideal system for assessing ecological changes along environmental and resource gradients. Steep gradients in light energy, decreased photosynthetic ability, and rapid turnover in the composition of coral communities with depth are likely to result in declines in the quantity and quality of resources available to coral consumers (Crossland et al. 1980, Crossland 1987, Anthony et al. 2002, Einbinder et al. 2009, Roberts et al. 2015). Moreover, although coral reefs are increasingly affected by anthropogenic climate change (Bellwood et al. 2004, Hughes et al. 2018), many stressors attenuate with depth (Marshall and Baird 2000, Hughes et al. 2010, Bridge et al. 2016, Muir et al. 2017, Baird et al. 2018). As light decreases, coral assemblages and morphologies change, resulting in reductions in complex branching forms that are key habitat providers for coral reef organisms (Coker et al. 2012). Moreover, energetic changes are likely to occur along the light/depth gradient, such as changes in energy acquisition and utilisation (Anthony and Fabricius 2000, Anthony et al. 2002, Alamaru et al. 2009, Einbinder et al. 2009). Because water quality is often poorer near the coast (e.g. Fabricius et al. 2005, Death et al. 2012), depth related effects of habitat and community structure may also vary with distance from shore.

Deep-reefs could offer a potential refuge for coral reef fishes vulnerable to shallow-reef habitat loss (Jankowski et al. 2015, Bridge et al. 2016), and fishes with broad depth ranges are considered at lower risk of extinction than species restricted to shallow depths (Graham et al. 2011). The ecological, behavioural, and condition responses of coral-dependent fishes to coral declines in shallow water are well established. Low densities of preferred coral genera are related to increased space use, increased effort in resource protection, and changed social dynamics (Hourigan 1989, Tricas 1989, Wrathall et al. 1992, Righton et al. 1998, Berumen and Pratchett 2006), as well as increased sub-lethal costs, including lower reproductive output (Kokita and Nakazono 2001, Pratchett et al. 2004, Berumen et al. 2005), with some coral-specialists experiencing double or triple jeopardy, and local or near-global extinctions (e.g. Munday 2004). However, if similar dynamics occur along depth gradients, sub lethal costs resulting in inadequate reproduction or recruitment (for example) may mitigate the refuge potential of deep reefs.

Numerous studies have examined depth distributions and the factors affecting them, but mostly over limited depth ranges of just a few meters (McGehee 1994a, Nanami et al. 2005). The few studies that have extended into deeper water on coral reefs suggest that both fish density and diversity decline with increasing depth (Bouchon-Navaro 1981, Friedlander and Parrish 1998, Brokovich 2008, Garcia-sais 2010, Jankowski et al. 2015). Moreover, depth stratification of species and assemblages, including during larval and settlement phases (Leis 1991, Huebert et al. 2011), is likely to strongly influence differential depth-related resilience benefits among taxa and functional groups (Brokovich et al. 2009, Graham et al. 2011). Due to the difficulty and time limitations of deep-water diving, however, there is a paucity of detailed ecological data among vulnerable taxa with extensive depth ranges on coral reefs (but see Srinivasan et al. 2003, Smallhorn-West et al. 2016) This has lead assessments of extinction threats, and commentary on the potential ability of depth to provide refuge for reef fish, to largely assume intraspecific ecology is static along steep depth gradients (Hawkins et al. 2000, Graham et al. 2011, Darling and Côté 2018) (but see Goldstein et al. 2016a, 2016b, 2017). However, this assumption has not been tested in strongly coral associated fishes.

Butterflyfishes, one of the most abundant and ecologically understood coral reef fish families, offer an ideal model group to assess dietary variation and plasticity responses to environmental and resource gradients among contrasting functional strategies (Nowicki et al. 2013). Butterflyfish occupy a broad spectrum of dietary specialization on corals and their feeding bouts are conspicuous, so it is possible to record proportional feeding effort on different resource types at the core and periphery of their ranges (Cole and Pratchett 2013, Pratchett 2013). More specialized coral feeders are known to be vulnerable to population declines due to coral loss (Pratchett et al. 2006, Wilson et al. 2006). Therefore, specialist corallivorous butterflyfishes are both vulnerable to anthropogenic coral loss, and gradients in their species distribution, environmental productivity, and disturbance exposure are likely to decline in parallel along a depth gradient. However, it is unknown whether the ecological strategies of coral-obligate fish observed in shallow waters are maintained along the extensive depth gradients most likely to confer increased resilience.

The overarching aim of this thesis was to understand the patterns and limiting processes of natural depth distributions in coral reef fishes and investigate depth-related ecological changes that may aid or hinder the ability of strongly coral associated species to succeed in deep reef environments. I hypothesize that deep reefs will show strong potential to act as refuges if: 1) Many species have broad or deep depth distributions, 2) Ecologically vulnerable species are not limited to shallow waters, 3) Deep-reef residents can efficiently secure resources without suffering sub-lethal costs, 4) Depth related resource changes are met by dietary plasticity or other compensatory mechanisms, 5) Deeper reef assemblages are more resilient to coral loss, and individuals from degrading shallow water environments can benefit from healthy deep-reef habitats. Kimbe Bay in Papua New Guinea is a low latitude reef system with abundant spread across a gradient from fringing reefs heavily influenced by terrestrial inputs through to offshore reefs in clear water with hard coral growth in depths >60 m. The occurrence of reefs with similar geomorphology across the bay provides an ideal location to examine changes in fish distributions, ecology, behaviour and condition across environmental gradients.

In **chapter 2**, I quantify what portion of a large part of the reef fish assemblage are limited to shallow waters and characterize the distributions, community structure, and habitat relationships of 123 coral reef fish species along depth (0 m - 40 m) and inshore-offshore gradients in Kimbe Bay, Papua New Guinea. Specifically, I use depth stratified abundance measures test whether: (1) reef fish abundance and diversity decline with depth and increase away from the shore. (2) individual species exhibit depth preferences within their overall depth range that result in distinct assemblages between depth strata, and whether these assemblages also extend deeper offshore. (3) whether coral habitat cover declines and structural characteristics change with increasing depth and distance from shore, with greater availability of deep complex coral habitat further offshore. (4) whether depth distributions of overall fish density, and of coral-associated fish species are limited by the availability of complex coral habitat. and (5) whether coral-fish associations decline with increasing depth.

In **chapter 3**, I use density distributions and trait measures to investigate the influence of pairwise interrelationships between dietary specialization, abundance and depth-range in 26 sympatric butterflyfish species along the same depth gradient. I further use quantitative modelling to examine whether species with vulnerability-conferring traits (i.e. High dietary specialisation, low abundance, and narrow depth distribution) are particularly associated with shallow-reef habitats and therefore greater exposure to habitat degradation. Specifically, I test the following questions: (1) Are species with broad depth distributions more abundant? (2) Are species and trait groups with broad depth distributions diet generalists? (3) Are diet generalists more abundant than diet specialists, and is this relationship stable along a depth gradient? (4) Are species with narrow ranges, low abundances, or high dietary specialization, restricted to shallow waters? And, does overlap occur among these traits? (5) Are distributions of dietary specialists skewed toward shallow water more than dietary generalists?

In **chapter 4**, I utilise an intensive set of insitu observational studies to quantify the behavioural and physiological costs of living at deeper depths and how this differs between specialist and generalist coralivores. First, I measure territory sizes along a depth gradient from 0 – 30m in two corallivorous butterflyfishes (*Chaetodon baronessa* and *C. octofasciatus*) and investigate depth related patterns in space use and resource access. I then quantify competitor densities, the number of competitive interactions, foraging distances and time spent pairing for each of the focal territories to examine depth related changes in ecology related to resource access. Finally, I measure five commonly used body condition metrics from individuals within these territories to examine potential physiological costs of living at the deep range margin. Specifically, I test whether 1) individuals' space use increased with depth; 2) lower resource densities resulted in fewer secured coral resources in deeper territories; 3) decreased resource availability led to behavioural costs related to accessing and securing resources at depth; and 4) individual body condition, energy storage and fecundity declined with depth.

In **chapter 5**, I utilise comprehensive feeding observations of the same individuals from these two obligate coral feeding species to examine whether flexibility in diets or feeding rates along the depth gradient could drive broad depth distributions and therefore increased resilience potential. I further use stable isotope analyses and lipid extractions from coral tissues to investigate whether compensatory mechanisms of energy provision in corals, and energy acquisition in their consumers, may occur at deep range-peripheries. Specifically I investigate whether: 1) Depth patterns occur in overall resource quantity and feeding effort, 2) Changing resource composition along the depth gradient results in dietary flexibility, 3) A reduction of feeding effort, on and selectivity for, preferred resources occurs at depth, and 4) compensatory mechanisms of energy provision in corals, and energy acquisition in their consumers may occur at the deep range periphery.

In **chapter 6**, I utilize a natural experiment to investigate whether deep-reefs can in fact provide refuge from habitat disturbance events, resulting in differential impacts and post disturbance outcomes among shallow and deep populations of the coral-obligate butterflyfish species *Chaetodon baronessa*. I further utilise a depth stratified tagging and competitor removal experiment in combination with naturally forced shallow-water habitat disturbances to test whether individual fishes in this species can migrate downward, away from degrading shallow-water habitats and inhabit an availability of healthy deeper-reef habitats. Finally, I use depth stratified observations of settlement and pre-adult density distributions to examine whether natural settlement patterns might be limited to shallow-water habitats.

Chapter 2 - DEPTH, BAY POSITION AND HABITAT STRUCTURE AS DETERMINANTS OF CORAL REEF FISH DISTRIBUTIONS: ARE DEEP REEFS A POTENTIAL REFUGE?

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Abstract

Increasing disturbance frequency and severity on coral reefs has caused declines in the abundance of structurally complex corals and many fish species that depend on them. However, most studies have focused on the shallowest 10 m, despite coral habitat extending to >30 m in many regions. Reefs in deeper water and offshore locations are less exposed to many stressors associated with coral decline and may offer a refuge for coral-associated fishes. Understanding how distributions and species-specific fish-habitat relationships vary along depth and distance-from-shore gradients is critical for assessing refuge potential. Here I examined the community structure, distributions and coral habitat associations of 123 reef fish species along a depth-gradient from <1 m to 40 m, from coastal to offshore reefs in Kimbe Bay, Papua New Guinea. Overall fish density and species richness declined with increasing depth but increased with distance offshore, such that deep offshore assemblages supported similar richness to shallow inshore sites. The most distinctive fish assemblage occurred at depths <1 m and ~25% of species were observed only in shallowest 5 m. However, ~60% of species occurred at or below 20 m and 24% were broadly distributed from <1 m to 30 m, with depth ranges of many species increasing with distance offshore. Strong relationships between fish abundance and coral habitat were observed, and 85% of species that were strongly associated with coral occurred at depths ≥20 m. My results suggest that while many species are restricted to vulnerable shallow depths, deep offshore reefs provide a potential refuge for a substantial proportion of coral-associated fish threatened by degradation of shallow coastal reefs and should be afforded greater consideration for conservation planning of coral reef fishes.

Introduction

Most species are distributed unevenly along environmental gradients such as latitude, altitude and depth (Schall and Pianka 1978, Gaston 2000, Connolly et al. 2003). These distributions are usually linked to either changes in the physical environment (e.g. temperature, rainfall, light and nutrient availability) or gradients in biotic habitat structure, such as vegetation type or canopy height (Gaston 2000, Hawkins et al. 2003). The extent to which a species' distribution is a response to either physical or biological factors is often unknown (e.g. Karr and Freemark 1983, Martin 2001), but may be elucidated through a detailed analysis of covariance between species, environmental and habitat variables. Species distributions are often influenced by multiple gradients and may reflect the interactions among them; for example, plants may have extended altitudinal ranges in warmer tropical environments (Cogbill and White 1991). A full understanding of species' distributions therefore requires an understanding of responses to gradients in several environmental dimensions. Understanding the influence of these important distribution drivers is becoming increasingly pertinent as species ranges are increasingly impacted by climate change (Parmesan and Yohe 2003, Poloczanska et al. 2013).

In aquatic environments, water depth represents a steep physical gradient that influences the distributions of many taxa. On tropical coral reefs, reef associated fishes are often restricted to particular depths and major changes in species composition can occur over narrow depth ranges of just a few meters (McGehee 1994, Nanami et al. 2005). Similar changes can occur along horizontal gradients from coastal to shelf-edge reefs (Williams 1982, Wismer et al. 2009, Emslie et al. 2010). To date, most studies on the factors affecting reef fish distributions have occurred in shallow water, where distributions are strongly influenced by benthic habitat structure, and particularly by the availability of live coral habitat (e.g. Bell and Galzin 1984, Syms and Jones 2000, Jones et al. 2004). The diversity (Roberts and Ormond 1987, Messmer et al. 2011), morphology (Nanami et al. 2005), and structural complexity (Luckhurst and Luckhurst 1978, Coker et al. 2012, Noonan et al. 2012) of coral habitats also strongly influence reef fish assemblages in shallow water.

The few studies that have extended into deeper water on coral reefs suggest that both fish density and diversity decline with increasing depth (Bouchon-Navaro 1981, Friedlander and Parrish 1998, Brokovich 2008, Garcia-sais 2010, Jankowski et al. 2015). However, fish assemblages in depths >15 m remain poorly described in most regions. The extent to which shallow-water fish-habitat associations are maintained at greater depths, and consequently the extent to which species' depth ranges are limited by habitat availability is currently unknown. Coral distributions and benthic habitat structure vary along depth gradients in response to decreasing light, temperature and wave energy (Done 1982, Kleypas et al. 1999, Roberts et al. 2015). In clear tropical waters, many coral species occur to depths of 50 m or more (Jarrett et al. 2005, Bridge et al. 2013, Muir et al. 2015). Greater light penetration and reduced terrestrial influence offshore (De'ath and Fabricius 2001, Fabricius et al. 2016) may enable complex coral habitats to occur at greater depths (e.g. Muir et al. 2015). If fish distributions are determined by habitat structure, deeper habitats in clear-water offshore locations could be expected to support greater fish diversity and abundance, with species exhibiting greater depth ranges further offshore.

Understanding the mechanisms underlying cross-shelf and depth distributions is becoming increasingly important as shallow and near-shore reefs become more degraded by climate change impacts and coastal development (e.g. Fabricius et al. 2005, Death et al. 2012). Shallow coral reefs have experienced ongoing widespread degradation, including declines in coral cover and structural complexity, and changes in benthic composition (Hughes et al. 2003, Wilkinson 2004, McWilliams et al. 2005). These habitat shifts have resulted in large-scale, long-term, multi taxon declines in reef fish abundances (Jones et al. 2004, Wilson et al. 2006, Wilson et al. 2009), temporally stable shifts in fish communities (Bellwood et al. 2012), and local extinction of highly-specialized coral-dependent species on shallow near-shore reefs (Munday 2004, Wilson et al. 2006). Disturbances such as coral bleaching and storm damage can attenuate relatively quickly with increasing depth (Bridge et al. 2013, Smith et al. 2014), and depth range is identified as a key factor both for mitigating extinction risk in corals and coral reef fishes (Carpenter et al. 2008, Graham et al. 2011) and for predicting recovery of reefs following disturbance (Graham et al. 2015). However, understanding species' potential for utilising deep-reef refuges requires accurate information on how species distributions, abundances and fish-habitat associations change along both depth and inshore-offshore gradients.

Here I characterize changes in coral reef fish distributions and their relationship with habitat structure along depth and inshore-offshore gradients in Kimbe Bay, Papua New Guinea. Kimbe Bay is a low latitude reef system with abundant spread across a gradient from fringing reefs heavily influenced by terrestrial inputs through to offshore reefs in clear water with hard coral growth in depths >60 m. The occurrence of reefs with similar geomorphology across the bay provides an ideal location to examine changes in fish distributions across environmental gradients. Specifically, I test whether: (1) reef fish abundance and diversity decline with depth and increases away from the shore, particularly at depths >10 m; (2) individual species exhibit depth preferences within their overall depth range that result in distinct assemblages between depth strata, and whether these also extend deeper offshore; (3) whether coral habitat cover declines and structural characteristics change with increasing depth and distance from shore, with greater availability of deep complex coral habitat further offshore; (4) whether depth-related distributions of overall fish density, and of coral-associated species are limited by the availability of complex coral habitat; and (5) whether coral-fish associations decline with increasing depth.

Methods

Study site

The study was undertaken in Kimbe Bay, Papua New Guinea (5° 30' S, 150° 05' E) during April-May of 2013, and June 2014. Ten reefs were surveyed from three positions across the bay ('Bay position'): 3 inshore, 4 mid-bay, 3 offshore reefs (Fig. S2.1). Inshore reefs were <1km from the coast, while mid-bay and offshore reefs experience progressively clearer water with less terrestrial influence. Inshore reefs in Kimbe Bay experienced high coral loss a decade previously (see Jones et al. 2004, Munday 2004, Gardiner & Jones 2005) and are currently in advanced stages of recovery but experience ongoing low level pulse perturbances. All reefs in the region consist of continuous reef substratum with abundant hard coral growth well beyond the maximum study depth, and therefore present no physical barriers to fish migration among depths. The maximum depth of scleractinian coral growth on Kimbe Bay reefs is unknown but extends to >60m in some cases (Pers. obs.).

Data collection

At each reef, divers recorded high definition digital video transects for both fish (30 m x 4 m) and benthic data (30 m x 1 m) at each of five depths: <1 m, 5 m, 10 m, 20 m and 30 m, transects were also recorded at 40m on two outer bay reefs. Four to six replicates were recorded for each depth at each reef (Table S2.1). Cameras faced forward for fish transects and directly into the reef for benthic transects. Transect widths were determined by pre-filming metric grids laid along the benthos. The use of video lights, a cyan balancing light-filter, high definition (1400 pixels) and high frame rates (60 frames per sec.) allowed on-screen identification of targeted taxa at all depths.

Reef fish from four non-cryptic, speciose and ecologically varied families (Pomacentridae, Chaetodontidae, Pomacanthidae and Acanthuridae) were identified to species based on Allen et al. (2003) and counted within a standardized lower section of the screen. Slower playback speeds and repeat viewings were used where species identification was not initially clear or large aggregations occurred. In the latter instance, counts were repeated, and consensus or mean abundance was used. If fish left the frame partially or entirely and re-entered immediately in the same position they were not counted again, otherwise all fish entering the frame were considered a new individual. Species richness was recorded as the total number of species observed within the four fish families in each transect.

The proportional cover of 10 benthic groups (massive coral, encrusting coral, laminar coral, complex coral, turf algae, crustose calcareous algae, sponges, coral rubble, sand and silt, and reef matrix) was recorded utilizing ‘Coral Point Count with excel extensions’ (Kohler and Gill 2006). Complex corals were defined as those considered to be most suitable complex habitat for the sheltering of small reef fishes. This included all branching, corymbose, hispidose, digitate, foliose and tabulate forms, but not laminar, massive, sub-massive or encrusting corals. Sixty random points were generated for each transect (six random points assigned within ten video frames extracted using a stratified-random design - equivalent to ten 1m^2 quadrats per transect, spaced approximately three linear meters apart), and the benthic component directly under each point was recorded.

Data analysis

Influences of depth and position on reef fish density and species richness

The total abundance and species richness of reef fish were tested for unequal distribution between depths (fixed factor) and bay positions (fixed factor), after accounting for differences between reefs (random factor nested within bay position) using Log$_{10}$ transformed data using Linear Mixed-Effects Models (lme) and ANOVA with the 'nlme' package in R (Pinheiro et al. 2015). Type III sums of squares were used due to unbalanced sample design, and effect size of each model component (R^2) was calculated by isolating variance components (Table 2.1, Model 1). To assess whether offshore sites supported higher fish densities than inshore sites at each depth, fish density data were grouped within depths and a priori contrasts were made between bay positions (with reef as a random nested factor) via ANOVA of lme models. Tukey's post-hoc pairwise comparisons of levels within significant factors were made using the 'lsmeans' package (Lenth and Hervé 2014).

Influences of depth and bay position on species distributions and community structure

The densities of a subset of 51 abundant species were assessed for uneven distributions between depths and bay positions using non-parametric, permutation-based ANOVA in the multivariate statistical program PERMANOVA, from the PRIMER package for ecological statistics (Clarke and Gorley 2006). The 51 'top ranked' species consisted of the 20 most abundant species from each depth, with some species being among the most abundant at multiple depths. Species depth ranges were determined using presence/absence data from each depth.

Changes in fish assemblage structure were analyzed in PRIMER using Bray Curtis dissimilarity matrices of square root transformed data. Very rare species (present <5% of all transects) were excluded, leaving 114 of 123 species. CLUSTER identified assemblage groupings with averagedlinkages, which were visualized on a MDS plot. Formal analyses of changes in community composition were undertaken using 3-factor MANOVA in PERMANOVA (Depth, Position(Reef)) . Fish species characteristic of communities at each depth and their proportional contribution to community were identified using SIMPER.

Habitat variation along the depth gradient

ANOVAs of lme models (built as per Model 1 above) were used to test for uneven cover of hard coral, complex coral, and laminar coral between depths and bay positions using square-root transformed data.

Relative influence of depth and habitat on reef fish distributions

I assessed the comparative influence of depth and habitat availability on total fish abundance ($\log_{10}$) and species richness ($\log_{10}$) by testing the level of fit of three lme models; Depth (Model 1a), Complex Coral Cover (square root) (Model 2) and Depth and Complex Coral Cover combined (Model 3). The best-fit model had the lowest AICc score, provided no model with fewer factors fell within two points of the best AICc score. R-squared values were used to represent the amount of variation in fish density explained by each model (Demidenko 2013).

Fish-habitat relationships along the depth gradient

The strength of correlation between overall fish density ($\log_{10}$) and cover of complex coral habitat (square root) was assessed at each depth and across all depths using linear models in R. I tested for correlation between abundances of the 123 fish species and the cover of benthic components within each depth stratum and across all depths using 'cortest' in R using a Dunn-Šidák adjusted alpha of 0.0073 based on the number of benthic components. Relationships between the compositions of the fish benthic assemblages were assessed using Spearman rank correlations of Bray Curtis dissimilarity matrices in RELATE (PRIMER). Data from 40m were included in exploratory analyses but excluded from all formal analyses because 40 m transects were recorded only for offshore reefs.

Results

Influences of depth and bay position on fish density and species richness

Overall fish density declined by ~40% between each successive depth stratum, resulting in a 10 fold decrease from a peak of ~350 individuals per $100m^2$ at <1 m to ~35 individuals per $100m^2$ at 30 m (Fig. 2.1a). This depth-associated decline alone accounted for ~50% of variation in fish abundance (Table 2.1 – Model-set 1a). The mean number of species present per transect within the four fish families also declined with increasing depth below 5 m, from 17 ± 0.58 (SE) and 15.5 ± 0.45 species per $120m^2$ at <1 m & 5 m to 9.3 ± 0.53 species at 30 m (Table 2.1, Fig. 2.1b). However, the total number of species declined by only ~15% along the depth gradient, from 72 species at <1 m to 61 species at the two deepest depths (Fig. 2.1c).

The mean number of fish species was significantly lower overall at inshore sites compared to mid-bay (Tukey's p = 0.0038) and offshore sites (Tukey's p = 0.0132) (Table 2.1, Fig. 2.1b). Mid-bay and offshore sites also housed 25-30% more species in total than inshore sites (99, 93 and 70 species respectively).

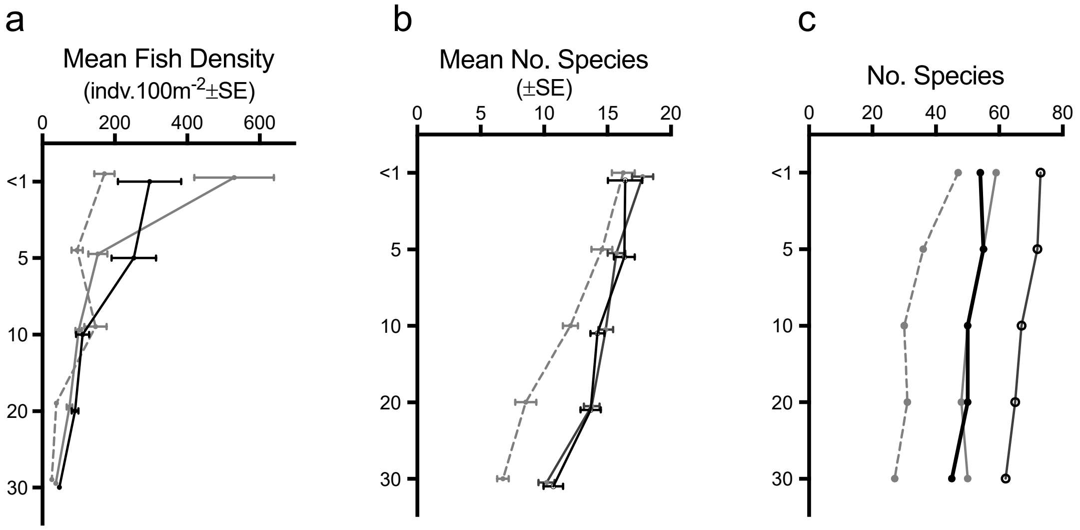

Figure 2.1: (a) The mean total fish density, (b) mean species richness, and (c) total species richness at each of 5 depth and 3 bay positions. Dashed lines represent the inner bay, solid grey lines the mid bay, and black lines the outer bay. Open circles on (c) represent total species count at each depth.

Reef fish density and species richness on deep reefs (20 m – 30 m) were both significantly higher away from inshore sites (Table 2.2, Table 2.1 – Model-set 1c). Overall densities at 20 m and 30 m depths were significantly higher offshore (~90 and ~47 indv.100m^{-2}) than at equivalent depths on inshore reefs (~39 and ~26 indv.100m^{-2}) and densities at 20 m sites offshore were equivalent to shallow sites (<1 -10 m) inshore (all *Tukey's* comparisons $p > 0.1$, Fig. 2.1a, Table S2.2). Likewise, the mean number of species per transect at 20m (8.6 ± 0.84 Spp.120m^{-2}) and 30 m (6.75 ± 0.46 Spp.120m^{-2}) on inshore reefs was lower than at equivalent depths on mid-bay (13.8 ± 0.61 and 10.2 ± 0.64 Spp.120m^{-2}) and offshore reefs (13.6 ± 0.8 and 10.7 ± 0.8 Spp.120m^{-2}) (Fig. 2.1b, Table 2.2), which also had ~40% more species in total at these depths (Fig 1c). In addition, total species numbers were higher at the deepest depths offshore than at the shallowest depths inshore (Fig. 2.1c). Differences in overall fish density between bay positions were more prominent but also more variable in shallow water. As a result, mean densities at <1 m were much higher on mid bay reefs than on inshore and offshore reefs but differences were not statistically significant (Table 2.2, Fig 2.1a).

Table 2.1 Summary statistics for 3 models: Model 1 tests for spatial organisation in the distributions of reef fish and coral across five depths and three bay positions. Model 2 tests for relationships between reef fish and complex coral distributions. Model 3 tests for the combined effects of depth and complex coral cover on Reef fish distributions. All model results give the influence of explanatory variables after first accounting for natural variation between reefs by incorporating reefs as a random factor. R^2 values represent the proportion of variation accounted for by the individual main effects (sub models a,b,c), and interaction terms in each model. Significance values: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p = 0.05$, NS = Not Significant ($\alpha = 0.05$). CV = Estimates of Components of Variance, and F_{perm} = pseudo-F-statistics based on permutation in PERMANOVA.

Model set		Explanatory Variables	Abundance (log10)					Species richness (log10)				Community Composition			
			df	F	p	R^2	AICc	df	F	p	R^2	df	F_{perm}	p	CV
1	1a	Depth	4,231	79.92	***	0.498	114.33	4,231	55.25	***	0.402	4,251	25.12	***	31.1
	1b	Position	2,7	4.48	.	0.048	286.49	2,7	6.95	*	0.074	2,251	15.9	***	15.9
	1c	Depth *Position	8,231	4.917	***	0.595	117.48	8,231	3.41	***	0.518	2,251	15.7	***	15.7
	2	Complex Coral	1,242	94.50	***	0.282	215.85	1,242	23.64	***	0.089	-	-	-	-
	3	Depth+ Complex Coral	1,234	3624.74	***	0.555	100.52	1,234	3859.1	***	0.397	-	-	-	-

Influences of depth and bay position on species distributions and community structure

The abundances of 41 of the 51 ‘top-ranked’ fish species (see methods) (81%) varied significantly with depth, and distribution patterns of 23 species (45%) varied with depth but not bay position (Table 2.4). Depth ranges varied greatly among all species surveyed, with 36 of the 123 species (29%) present at only one depth (Fig. 2.2a), 29 (24%) present at all depths to 30m and a further 16 species (12%) recorded at all depths to 40 m on outer-bay reefs (e.g. *Chaetodon baronessa, Ctenochaetus tominiensis)*. At least one species was uniquely observed at each study depth, however the greatest proportion of ‘single depth’ species occurred at <1m (Fig 2b). Twenty-nine species (24%) occurred only at depths ≤5m (e.g. *Chrysiptera cyanea, Chromis viridis*), while 77 species (62%) occurred at depths ≥ 20m (Fig. 2.2c).

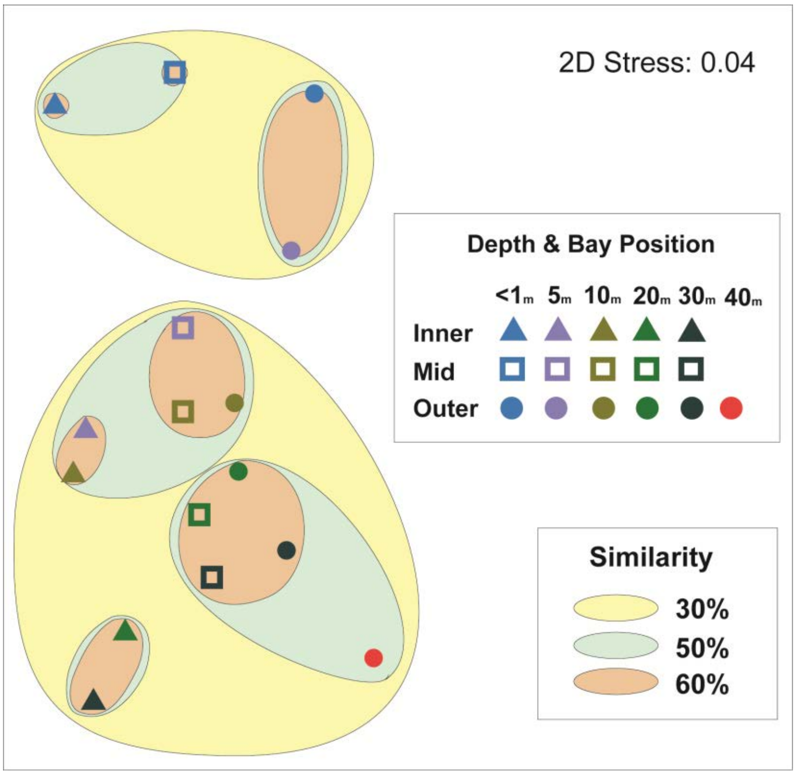

Figure 2.2: MDS plot showing similarities and differences in the composition of the reef fish community at each combination of depth and bay position. Similarity groupings are calculated via cluster analysis.

Table 2.2: Summary table for pre-planned within-depth contrasts of fish abundance between bay positions at each depth. Contrasts = significant contrasts (Tukey's adjusted α), I = inshore, M = mid-bay, O = offshore.

Depth (m)	Reef Fish Abundance (log10)				Reef Fish Species Richness (log10)				Complex Coral Cover (sqrt)			
	df	F	p	Contrasts	df	F	p	Contrasts	df	F	p	Contrasts
1	2,7	4.33	0.064	-	2,7	0.423	0.670	-	2,7	6.97	0.022	I<M
5	2,7	2.72	0.144	-	2,53	1.278	0.287	-	2,7	3.6	0.082	-
10	2,7	0.91	0.449	-	2,7	2.683	0.138	-	2,7	0.59	0.57	-
20	2,7	12.09	<0.001	I<M, I<O	2,45	14.5	<0.001	I<M, I<O	2,7	0.756	0.50	-
30	2,7	6.61	0.032	I<M, I<O	2,7	5.449	0.041	I<M, I<O	2,7	0.267	0.70	-

Depth patterns in species distributions resulted in significant differences in community composition between all depths (Table 2.1) (all comparisons; $p_{perm}<0.001$) and three major depth-related clusters were identified. The fish community at <1 m depth was best characterised by fourteen species (Fig. 2.3) and was <30% similar to a second community cluster that incorporated all other depths (Fig. 2.4). Of the fourteen species characteristic of <1 m only four were also characteristic the assemblage at 5m and none were characteristic of assemblages below 10 m. The next split in the fish community separated assemblages at 5-10 m from those at 20-30 m, with <40% similarity between the two groups. Fewer species characterised the deeper assemblage and those that did were mostly a subset of species characteristic of the assemblage at 5 m (Fig. 2.3).

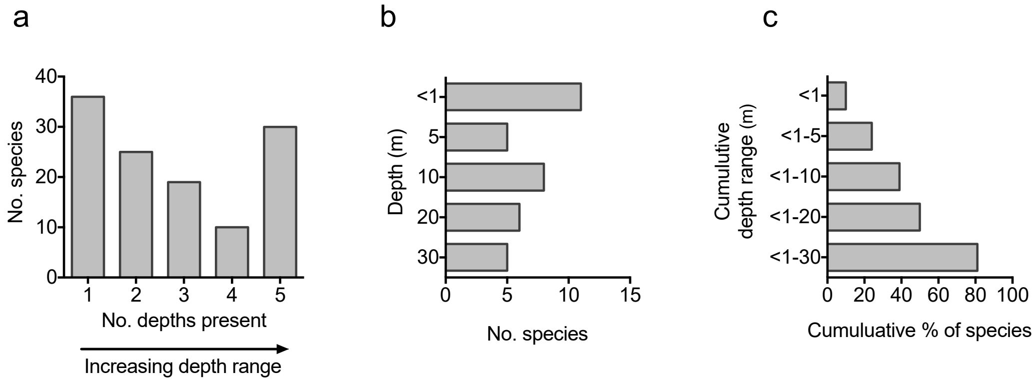

Figure 2.3: (a) The number of species recorded at 1 to 5 of the study depths (n=123). (b) The number of species that occurred at a single depth only, within each depth. (c) The percentage of species with occurrence restricted to each cumulative depth bracket.

The distributions of 18 ‘top-ranked’ species (40%) varied among bay positions (e.g. *Chrysiptera viridis*, *Chaetodon ornatissimus*) and while the community was similar between mid-bay and offshore positions within the same depths (p_{perm}= 0.232), inshore assemblages differed from both mid-bay and offshore assemblages (p_{perm}< 0.001, p_{perm}= 0.019 respectively),

Approximately half of the 'top-ranked' species were recorded at greater depths or in greater abundance at deeper depths offshore than on inshore reefs (25 spp.), and 18 species distributions were significantly influenced by the interaction of depth and bay position (Table 2.3). Eleven of these interactions between depth and bay position (60%) occurred in species distributed in the shallowest 5m, where small damselfish species had high peak densities in one or two bay positions only. Some characteristic deep-water species increased in density toward the outer bay (e.g. *Chromis amboinensis*, *Chromis delta, Chromis retrofasciata* and *Ctenochaetus tominiensis*), whereas others were more numerous in the inner bay (eg. *Chaetodon octofasciatus, Chrysiptera rollandi* and *Pomacentrus nigromanus*). In one example the coral feeding butterflyfish *Chaetodon lunulatus*, was very rare below 10m at inshore sites but equally abundant at all depths to 30m in the mid-bay and offshore reefs. These species patterns resulted in the depth related separation of the fish assemblage being strongest inshore, with the deep assemblages (20 m - 30 m) in the mid-bay and offshore positions being more similar to the mid-water (5-10 m) assemblages (Fig. 2.4).

Habitat variation along the depth gradient

Total hard coral cover (HCC) was relatively high (48-60%) at all sites (Fig. 2.5a), though small (<12% cover) significant changes did occur among depths and bay positions, with no significant interaction between the two (Table 2.4, Fig. 2.5a). Total coral cover was significantly higher at 5m and 10m than at 30m (*Tukey's* p = 0.008 and p = 0.001), and was generally ~12% higher in the mid-bay than the outer bay (*Tukey's* p = 0.025). The functional composition of coral growth forms changed more substantially over the depth gradient. For example, where complex coral cover declined overall below 10m (Fig. 2.5b, Table 2.4), laminar corals increased with depth at all bay positions (Fig. 2.5c, Table 2.4), with depth accounting for ~20% of variation in complex coral cover (R^2=0.189, Table 2.4).

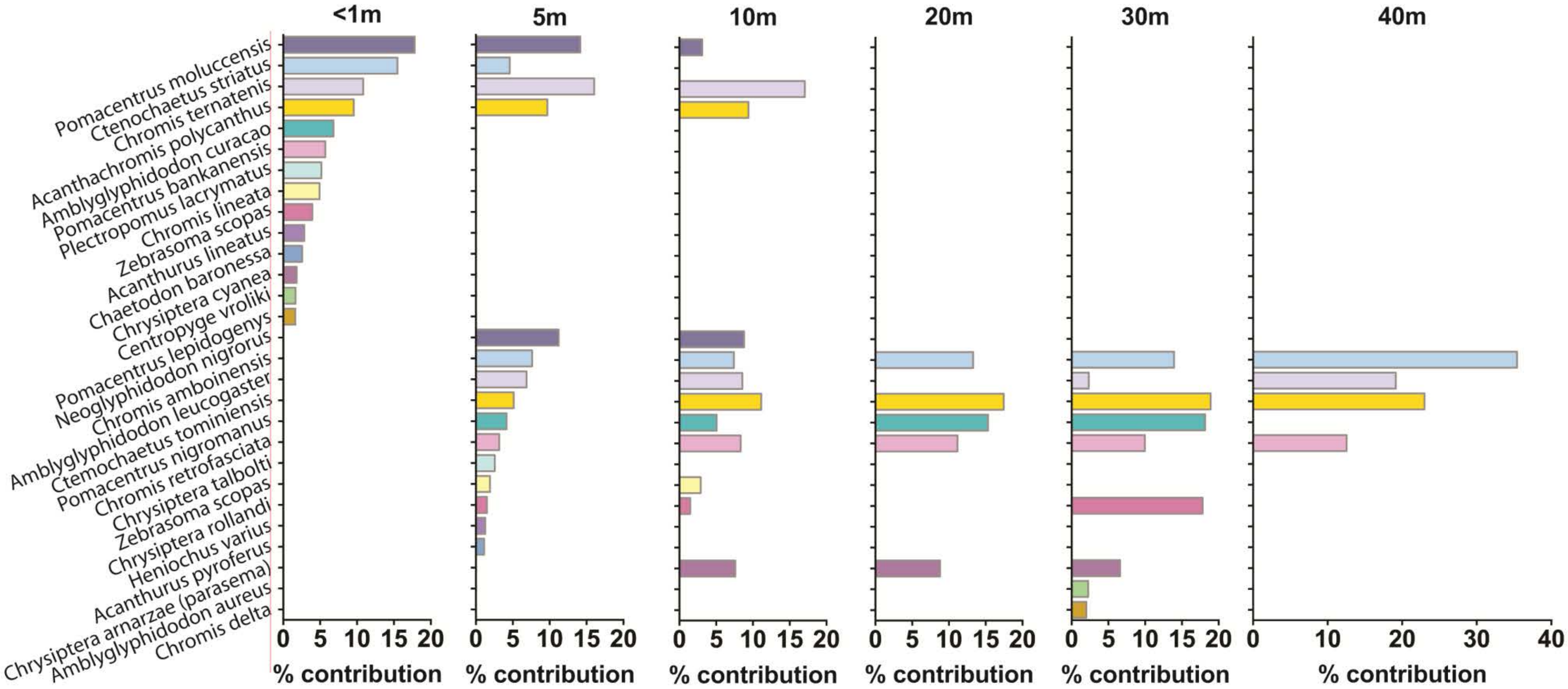

Figure 2.4: The species most characteristic of the assemblage at each depth, and their proportional contribution to within-depth similarities.

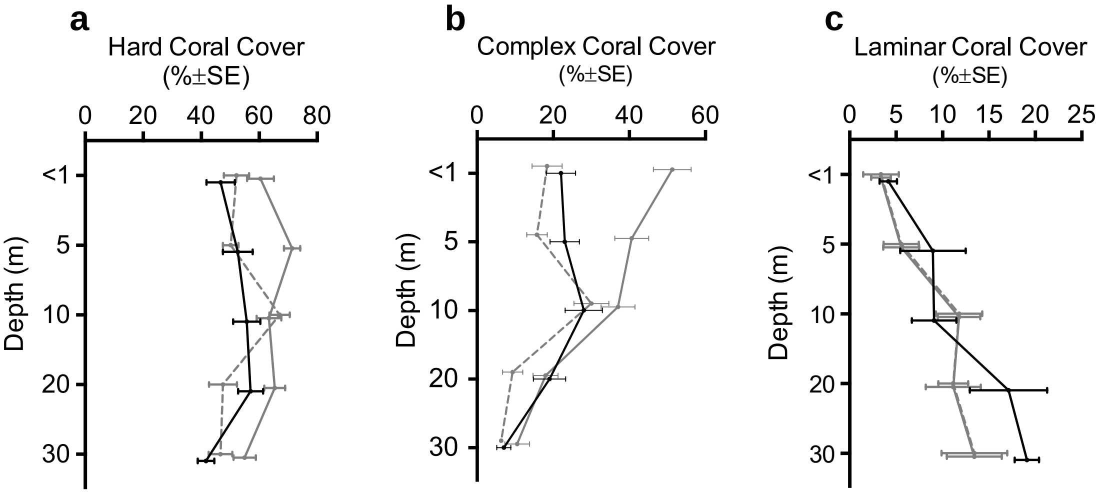

Figure 2.5: The mean per cent cover of (a) All Hard Corals, (b) Complex Corals, (c) Laminar and Tiered Corals, at each of five study depths, and three bay positions, inner bay (dotted grey lines), mid bay (solid grey lines), and outer bay (dark lines).

The highest cover of complex coral habitat was in shallow water (≤10 m) on mid-bay reefs (~51%), (all Tukey's comparisons <1-10 m $p > 0.9$, all comparisons <10 m against >10 m $p < 0.05$), and varied substantially in the shallowest 1 m (Table 2.2). Although complex coral cover was twice as high at 20 m on mid-bay (~17%) and offshore reefs (~19 %) than inshore reefs (~9%), cover was not significantly different between bay positions at depths below 5 m (Table 2.2).

Relative influence of depth and habitat on reef fish distributions

Depth distributions were not strongly habitat limited. After accounting for between-reef differences, the combined influences of depth and complex coral cover explained 55% of the variation in overall fish density and was the best-fit model (Table 2.1, Model-set 3). However, depth alone explained a similarly high proportion of variation (50%) (Table 2.1, Model-set 1a), which was almost twice that explained by complex coral cover alone (28%) (Table 2.1, Model-set 2). Similarly, more than double the number of density distributions in the 51 'Top-ranked' species varied with depth (41 species - 80%) than with complex coral cover (13 species - 25%) (Table 2.4). Eleven of the thirteen Top-ranked species (85%) with correlations to complex coral cover however were broadly distributed to 20 m or deeper with the other two species limited to the shallowest 5 m.

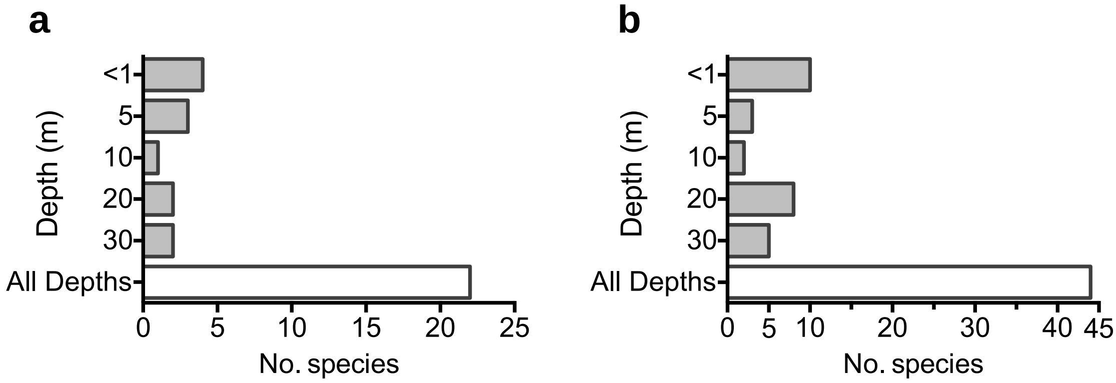

Figure 2.6: The number of species with distributions that have a significant positive correlation (α = 0.0031 with Bonferoni adjustment) within each depth, and across all depths, to (a) complex coral cover and (b) one or more benthic habitat types at each depth.

Fish-habitat relationships along the depth gradient

Fish-habitat relationships were not strongly depth dependent. The strength of relationships between total fish density and the availability of complex coral cover did not decline uniformly with depth (Fig. 2.7, Table 2.5). Positive correlations between the two occurred at <1 m and at 20 m, but not at other depths. Overall, 18% of all species distributions (22 of 123 spp.) were positively correlated to the availability of complex coral habitat when considered across all depths (Fig. 2.6a), 36% (44 spp.) were correlated to at least one benthic habitat category (Fig. 2.6b). Again there was no uniform decline with increasing depth in the number of species distributions correlated to the cover of complex coral habitat or other benthic habitats (Fig. 2.6). However, association with complex coral habitat was stronger among fish species characteristic of shallow-water assemblages than characteristically deep-water species. The distributions of eight of the fourteen (57%) species most characteristic of the fish assemblages between <1m and 5m (see Fig. 2.4) were correlated to the availability of complex coral habitat when habitat availability was considered across all depths, and 71% (10 spp.) were negatively correlated to laminar coral cover. In contrast, the densities of 55% of fish species characteristic of assemblages below 10 m (5 of 9 spp.) were positively correlated with laminar coral cover, and three species were negatively related to the availability of complex coral habitat. Only two characteristically deep-water species were correlated strongly with complex coral habitat cover.

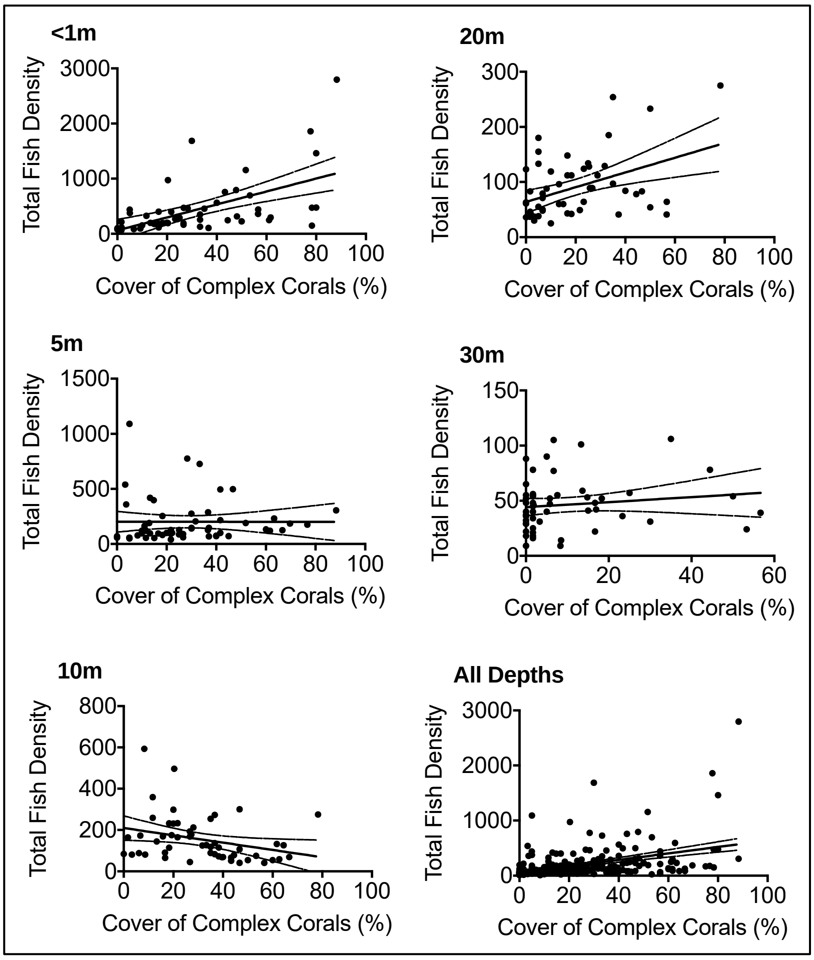

Figure 2.7: Correlations between total fish density and cover of complex corals at five depths along a gradient from <1m-30 m, and across all depths. Regressions at <1 m, 10 m, 20 m, and across all depths are significant. Dotted lines represent 95% confidence intervals.

Table 2.3: Mean abundance of 51 ‘Top-Rank’ species at each depth, factors of spatial organization and their correlations to complex coral habitat. Bold numbers indicate depths at which a species is among the top 20 most abundant. Significance values from PERMANOVA: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, NS = Not Significant ($\alpha = 0.05$). Significant correlations to complex coral; $\alpha = 0.0073$.

Species	Mean density (ind. 100 m ^{2})						Spatial organisation (PERMANOVA)				Sig. cor. complex coral (r)
	<1 m	5 m	10 m	20 m	30 m	40 m	Depth	Pos.	Depth × Pos.	Reef	All depths
Chromis ternatensis	**151.08**	**49.87**	**38.92**	**6.82**	**0.74**	0.00	***	*	***	***	0.515
Chromis lineata	**64.40**	**26.44**	0.00	0.00	0.00	0.00	***	**	**	***	-
Pomacentrus moluccensis	38.09	**13.63**	**4.67**	**1.69**	**1.28**	0.00	***	NS	*	***	0.426
Chrysiptera arnazae	0.00	**3.68**	**23.39**	**11.31**	**3.72**	**3.31**	**	NS	NS	***	-
Acanthochromis polyacanthus	**14.25**	**8.04**	**8.77**	**4.26**	**1.31**	**0.11**	***	*	NS	NS	0.252
Chromis amboinensis	0.15	**5.26**	**4.69**	**7.15**	**4.80**	**11.77**	***	NS	NS	***	-
Pomacentrus nigromanus	0.39	**5.28**	**4.00**	**8.08**	**5.03**	0.00	***	*	*	***	-
Chromis atripectoralis/viridis	**9.23**	**9.47**	0.00	0.00	0.00	0.00	*	**	**	*	0.221
Ctenochaetus striatus	**14.90**	**2.27**	**0.42**	0.28	0.11	0.00	***	*	NS	NS	0.250
Chromis retrofasciata	0.09	**2.05**	**5.25**	**6.02**	**3.65**	**6.86**	***	NS	*	***	-
Ctenochaetus tominiensis	0.01	**2.79**	**4.39**	**4.25**	**3.00**	**3.09**	***	***	**	NS	-
Amblyglyphidodon leucogaster	0.40	**3.89**	**4.96**	**3.65**	**1.38**	**2.29**	***	***	***	***	0.292
Chrysiptera cyanea	**13.41**	0.00	0.00	0.00	0.00	0.00	**	NS	*	***	-
Neoglyphidodon nigrorus	0.62	**6.75**	**4.30**	**1.35**	0.06	0.00	***	NS	NS	***	0.293
Amblyglyphidodon curacao	**11.14**	0.46	0.24	0.00	0.00	0.00	***	NS	NS	***	0.196
Chrysiptera rollandi	0.16	**2.20**	**0.94**	**1.48**	**3.38**	**0.46**	***	**	**	**	-
Zebrasoma scopas	**2.86**	**1.09**	**1.18**	**0.48**	**0.17**	0.00	***	***	NS	NS	0.320
Acanthurus thompsoni	0.01	0.49	**0.89**	**2.48**	**1.78**	**0.57**	*	NS	NS	***	-
Pomacentrus aurifrons	0.00	**2.26**	**2.70**	0.14	0.00	0.00	*	NS	**	*	-
Amblyglyphidodon aureus	0.22	**1.22**	**0.82**	**1.48**	**1.20**	**0.69**	**	NS	NS	***	-
Plectroglyphidodon lacrymatus	**4.61**	0.20	0.00	0.00	0.00	0.00	***	*	***	***	-
Acanthurus lineatus	**4.42**	0.04	0.00	0.00	0.00	0.00	***	NS	NS	***	0.206
Pomacentrus bankanensis	**4.19**	0.13	0.05	0.00	0.00	0.00	***	NS	NS	**	-
Abudefduf vigiensis	**2.28**	**1.43**	0.00	0.00	0.00	0.00	**	NS	NS	***	-
Chrysiptera talboti	0.00	**1.60**	**0.80**	**0.80**	0.00	0.00	**	NS	NS	NS	-
Chaetodon lunulatus	**0.68**	0.44	**0.60**	**0.45**	**0.22**	0.00	NS	*	NS	*	0.200
Chromis margaritifer	**1.17**	0.74	0.00	0.00	0.00	0.00	***	*	*	***	-
Chaetodon baronessa	**1.13**	0.46	0.14	0.12	0.02	**0.11**	***	NS	NS	NS	0.288
Naso hexacanthus	0.00	0.22	0.00	0.09	**0.17**	**10.29**	NS	NS	NS	NS	-
Chromis xanthura	0.34	**1.39**	0.00	0.00	0.00	0.00	**	***	**	NS	-
Zanclus cornutus	0.46	0.29	**0.78**	0.23	0.08	0.00	**	NS	NS	**	-
Pygoplites diacanthus	0.56	0.49	0.25	0.26	**0.20**	**0.23**	NS	***	*	NS	-
Heniochus varius	0.41	0.62	0.27	0.25	0.15	**0.11**	*	***	NS	NS	-
Forcipiger flavissimus	0.07	0.25	**0.47**	**0.54**	**0.17**	**0.23**	*	***	NS	NS	-
Neopomacentrus azysron	**1.33**	0.08	0.00	0.00	0.00	0.00	***	NS	***	NS	-
Pomacentrus adelus	**1.39**	0.00	0.00	0.00	0.00	0.00	**	**	***	**	-
Acanthurus pyroferus	0.43	0.53	0.14	0.09	0.08	**0.11**	NS	**	NS	NS	-
Chromis delta	0.00	0.00	0.05	**0.51**	**0.74**	**0.11**	**	NS	NS	***	-
Pomacentrus lepidogenys	**1.23**	0.03	0.00	0.00	0.00	0.00	**	NS	NS	***	-
Centropyge vroliki	**0.93**	0.17	0.09	0.00	0.02	0.00	***	*	NS	***	-
Chaetodon octofasciatus	0.00	0.08	0.30	**0.51**	**0.28**	0.00	*	NS	NS	NS	-
Chaetodon ornatissimus	0.21	0.27	0.20	0.17	**0.18**	**0.34**	NS	***	NS	NS	-
Centropyge nox	0.04	0.07	0.16	0.43	**0.28**	**0.11**	***	NS	NS	NS	-
Pomacentrus reidi	0.00	0.06	0.02	0.35	**0.46**	0.00	**	NS	NS	***	-
Naso literatus	0.09	0.11	0.13	0.09	0.06	**0.34**	NS	NS	*	NS	-
Neoglyphidodon thoracotaeniatus	0.00	0.01	0.05	0.18	0.14	**0.23**	*	NS	NS	*	-
Pomacentrus nigromarginatus	0.00	0.00	0.02	**0.55**	0.11	0.00	NS	NS	NS	NS	-
Dascyllus flavicaudis	0.00	0.00	0.00	0.00	0.00	**1.83**	***	NS	NS	NS	-
Heniochus monoceros	0.01	0.01	0.00	0.03	0.11	**0.11**	NS	NS	NS	NS	-

Twenty-three per cent of overall variation in the composition of the fish community was explained by changes in the benthic structure and the structures of fish and benthic communities were significantly correlated within three of the five depth strata (Table 2.5). Again, however, there was no linear trend through the depth gradient. While the strongest correlations were in the shallowest water (<1 m), there was no correlation at either 5 m or 10 m, and significant correlations occurred at 20 m and 30 m.

Table 2.4: Summary statistics tests for spatial organisation in the distributions of coral habitat across five depths and three bay positions. R^2 values represent the proportion of variation accounted for by the individual main effects (sub models a,b,c), and interaction terms in each model. Significance values: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $p = 0.05$, NS = Not Significant ($\alpha = 0.05$). F_{perm} = pseudo-F-statistics based on permutation in PERMANOVA.

Model set		Explanatory Variables	Coral Cover											
			Hard Coral Cover				Complex Coral Cover				Laminar Coral Cover			
			df	F	p	R^2	df	F	p	R^2	df	F	p	R^2
1	1a	Depth	4,231	4.79	*	0.018	4,231	22.61	***	0.189	4,231	16.27	***	0.159
	1b	Position	2,7	15.25	**	0.101	2,7	7.25	*	0.113	2,7	0.225	NS	0.011
	1c	Depth*Position	8,231	1.65	NS	0.120	8,231	3.89	*	0.383	8,231	0.893	NS	0.188

Discussion

The presence of contiguous reef habitat to depths of ≥40m in Kimbe Bay allowed me to address a number of questions concerning depth distributions of reef fish and the extent to which depth ranges are influenced by habitat availability and bay position across a wide depth range from the surface to upper mesophotic depths. Overall, my results suggest that a considerable proportion of fish species can occur across a broad depth range and may be capable of utilising deep refuges if habitat degradation is depth-dependent. Furthermore, depth ranges and/or abundances at greater depths increased with distance offshore for many species suggesting that deep habitats on clear-water, offshore reefs may be particularly important refuges. However, approximately 25% of all species were restricted to shallow depths (<5 m), suggesting some species are unlikely to benefit from potential depth refuges unless their depth ranges shift.

As expected, the overall abundance and mean species richness of reef fishes per unit area declined significantly with increasing depth, while the total number of species declined by only 15% between <1 m – 30 m. The abundance of the majority of individual fish species also varied with depth, with the greatest changes in community composition occurring between the shallowest depth (<1 m) and all other depths. While some species were restricted to a narrow depth range, others were broadly distributed throughout the depth gradient, particularly on offshore reefs. At greater depths (20 m – 30 m), more fish species and higher abundances occurred on offshore reefs. This resulted in similar total fish abundance and species richness between deep offshore and shallow inshore reefs.

Although depth was the most important single factor influencing fish distributions, some species were also strongly associated with habitat structure. Despite high hard coral cover at all depths and bay positions, the functional composition of coral habitat varied with depth, which facilitated deep distributions of some fish species, including some coral specialists, but not others. The strength of association between fishes and complex corals did not decline uniformly with depth, with some of the strongest correlations occurring at 20 m.

Fish distributions along the depth gradient

The general depth-related declines in abundance and species richness observed in Kimbe Bay are consistent with previous studies (eg. Bouchon-Navarro 1981, Nagelkerken 2001, Brokovich 2008, Kahng et al. 2010). Species depth distributions varied substantially and species with narrow depth ranges occurred most often in shallow depths, which is consistent with previous observations and experiments showing narrower distributions in shallow-water specialists versus deep-water specialists (Bean et al. 2002, Srinivasan 2003, Jankowski et al. 2015).

The average depth distributions in Kimbe Bay were narrower than those reported for a comparable, but deeper gradient in Puerto Rico. In this study 25% of all species occurred only in shallowest 5m, a further 25% of species occurred from <1 to 30 m, and more than half of all recorded species occurred at depths ≥20 m, with a further 10% distributed from <1 m to 40 m on offshore reefs. Garcia-Sais (2010) surveyed at 30 m and 40 m, and from 15 – 50 m in two different Puerto Rican locations and reported species assemblages similar to nearby shallow reefs, with three-quarters of all species observed deeper than 30 m, and two thirds observed at all depths. Similarly, ~80% of species surveyed from 32 – 78 m at Johnston Atoll in the central Pacific are also known from shallow water surveys (Wagner et al. 2014). The inclusion of the more unique fish assemblage in shallower water in this study, as well as regional differences in fish biodiversity and the differing taxonomic breadth of the studies may account for some of these differences. The inclusion of more fish families, particularly larger bodied species and some planktivores (e.g. Anthiinae) that tend to have broader and deeper depth ranges (e.g. Kulbicki et al. 2015, Bridge et al. 2016) would likely increase proportional species richness at deeper depths in Kimbe Bay. Additionally, many species of the parrotfish and wrasse families commonly have distributions centred on the reef flat and future depth distribution studies should focus on these families also.

Influence of bay position on depth-distributions

Our study confirmed that both depth and bay position influence the composition of fish communities in Kimbe Bay. The effects of bay position, including changes in species richness and composition offshore, were similar to previous studies along cross-shelf gradients in other regions (e.g. Williams 1982, Malcolm et al. 2010), with differences generally separating inshore reefs from those further offshore. The simultaneous assessment of both depth and bay position here enabled us to provide the first analysis of the interaction between these two factors. Half of the species distributions that varied by depth also varied among bay positions. Many species had broader depth ranges on offshore reefs, where community assemblages were more similar between depths. Importantly, deep offshore reefs in this study showed substantial ecological value, supporting high fish diversity and densities equivalent to shallow inshore reefs.

Depth influences on habitat availability and fish-habitat relationships

Hard coral cover was prominent throughout the depth gradient and was high at 30 m compared to most contemporary shallow reef systems (Gardner et al. 2003, Bellwood et al. 2004, Wilson et al. 2009, Chong-Seng et al. 2012, De'ath et al. 2012). The cover of habitat-forming complex coral declined with increasing depth in Kimbe Bay, but was comparable or higher at 20 m and 30 m than on shallow reefs that have 'recovered' from severe disturbances in other regions (e.g. Wilson et al. 2009, Chong-Seng et al. 2012). Bay position exerted less influence on coral cover and habitat structure than expected, and was most prominent in shallow mid-bay habitats, where complex coral cover was twice as high compared to equivalent depths either inshore and offshore. This potentially results from mid-bay reefs being less exposed to storms than offshore reefs (sensu Roberts et al. 2015) and less influenced by anthropogenic and terrestrial pressures than reefs inshore (Jones et al. 2004). There was some evidence to suggest deeper extensions of complex coral habitat availability on offshore reefs, where cover at 20 m was generally ~50% higher than on inshore reefs, although there was some variability among reefs.

The strength of relationships between reef fish distributions and benthic habitat structure overall was similar to other studies from shallow depths (e.g. Wilson et al. 2008), with the strongest relationships observed at the shallowest depth (<1 m). Surprisingly however, the strength of relationships did not decline uniformly with depth; instead, fish-habitat relationships were weak or non-existent at 5 m and 10 m, but strong at 20 m. Jankowski et al. (2015) recently reported an increasing strength of fish-coral habitat relationships with depth to 20 m on the GBR, suggesting general depth patterns may differ from expectations of a general decline in fish-coral associations with increasing depth.

The relatively weak fish-habitat relationships at 5 m - 10 m were surprising given some species observed at these depths are known to associate strongly with live coral (Srinivasan and Jones 2006, Bonin 2012, Boström-Einarsson et al. 2013). Potentially, variation in microhabitat structure among depths may account for this observation and further, more detailed analysis within depths may be warranted to further elucidate fine-scale patterns of microhabitat use.

The distributions of characteristic shallow-water species tended to correlate positively with complex coral habitat availability and/or negatively with laminar coral cover, whereas the distributions of characteristic deep-water species were more often positively correlated with laminar coral cover. However, the distributions of some deep-water species were related to the continued presence of complex corals to at least 30 m. For example, *Chrysiptera arnarzae* (formerly *Chrysiptera parasema)* associates strongly with complex coral habitat in waters ≤ 10m (Srinivasan and Jones 2006, Bonin 2012, Boström-Einarsson et al. 2013), and is considered highly vulnerable to coral habitat loss in shallow water (Bonin 2012). The relationships in deeper water recorded here may therefore reduce the vulnerability of this and similar species from shallow water coral loss.

Comparing the influences of depth and habitat availability

Depth-related changes in habitat structure significantly influenced overall reef fish abundance and many species' distributions along the depth gradient. However, depth alone explained more variation in overall fish abundance and influenced more species distributions than did depth-related variation in habitat availability. Though finer scale surveys of micro-habitat association may reveal more about the importance of fish-habitat relationships at deeper depths, it is probable that depth influences other important ecological processes apart from its influence on habitat composition alone, as suggested by experimental studies (Srinivasan and Jones 2006).

It is unclear why some coral-associated species did not occur in deep water even where suitable habitat was available, while others did. Depth preferences may be related to other ecological processes that control species niches such as differences in settlement depth of juveniles (Leis 1991, Srinivasan 2003), adult dispersal capacity (e.g. Frederick 1997), interspecific competition (e.g. Böstrom-Einarsson 2013), or predation pressure (e.g. Beukers and Jones 1998). Likewise, subtle physiological differences may also influence the success of species, or individuals on deep reef habitat (e.g. Brokovich et al. 2010). It is not clearly understood if deeper habitat use incurs higher energetic costs, though some shallow water species experience a greater cost of being outside their preferred depth range than deeper species (Srinivasan and Jones 2003), while one species of rubble-dwelling damselfish is known to alter energy allocation according to depth (Hoey et al. 2007).

Are deep reefs a potential refuge?

Shallow coastal reefs are often more vulnerable to degradation and are likely to be at greater risk from disturbances such as storms, bleaching and sedimentation than reefs in deeper water and further offshore (Bridge et al. 2013). Consequently, fish species restricted to shallow, inshore habitats and that are strongly dependent on live coral are most at risk from habitat degradation (e.g. Munday 2004, Wilson et al. 2008, Graham et al. 2011). Deep, offshore reefs may help mitigate disturbance-associated declines at local to regional scales by providing a refuge for species with more general habitat requirements or coral-associated species with broad depth distributions. Approximately a quarter of my study species occurred exclusively in the shallowest 5 m and the fish community at <1 m was more abundant, more diverse and had the stronger relationships to complex coral habitat at both community and species levels than at deeper depths. This suggests that a considerable proportion of species are likely to be substantially affected by reef degradation (Jones et al. 2004, Munday 2004, Wilson et al. 2008, Graham 2011) and are unlikely to benefit from a depth refuge. However, the majority of species in Kimbe Bay can occur in relatively deep water and may be capable of persisting through disturbance events in deep, offshore habitats. Deep offshore sites supported a high abundance of complex coral habitat and were occupied by many fish species with both general and highly specialized habitat requirements. Many species were highly flexible in their spatial distribution and/or habitat requirements, with as many as half extending into deeper water further offshore. A quarter of all species were broadly distributed from <1 m to 30 m, and half were present at 20 m. In addition, more than half of the most abundant species were distributed independently of complex coral habitat availability. Surprisingly, a high proportion of the abundant species with distributions correlated to complex coral availability were present to at least 20 m and in most cases 30 m, suggesting that depth offers a potential refuge even for some coral specialists.

My study contributes to an emerging body of work that suggests deep reefs may act as a refuge for reef fishes if deeper reefs are less exposed to disturbances. A more complete understanding of the refuge potential will require further detailed assessments of the ecological and physiological processes that control species niches and depth ranges along extended depth gradients. Tests for the detrimental impacts and sub-lethal effects of changes in micro-habitat use, diet, prey quality, movement ecology and competitor densities are well established along horizontal ecological gradients for many reef fish species and should be easily adapted to studies along depth gradients.

Chapter 3 - BROAD DEPTH RANGES AND HIGH ABUNDANCES MEDIATE RISKS FOR A CORAL-SPECIALIST REEF FISH GUILD

Abstract

Interrelationships among distribution breadth, abundance and degree of resource specialization form the basis of many general models in ecology. Widely distributed species are often more abundant than those with narrow distributions, and resource specialists often exhibit narrow distributions and numerically rarity. Understanding whether these ecological generalizations hold is important in conservation ecology, as species with narrow distributions, low abundance and/or specialized resource requirements are increasingly at risk from habitat loss. On coral reefs, specialized coral-associated fishes may be highly vulnerable to declining coral cover in shallow-water. However, risk assessments incorporating detailed vertical distribution data are rare. To evaluate whether depth may mediate risk in coral-specialist fishes I tested: (1) whether the pair-wise relationships between depth distributions, local densities and diet specialization are consistent with traditional expectations, and (2) what proportion of species with traits conferring vulnerability, (narrow depth-distributions, low abundance or high diet-specialization) were restricted to shallow-reef habitats. To do this, I quantified depth distributions and abundance for 25 Chaetodontidae species, between 0 and 40 m in Kimbe Bay, Papua New Guinea, and utilized dietary specialization indices for eight species, from the literature. As predicted, species with the broadest depth-distributions were also the most abundant. However, contrary to expectation, the most specialized species were also the most abundant and the most broadly distributed. Further, no specialist-species experienced combined vulnerability traits, and no specialists were wholly restricted to shallow-water, where habitat disturbance is often highest. However, despite the resilience potential broad depth ranges and high abundances may confer to dietary specialists, their distributions were strongly biased toward shallow-water. My results support the conclusion that interrelationships among vulnerability traits and occupancy depths do not necessarily follow traditional ecological expectations, but on coral reefs they do work to mediate substantial risks in a family of reef fish vulnerable to shallow-water coral habitat losses.

Introduction

Interrelationships among distribution breadth, abundance and degree of resource specialization form the basis of a number of general models in ecology (Brown 1984, Gaston et al. 1997, 2000). They also inform vulnerability assessments in conservation biology (Rabinowitz 1981, Julliard et al. 2004, Graham et al. 2011). Most often, narrow species ranges are related to lower overall abundances (Hanski 1982, Brown 1984, Swain and Wade 1993, Gaston 1996, Gaston et al. 1997, Lawton 1999, Frisk et al. 2011), and resource specialists often have low abundances and narrow ranges, due to the limited distribution and abundance of their prey (Gaston et al. 1997, Lawton 1999, Harcourt et al. 2002). However, these generalizations do not always hold. For example, resource specialists can reach high abundances where they exploit locally dense resources (Gaston et al. 1997), and resource specialists that utilize widespread resources should themselves have broad distributions (e.g. Quinn et al. 1997, Gaston et al. 1997, Gregory and Gaston 2000, Jones et al. 2002). Therefore, links between distribution, abundance and resource specialization remain equivocal, with studies both supporting (Harcourt et al. 2002, Munday 2004, Pratchett 2013) and refuting (Gaston et al. 1997, Gregory and Gaston 2000, Jones et al. 2002) such generalizations, in both terrestrial and marine systems. Further, the pair-wise relationships between distribution, abundance and resource specialization may be context specific (Gaston et al. 1997) and need to be evaluated for a wider range of species, ecosystems, and regions - especially where organisms are likely to experience heightened vulnerability due to elevated environmental change.

Species with small distributional ranges, low local abundance or high levels of specialization, will be particularly susceptible to localized disturbances (Mckinney 1997), the risks of small population size (Williams et al. 2008), and loss of a resource (Gaston et al. 1997). Species that are subject to two or three different sets of these risk factors are considered to be in “double jeopardy” or “triple jeopardy” (e.g. Harcourt et al. 2002, Munday 2004, Swartz et al. 2006, Hughes et al. 2014), and may be more vulnerable to local extinction (Gaston 1996, Johnson 1998). However, the extinction risk really depends upon how much species with these vulnerability trait combinations are subject to an increasing array of environmental disturbances.

Increases in climate change related habitat disturbances and species displacements have strengthened the impetus to understand links among distribution, abundance, resource specialization, and their associated vulnerability risks (Thomas et al. 2004, Harris and Pimm 2008, Angert et al. 2011, Chen et al. 2011). Disturbances are often spatially patchy and can attenuate along environmental gradients. For example, fire disturbance frequencies attenuate with decreasing aridity along latitudinal (Pausas and Bradstock 2007) and elevation gradients (Harmon et al. 1984, Bekker and Taylor 2010). Strong overlaps between disturbance pressures and the central ranges of vulnerable organisms will elevate extinction risks (Thomas et al. 2004). However, species may mediate risk through low spatial overlap with disturbances, or by having broad distributions, high abundances, and/or generalist resource requirements (e.g. Roberts and Hawkins 1999, Hawkins et al. 2000, Munday 2004, Graham et al. 2011). In terrestrial systems, vertical gradients in disturbance, distributions, and ecological processes can strongly influence these resilience outcomes (Parmesan and Yohe 2003, Raxworthy et al. 2008, Chen et al. 2011). However, the ecological correlates of depth ranges and the influence of depth on pair-wise relationships among vulnerability traits are grossly under-studied in marine systems, and generalizations from terrestrial theory may not hold.

Coral reef ecosystems offer a good testing ground for ecological theories of the spatial distributions of vulnerability traits and disturbances; they support high abundance and diversity, and depth offers steep environmental and habitat gradients over short spatial scales, with few physical barriers to vertical dispersal. Moreover, shallow-water coral reefs are immediately imperilled by climate-change related habitat degradation (e.g. Bellwood et al. 2004, Hughes et al. 2018), and improved knowledge of how risk and resilience factors play out among vulnerable species groups is imperative (Munday 2004, Graham et al. 2011). In shallow waters, interrelationship patterns among vulnerability traits for reef fish are equivocal (Bean et al. 2002, Jones et al. 2002, Munday 2004, Ollerton et al. 2007, Hobbs et al. 2010, Lawton et al. 2012, Pratchett et al. 2013). However, coral resource specialists are consistently the most vulnerable to habitat losses (Hawkins 2000, Jones et al. 2004, Wilson et al. 2006, Pratchett et al. 2008). Some such coral-specialists experience double or triple jeopardy, and local or near-global extinctions (e.g. Munday 2004). However, a broad availability of key coral resources in shallow waters largely results in broad shallow-water geographic (SWG) distributions (Jones et al. 2002, Lawton and Pratchett 2012) and high local abundances (Pratchett et al. 2008) that currently mediate some risk in the majority of this group. As severe warm-water and storm-related habitat degradation becomes more geographically and temporarily ubiquitous in shallow waters (e.g. Hughes et al. 2018) this resilience is likely to be compromised. However, because such events often have differential impacts along depth gradients (e.g. Bridge et al. 2013), depth range and depth influences on specialization and abundance traits are likely to become increasingly important components of risk mitigation strategies and resilience outcomes for reef fishes (e.g. Roberts and Hawkins 1999). In general, depth is expected to exert strong environmental filters on coral resources and coral specialization traits, which would limit the depth refuge potential for many vulnerable coral-specialist reef fishes. However, to date, the influence of depth on ecological determinants of reef-fish distributions, and the relationships between vulnerability traits and depth distributions are poorly understood outside of very shallow waters (< 12 m).

Here I investigated the influence of pairwise interrelationships between dietary specialization, abundance and depth-range in 26 sympatric butterflyfish (Chaetodontidae) species between 0 m and 40 m depths on coral reefs in Kimbe Bay, Papua New Guinea. I also examined whether species with vulnerability-conferring traits were particularly associated with shallow habitats. Chaetodontidae is a ubiquitous family and frequently used as a model group in shallow-water ecological studies. Coral dietary specialization ranges from obligate and facultative coral feeders to non-coral invertebrate feeders (Pratchett 2013), which are the three reef fish dietary groups facing the greatest extinction threats (Graham et al. 2011). Risk and resilience potential are often assessed among such diet-trait groups. However, the finer degrees of trait expression that occur within groups may further differentiate these potentials (e.g. Lawton et al 2012b), and dual assessments among and within trait groups may highlight the broad-scale applicability of vulnerability and resilience measured at trait-group levels. I therefore investigated patterns at both levels. Specifically, I tested the following questions: (1) Are species with broad depth distributions more abundant? (2) Are species and trait groups with broad depth distributions diet generalists? (3) Are diet generalists more abundant than diet specialists, and is this relationship stable along a depth gradient? (4) Are species with narrow ranges, low abundances, or high dietary specialization, restricted to shallow waters? And, does overlap occur among these traits? (5) Are distributions of dietary specialists skewed toward shallow water more than dietary generalists?

Methods

Field methods

I recorded the abundance of 26 Chaetodontidae species (butterflyfish) at each of five depths (<1m, 5m, 10m, 20m, 30m), on 10 reefs in Kimbe Bay, Papua New Guinea, with diver operated video. Opportunistic transects were recorded at 40 m depth on two of these reefs. I recorded 4 – 6 transects per depth, per reef, with a total of 273 30 m x 4 m fish transects.

Dietary specialization

All Chaetodontidae species were classified into one of three diet-trait groups, Obligate (OBL), facultative (FAC), or non-coral benthic invertebrate (NON) feeders, according to Cole et al. (2008). The groups represent a gradient of decreasing dietary reliance on corals. I further assigned dietary-specialization levels to ten species from literature with comparable indices (Pratchett 2007, supplemental table S3.1); little variation occurs in dietary specialization levels among my study location and the location where indices were developed (Lawton et al. 2012b). To limit potentially spurious range estimates (e.g. Brown 1984, Gaston et al. 1997), rare species (occurring < 2 % of transects) were removed from all analyses except where grouped total abundance counts utilized multiple species (supplemental table S3.2).

Analyses

I undertook all analyses in R version 3.3.2 (R Core Team 2016). I tested for differences in mean depth ranges among trait groups using general linear models (GLM) with each member species' total depth range. I analyzed the influence of species-level dietary specialization on depth ranges using simple linear regression models (LM). I also used LMs to test abundance ~ depth-range relationships across all species, as well as among species within each diet-trait group. Species abundance was log-transformed to meet normality assumptions. I tested for differences in overall and within-depth abundances among the three trait groups by building generalized linear mixed models (GLMM) from raw count data using the package 'lme4'. I used the negative binomial error family with a log link to constrain model dispersion. I tested for overall differences in counts among diet trait groups (Count~Group), and also for the predicted variation in those patterns with increasing depth (+Group:Depth). I tested models for goodness of fit and over-dispersion by comparing sums of squared Pearson residuals to residual degrees of freedom. I also tested models for heteroskedastic variance, zero-inflation and spatial autocorrelation using the 'DAHRMa' package. All tests were passed. I then used 'car::Anova' and 'lsmeans::contrasts' to compare factors and levels of interest. All effect and error estimates were back-transformed using the exponent as the inverse of the log link before presenting results. I also tested for depth related variation in species level abundance-specialization relationships with LMs of mean species abundance as a function of dietary specialization, across all depths and within each depth.

I assessed whether species with any of the three vulnerability traits (narrow distribution, low abundance, and high dietary-specialization) were restricted to shallow water by regressing each risk trait against the shallowest and deepest depths occupied by species using LMs. Narrow-range was set at < 15m, low-abundance at 20 individuals (a mean of < 2 individuals per reef), and high-specialization was set at the level where substantial shallow water attrition and sub-lethal costs have been recorded in response to habitat loss (here, > 4.25 on a logX^2 scale).

I investigated differential distributions along the depth gradient among levels of dietary specialization using hierarchical logistic regression models (Huisman et al. 1993, Jansen and Oksanen 2013) of presence/absence data for the three diet trait groups (OBL, FAC and NON), and for four focal species from the OBL group. I determined the best model fit for each distribution using Akaike information criteria (AICc) and by comparing Akaike weights (w_i) between each of seven model types (see supplemental methods note) in 'eHOF' (Jansen and Oksanen 2013). I then tested model selection stability across 1000 bootstrapped iterations. I set the species occurrence cut-off at 30, and the frequency of species occurrences ranged moderately from 0.13 - 0.30 (see Supplemental table S3.2).

Results

Interrelationships

There was no relationship between depth-range and abundance at the trait group level, with high variation occurring within facultative and non coral-feeding groups (OBL, $F_{1,4} = 6.54$, $p = 0.063$, FAC, $F_{1,2} = 1.19$, $p = 0.39$; NON, $F_{1,5} = 1.40$, $p = 0.29$) (Fig. 3.1a). However, at the species-level, there was a significant relationship, with abundant species utilizing broader depth ranges than rarer species (log-linear: $R^2 = 0.39$, $F_{1,15} = 9.55$, $p = 0.008$) (Fig. 3.1b).

Dietary specialization did not significantly influence depth ranges among trait groups ($F_{2, 21} = 1.092$, $p = 0.35$) (Fig. 3.1c), with the depth ranges of obligate coral feeders being no more constrained than facultative or non-coral feeders. However, a strong positive log-linear relationship was evident across all 26 species ($R^2 = 0.84$, $F_{(1,6)} = 30.53$, $p = 0.002$), with more specialized species having broader depth ranges (Fig. 3.1d).

Higher abundance was clearly related to higher dietary specialization at the trait group (Chi-sq = 75.18, df = 2, $p < 0.001$), and species levels ($R^2 = 0.58$, $F_{1,7} = 9.66$, $p = 0.02$), when considered across all depths. Obligate coral feeders were approximately three times more abundant than both the facultative and non-coral feeders overall (Fig. 3.1e), and the most specialist species was ~25 times more abundant than the most generalist species (Fig. 3.1f).

The relationship between abundance and dietary specialization varied among depth strata (Fig. 3.2). Obligate corallivores were the most abundant trait group within each depth up to, but not including, 40 m (Chi-sq = 70.52, df = 15, $p < 0.001$). However, facultative feeders were only more abundant than non-coral feeders at the shallowest depth, with a clear crossover in abundances occurring at 10 m depth (Fig. 3.2a; and see Supplemental figure S1 for estimates of pairwise differences). The species level relationship attenuated more strongly with depth (Fig. 3.2b) and was only supported in shallow waters of ≤ 5m depth (< 1 m, $R^2 = 0.58$, $F_{1,7} = 9.46$, $p = 0.02$; 5m, $R^2 = 0.60$, $F_{1,7} = 10.38$, $p = 0.014$). There was a significant decrease in slopes of the relationship with increasing depth ($F_{5,41} = 3.274$, $P = 0.014$) (Fig 2b). For example, at <1 m the most specialized species was ~ 38 times more abundant than the least specialized species, but by 5 m the difference was ~ 8 fold, and at 10 m there was no detectable difference. Model effect size (R^2) also decreased with depth ($R^2 = 0.77$, $F_{1,3} = 9.92$, $p = 0.051$) (Supplemental figure S2).

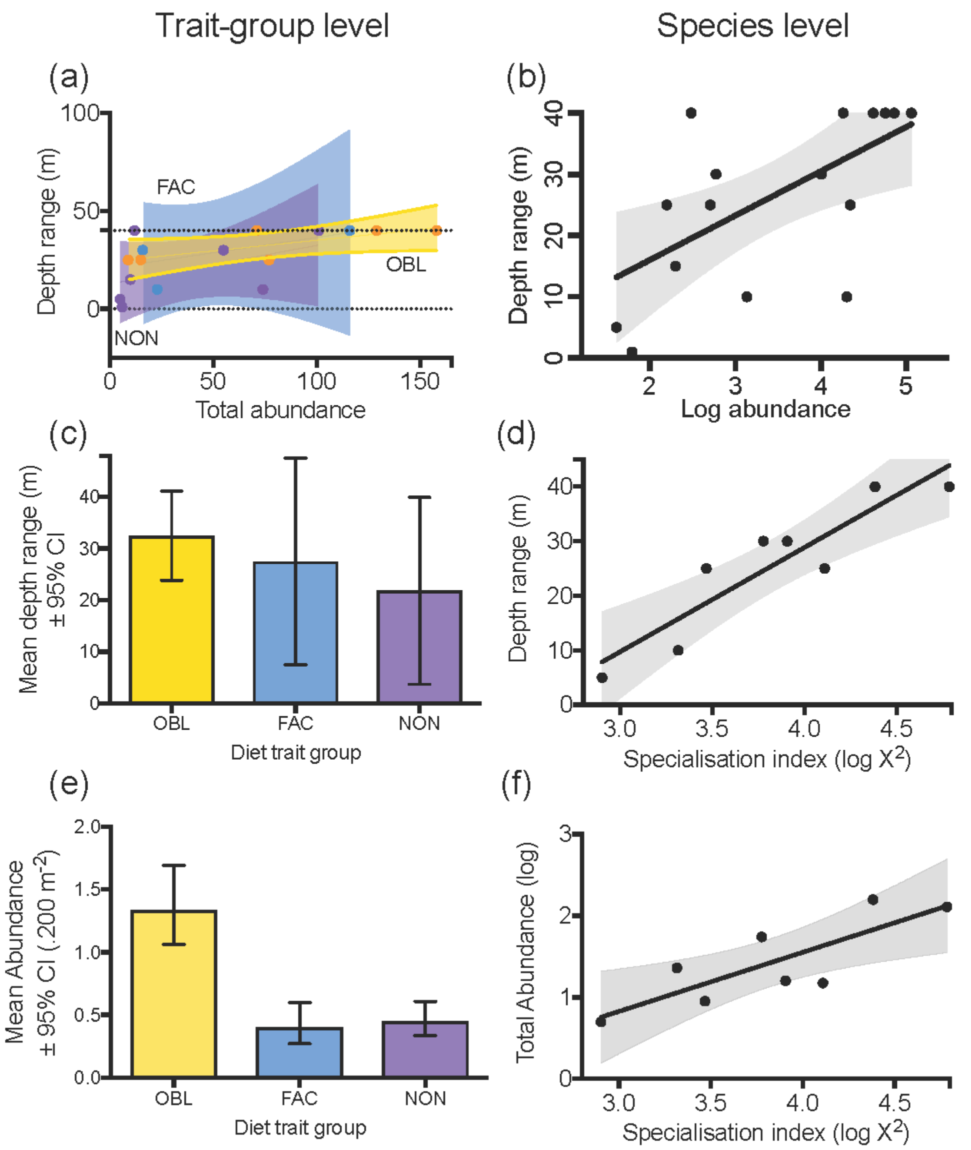

Figure 3.1: Plots of pairwise interrelationships between dietary specialization, abundance and depth-range among diet trait groups (left column) and species (right column) in the family Chaetodontidae; (a-b) relationships between depth range and abundance for 3 trait groups (a), and 25 species (b); (c-d) relationships between depth range and dietary specialization; (e-f) relationships between abundance and dietary specialization. The three dietary trait groups on the left side represent a gradient in dietary reliance on corals from Obligate (OBL, yellow), to facultative (FAC, blue), and non-coral (NON, purple) feeders. Error bands and error bars represent the 95% confidence intervals and the solid lines on the right side plots represent mean model fits. The dotted lines in (a) represent the depth range within which data were collected.

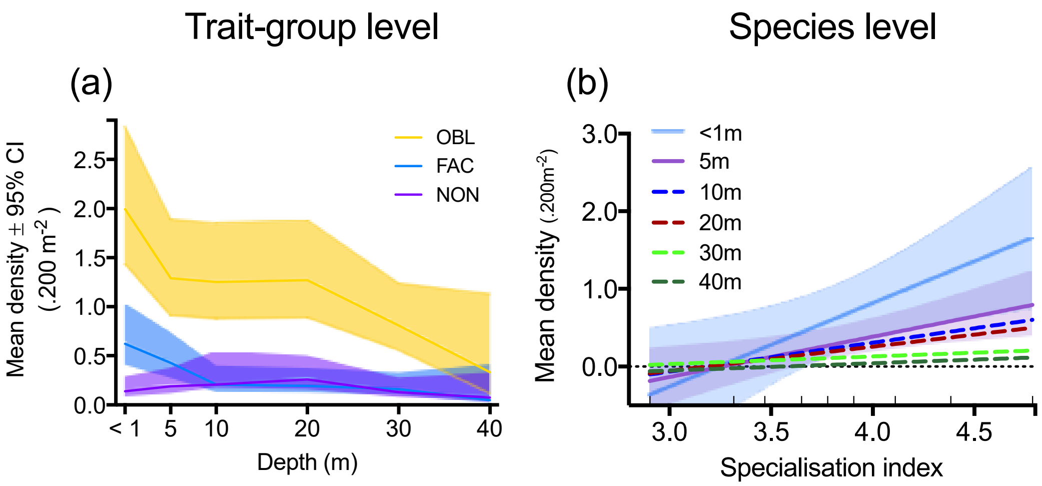

Figure 3.2: (a) Comparisons among mean densities of the three major diet trait groups in the coral reef fish family Chaetodontidae (butterflyfish), at each of six depths in Kimbe Bay, PNG. Error bands are 95% confidence intervals. OBL (yellow) = obligate coral feeders, FAC (blue) = facultative coral feeders, NON (purple) = non-coral benthic invertebrate feeders. Plot (b) shows the relationship between mean species abundance and dietary specialization among eight species within each of six study depths. Colors in (b) indicate water depth as per legend; solid lines represent statistically significant regressions (plotted with 95% confidence bands), and dashed lines represent non-significant regressions (α = 0.05).

Association of vulnerability traits with shallow water

Three species had narrow ranges that occurred wholly in the shallowest 15 m, with no species occurring solely in deep water (Fig. 3.3a). The deepest depth occupied by a species was strongly positively related to its overall depth range ($R^2 = 0.96$, $F_{1,14} = 400.7$, $p < 0.001$) (Fig. 3.3a - black), and all three species with depth ranges of ≤ 10m occurred solely in the shallowest 10 m. Species that had any part of their distribution in the shallowest depth (< 1 m) also had the broadest depth ranges ($R^2 = 0.42$, $F_{1,15} = 11.03$, $p = 0.005$) (Fig. 3.3a - white).

Two species with low abundance also occurred wholly in the shallowest 15 m. Species with shallower overall distributions generally had lower abundances. The deepest depth occupied by a species was moderately positively related to its overall abundance ($R^2 = 0.50$, $F_{1,14} = 13.95$, $p = 0.002$, log-linear, (Fig. 3.3b - black). However, some species with low abundances also occurred in depths ≤ 20 m, and species that had some occupancy in the shallowest depths (< 1 m) also generally, though not always, had the highest abundances (R^2 = 0.36, $F_{1,14}$ = 7.90, p = 0.014) (Fig. 3.3b - white).

No highly specialized species was limited to shallow water. Further, there was no general relationship between shallow-water association and dietary specialization (Deepest occupied depth ~ specialization index, R^2 = 0.12, $F_{1,6}$ = 0.80, p = 0.41; Shallowest occupied depth ~ specialization index, R^2 = 0.15, $F_{1,6}$ = 1.04, p = 0.35) (Fig 3c). All species with dietary specialization data available had some occupancy in waters ≤ 5m in depth. However, most (75%) also had some occupancy at depths ≥ 30m

Double jeopardy

Three species had narrow depth ranges, seven species had low abundance, and two of these species overlapped, creating a double jeopardy (Fig 3d). Two species had high dietary specialization, but both species had broad depth ranges and high abundance. Therefore, no species expressed a triple jeopardy situation. One highly specialized species (*Chaetodon trifascialis*) was too rare to include in formal analyses of depth ranges (4 individuals in 32,760 m^2). It also expresses double jeopardy (Fig. 3.3d – dotted lines), though depth may offer some risk mediation, as one of the four observed individuals was at 20 m depth.

Shallow biased specialists

Distributions were skewed toward shallow water among trait groups with higher reliance on corals (Fig. 3.4a) and among coral-obligate species with higher dietary specialization (Fig. 3.4b), but not among dietary generalists at either level. Occurrence probabilities declined monotonically with increasing depth for both the obligate and facultative coral feeding groups (max slopes: OBL, y = - 0.49x; FAC, y = - 0.37x). In contrast non-coral feeders were symmetrically distributed along the gradient, with peak distributions occurring in mid depths of 10 m – 20 m (Fig. 3.4a). Depth distributions differed among all four focal coral-obligate species, with a positive relationship apparent between increasing dietary specialization and increased distribution asymmetry toward shallow-water (Fig. 3.4b). *C. baronessa* was the most specialized species and the most common in shallow water, but its probability of occurrence declined steeply from ~ 0.6 at <1 m to ~ 0.2 by 10 m (max slope y = - 1.43x), though the rate of decline decreased in deeper water. *C. lunulatus* occurrence probabilities also declined monotonically with depth, though at a lesser rate than *C. baronessa,* from ~ 0.4 at <1 m to ~ 0.2 at 30 m (max slope y = - 0.33x), and in a linear fashion (Fig. 3.4a). *C. ornatissimus* did not respond to the depth gradient, with a probability of occurrence of ~ 0.18 at all depths (Fig. 3.4b). The fourth and most generalized of the species, *C. octofasciatus* had an asymptotic threshold response to the depth gradient, where it was almost completely absent from waters ≤ 5 m, but occurrence probability was equal (~ 0.2) at all depths beyond 10 m (Fig. 3.4b).

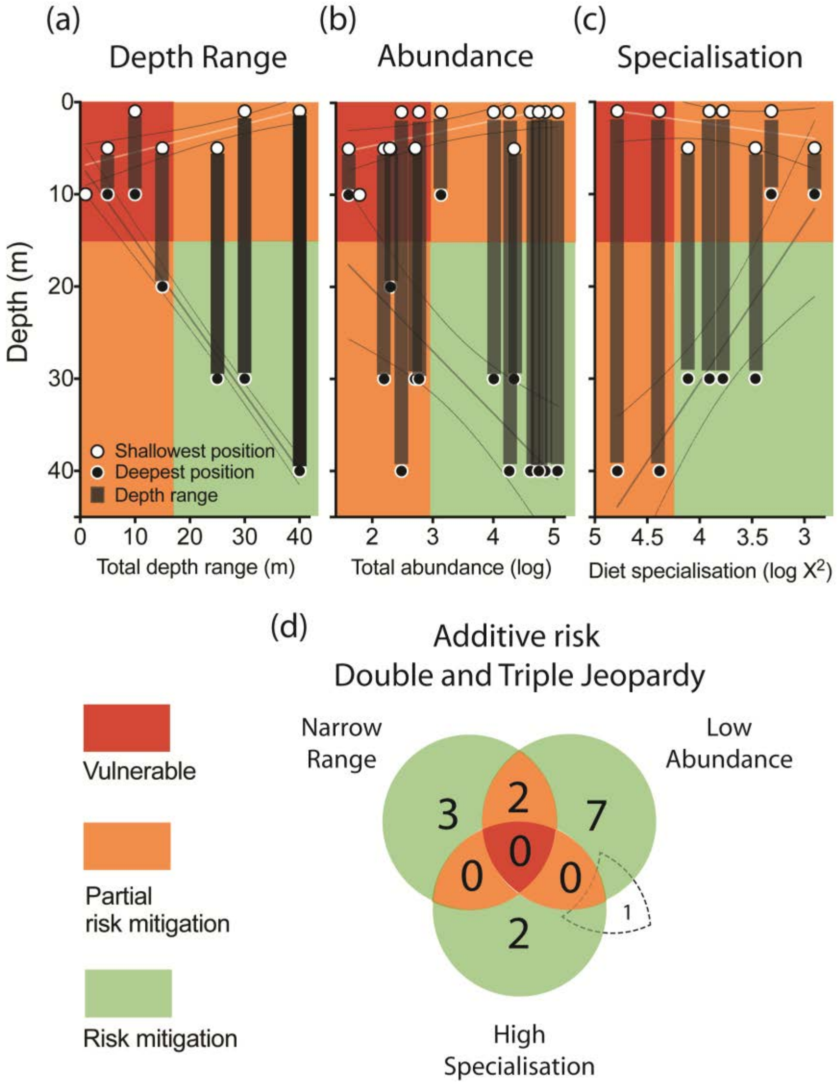

Figure 3.3: Relationships between shallow-water occupancy and: (a) depth ranges; (b) local abundance; and (c) diet specialization, among 26 species in the coral-reef fish family Chaetodontidae, in Kimbe Bay, PNG. White dots represent the shallowest depth occupied by a species, black dots represent the deepest occupied depths, and grey translucent bars represent the full depth range. Because surveys were depth stratified, multiple species in (a) have the same depth-ranges and overlap entirely. Solid lines are mean model fits (white = shallowest depth and black = deepest depth on the y axis). Dotted bands are 95% confidence intervals. Red, orange and green sections represent quadrants of hypothetical stress exposures in a-c, and increasing extinction risk in (d). The dotted petal in (d) represents one rare species with high dietary specialization excluded from formal analyses due to lack of confidence in range estimates.

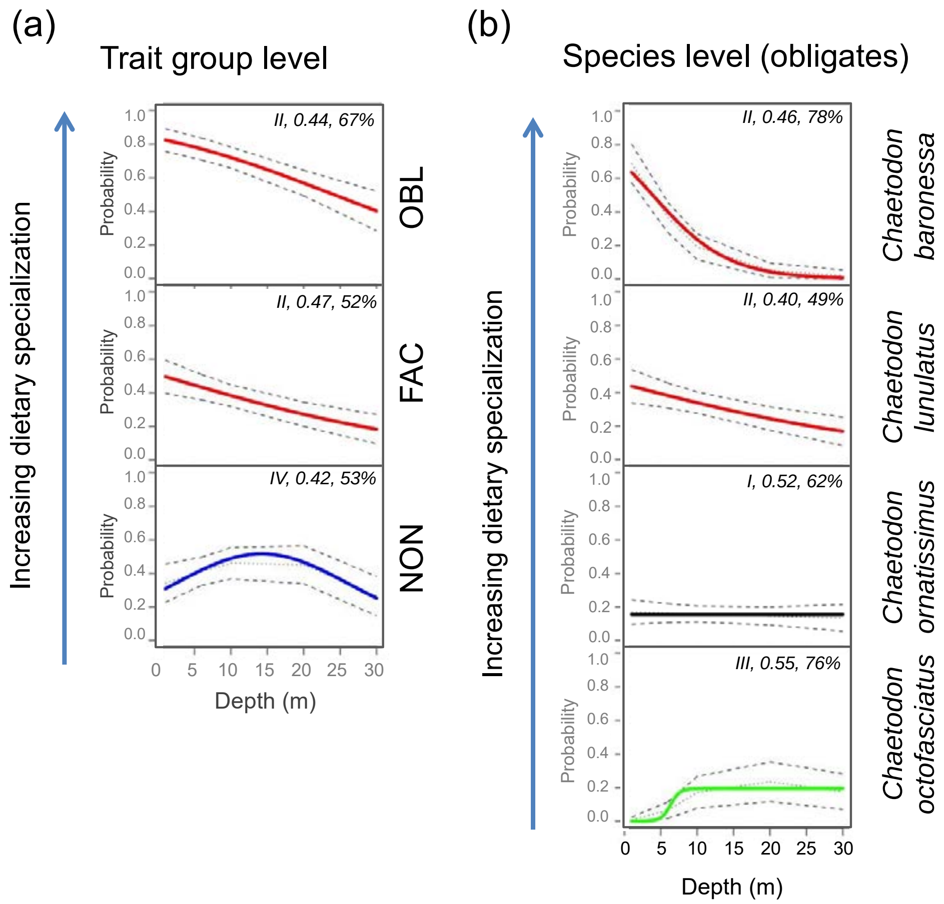

Figure 3.4: Distribution responses to the depth gradient among (a) three dietary trait groups, and (b) four focal obligate coral feeding species of the coral-reef fish family, Chaetodontidae. Each column is arranged in increasing level of dietary specialization from the bottom plot to the top plot. Modelled data are probability of occurrence. OBL = obligate coral feeders, FAC = facultative coral feeders, NON = non-coral benthic invertebrate feeders. Bold solid lines represent the best-fit of constrained hierarchical logistic regression (or, HOF) models. Dotted lines (sometimes obscured) represent best-fit GAM models, which give an unconstrained representation of the data. Dashed lines are 95% confidence limits for the GAM fits. Line colors indicate different types of HOF model fits (I-VII), which are indicated in the top right of each plot with roman numerals. After the model type, the weighted AICc score (0.0 – 1.0) of the model, and the percent of bootstrapped models confirming HOF fits, over 1000 iterations, are given.

Discussion

The interrelationships among depth distributions, local densities and diet specialization among butterflyfish in Kimbe Bay were not consistent with all traditional ecological expectations. Species with broad depth distributions reached greater local abundances as predicted; hence, rarer species had narrower distributions and narrow distributions should increase extinction risk from localized environmental change. However, contrary to expectations, the most-specialized coral-feeders (the group most vulnerable to habitat loss and extinction in shallow water, also had the broadest depth ranges and highest local abundances. Only three of the twenty-six study species (12%) occurred entirely in shallow water (< 15 m), where the greatest coral-habitat losses are likely to occur. Two of these species expressed a double-jeopardy situation by also having low abundances. However, all three species limited to shallow-water again had non-specialist (facultative or non-coral) diets. Therefore, the species most at risk from numerical rarity and restricted depth ranges may not be those with high dietary specialization, and lower coral reliance among these generalist species may therefore mediate some of the risk associated with shallow ranges. Overall, the results point to an unexpected resilience for some fish species previously considered vulnerable to shallow-water habitat losses on coral reefs and suggest deep reef slopes may offer them a potential refuge.

Despite the resilience potential conferred to dietary specialists by broad overall depth ranges, they are unlikely to be a panacea. As predicted, obligate coral-feeders, particularly specialist species, were strongly aggregated in shallow waters. If these distribution patterns are symptomatic of energetic or demographic costs that limit the success of deep-water residents, and downward vertical migration is not possible, habitat disturbances limited to shallow waters may lead to disproportionate numerical losses among the fittest members of coral-specialist species. In such cases, hypothetical refuge-populations of coral-specialists in deep-water might remain small, thus introducing a new set of risk factors.

Range and abundance

The ecologically common combination of narrow distributions and small populations (see Gaston et al. 2000) puts species at risk from both environmental change (Mckinney 1997) and population fluctuations (Williams et al. 2009). The classic examples of positive range ~ abundance relationships occurred at multiple spatial scales, across diverse taxa (Brown 1984). However, positive range ~ abundance relationships among reef-fish species have not been supported previously in broad SWG investigations, with some studies finding no relationships (Butterflyfishes: Jones et al. 2002, Lawton et al. 2012a), and others finding negative relationships (Angelfishes: Hobbs et al. 2010, Multiple taxa: Hughes et al. 2014). My results counter the findings of SWG reef-fish studies, and instead are congruent with general ecological theory. Butterflyfish species with broad depth-distributions had greater local abundances, and rarer species had narrower distributions.

One consequence of positive depth-range ~ abundance relationships is that rare species have the dual risk of population losses where environmental disturbances on reefs are patchy and vertically constrained. However, another potential ecological byproduct is the ‘rescue effect’, where members of abundant species migrate from the range core toward peripheries and reduce extinction risk at range margins (Hanski and Gyllenberg 1993, Lawton 1993). Therefore, abundant coral-specialists may have two sources of compensation for localized disturbances. Firstly, a greater number of individuals may buffer population losses, and secondly, such species have a greater potential for downward population range-shifts and additional re-seeding from deep range margins post disturbance. However, these benefits will be limited to cases where deep range margins provide viable habitats, and populations within core source habitats (e.g. shallow water) are not fully depleted.

Range and specialization

Specialist species are also expected to be vulnerable to environmental change because their distributions are spatially limited to locations where specific resource needs are met (Gaston et al. 1997). Range ~

specialization relationship have not been supported among reef fishes when considered across SWG ranges (Butterflyfishes: Jones et al. 2002, Anenomefishes: Jones et al. 2002, Ollerton et al. 2007, Anglefishes: Hobbs et al. 2010). Here, the most specialized coral-feeders also had the broadest vertical ranges, which was contrary to expectations from generalized ecological theory and from SWG range studies. However, previous studies have theorized and demonstrated that resource specialists utilizing widespread resources should themselves have broad distributions (e.g. Quinn et al. 1997, Gaston et al. 1997, Gregory and Gaston 2000). This suggests locations with suitable deep-water coral habitats can accommodate coral-specialist species, relieving some of the predicted, and increasingly evident pressures of shallow-water coral-habitat losses (Hughes et al. 2018). However, the comparatively limited depth-range of generalist species here also means that generalists themselves are not immune to risk from shallow-water habitat losses, especially because the loss of structural complexity associated with disturbances such as storm damage or successive bleaching events leads to high attrition rates even among facultative coral-feeders (Graham et al. 2009) and some non coral-associates (Jones et al. 2004).

Specialization and abundance along a depth gradient

Resource specialists also have higher extinction risks because the limited distribution and density of their prey results in low total abundances (Gaston et al. 1997, Lawton 1999, Harcourt et al. 2002). In turn, low abundance increases the risks associated with stochastic population dynamics (Williams et al. 2008). In shallow waters, reef fish abundance ~ specialization relationships have equivocal support, with multiple studies finding negative relationships (gobies: Munday 2004), no relationships (multiple families: Jones et al. 2002, angelfishes: Hobbs et al. 2010), and positive relationships, including among butterflyfishes (triggerfishes: Bean et al, 2002, butterflyfishes: Pratchett et al. 2013). My results supported positive abundance ~ specialization relationships, and confirm this unusual relationship in butterflyfishes from shallow water studies. High abundances may therefore partially mediate vulnerability to shallow-water habitat loss among some coral-specialists. This unexpected pattern has previously conferred long-term resilience to species in other systems. For example, in wet tropical rainforests, seemingly at-risk specialists have surprisingly maintained high populations and persisted over evolutionary time periods that included multiple intensive disturbances (Williams et al. 2009). The presence of this pattern across depths, as well as within shallow waters at the SWG scale demonstrates that resilience factors can operate concurrently at multiple spatial scales and resilience may be maintained if large tracts of shallow-water coral habitats are lost in the future.

Additive risk – multiple vulnerability traits and shallow water

Species with two or three way vulnerability combinations have increased extinction risks (Gaston 1996, Johnson 1998), particularly where ranges are restricted to highly disturbed locations (Thomas et al. 2004). To date, studies quantifying the proportion of species expressing single or multiple vulnerability traits and whose ranges also wholly or mostly overlap shallow waters have been surprisingly rare within coral-reef systems. Among the 26 butterflyfish species assessed here, twelve (33%) expressed at least one vulnerability trait. Two species (8%) experienced ‘double-jeopardy’, from combined narrow depth-range and low abundance. However, no species experienced ‘triple-jeopardy’, as all species with secondary vulnerability traits had broad dietary niches or were non-corallivores. Three species (12%) expressed at least one vulnerability trait and had a shallow range, but none of these were highly specialized coral-feeders. The fact that highly coral-specialized Chaetodontidae family members do not appear to suffer double jeopardy, nor are restricted to shallow waters in my study system, is encouraging for their persistence prospects under current and future conditions.

Potential costs of range contractions

Abundances have long been known to decline toward range margins (Grinnell 1922). Here the most coral-specialized species had strong biases toward shallow water and much lower abundances at deep range margins. This relationship held across trait groups, as well as among coral-obligate species. This pattern was expected but is striking here because the most coral-specialized species were also the most abundant and had the broadest depth ranges in this study system. Asymmetric distributions may follow asymmetric availability of quality resources (e.g. MacDonald et al. 2016), or be driven by population dynamics that differentially enhance and limit success between shallow and deep locations (sensu Holt and Keitt 2000). In the later cases, core source populations often feed more marginal sink locations (e.g. Lawton 1993), and future range contractions toward deep-water may compromise the persistence of specialist species if current deep ranges are strongly reliant on population substitution from shallow-water sources. Greater knowledge will be needed about possible ecological limitations to (e.g. Srinivasan et al. 2003, Bridge et al. 2016, MacDonald et al. 2018), and the potential energetic costs of (e.g. Smallhorn-West et al. 2017), deep residence in this group of vulnerable fishes. In addition, if shallow-water does provide keystone habitats (sensu Hitchman et al. 2018) and species are not able to reside solely at depth across multiple generations, range-only estimates of extinction risk may overestimate the mitigation factor of deep residence

Conclusions

Vertical ranges are often a good predictor of resilience to global environmental change in terrestrial systems (Parmesan and Yohe 2003, Raxworthy et al. 2008, Chen et al. 2011). Similarly, broad depth-ranges are likely to become an increasingly important factor in ecological resilience/recovery, and species persistence, among coral–reef taxa as shallow-limited species become increasingly more exposed to habitat disturbance (e.g. Graham et al. 2011, 2015). My results demonstrate that interrelationships among vulnerability traits along depth gradients in coral reef systems do not necessarily follow generalized expectations from ecological theory, or from coral reef studies in shallow waters. However, the results do support the conclusion that interrelationships among vulnerability traits and occupancy depths mediate a substantial component of risk among a family consisting mostly of vulnerable coral-reef fishes. Specialization is considered a fundamental trait that increases extinction risk across widespread taxa (Foufopoulos and Ives 1999, Fisher et al. 2003, Julliard et al. 2004), and this is also the case among reef-fish (Roberts and Hawkins 1999, Wilson et al. 2006, Graham et al. 2011). However, the most specialized species here were also the most abundant and the most broadly distributed, with no specialist species experiencing double or triple jeopardy or being wholly restricted to shallow water, where habitat disturbance is often highest. Thus, deep distributions and high abundances appear to mediate some risk associated with strong habitat reliance in this group. On the other hand, the distributions of specialist species were also strongly biased toward shallow waters. The underlying reasons for declining abundance with depth are not clearly established, and further work is needed to determine the potential for deep water to act as a temporary or permanent refuge for strongly coral associated reef fish species.

Chapter 4 - MARGINAL SINKS OR POTENTIAL REFUGES? DEEP HABITATS INCREASE RESOURCE ACCESS AND CONFER NO SUB-LETHAL COSTS IN A VULNERABLE GUILD OF CORAL-OBLIGATE REEF FISHES.

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Abstract

Escalating climate-related disturbances and asymmetric habitat-losses will increasingly result in species living near current range margins. Marginal habitats may represent important refuges for these species, as long as individuals can acquire adequate resources to survive and reproduce. However, the costs of securing sparsely distributed resources at range margins can be substantial and may result in sub-optimal individuals forming non-self-sustaining sink-populations. Shifting resource availability is likely to be particularly problematic for dietary specialists. Here, I use extensive in-situ behavioural observations and physiological condition measurements to examine the costs and benefits of resource-acquisition along a depth-gradient in two obligate corallivore reef fishes with contrasting levels of dietary specialisiation. I show that the space utilised to secure coral-resources increased towards the lower depth limit as expected. However, increased territory sizes resulted in equal or greater total resources secured within deep territories. I observed no differences in foraging-distance, pairing-behaviour, body condition or fecundity at greater depths, as well as decreased competition. Contrary to expectation, my results demonstrate that deep-water coral-obligate fishes can select high-quality coral patches to access equal or greater resources than their shallow-water counterparts, with no extra costs. This suggests depth offers a viable potential refuge for some at-risk coral-specialist fishes.

Introduction

Rapid climate change has increased ecosystem degradation and extinction risk across most of the earth's biomes and taxonomic groups, with many species experiencing range contractions or displacements from core ranges (Parmesan and Yohe 2003, Thomas et al. 2004, Lenoir and Svenning 2015, Scheffers et al. 2016, Pecl et al. 2017). Many currently extant species radiated from organisms that survived past global-scale environmental change (e.g. Quaternary glacial cycles) in cryptic refugia at range peripheries (Stewart and Lister 2001, Provan and Bennett 2008). Successful survivorship and reproduction in small refuges, often at range peripheries (Scheffers et al. 2014), is likely to be important for many species' long-term resilience to asymmetric impacts from current rapid climate changes (Ashcroft 2010, Keppel et al. 2012). The potential for peripheral habitats to act as refuges largely depends on individual performance at these ecological extremes. Species presence does not always relate to individual success or population viability, therefore understanding the ecological factors that limit population success at range margins is critical for predicting future trajectories.

Individuals occupying a species' range margin face many potential costs. While species' realized-niches are ideally centred on regions of optimal performance along gradients (e.g. (González-Guzmán and Mehlman 2001, McGill et al. 2006)), source-sink dynamics, density-dependence, and intra-trophic competition cause species to extend beyond ideal niches (Terborgh 1977, Lawton 1993, Pulliam 2000). At range margins, habitats and populations often become more fragmented (Brown 1984, Thomas and Kunin 1999), occupancy decreases (Kawecki 2008), and individuals may exhibit behavioural changes and/or experience physiological costs (Zammuto and Millar 1985, Badyaev and Ghalambor 2001, Smallhorn-West et al. 2017) in relation to securing sparcer resources. For example, the summer ranges of roe deer are much larger at higher altitudes, where food resources are sparser (Mysterud 1999), and greater reliance on high-altitude habitats results in lower body condition among red deer (Mysterud et al. 2001), and lower avian fecundity (Krementz and Handford 1984).

Despite these costs, occupying range margins may also present advantages, such as reduced competition (Goldberg and Novoplansky 1997, Choler et al. 2001). In addition, although population abundances may be lower in fragmented peripheral habitats, inhabited patches may not differ greatly from ideal conditions within range centres (Carter and Prince 1981, Holt et al. 2005). In such cases, margin dwellers may incur little fitness cost (Prince and Carter 1985, Samis and Eckert 2009, Sexton et al. 2009). Asymmetric disturbance impacts may also result in previously optimal habitats becoming suboptimal, while marginal habitats remain stable. Consequently, marginal habitats can serve as good candidates for refuge populations if costs are not high. Assessing individual performance among marginal populations requires detailed knowledge of changes in key ecological strategies and demographic traits between the range core and periphery habitats. However, range peripheries are typically under-sampled, and detailed ecological assessments of individual space-use, resource-access, and physiological-condition at range margins constituting potential refuges are rare among animals (Feldman and McGill 2013).

Coral reefs are highly diverse ecosystems and exhibit strong ecological gradients over small spatial scales (e.g. (Done 1982, Williams 1982, McGehee 1994b, Berumen et al. 2005)). Coral habitats are also highly vulnerable to global-scale degradation (Pandolfi et al. 2003, Bellwood et al. 2004, Hughes et al. 2017), however, highly divergent responses often occur at smaller spatial scales (e.g. (Nyström and Folke 2001, Graham et al. 2015, Roche et al. 2018)). Therefore coral reefs provide an ideal model ecosystem for assessing drivers of differential responses to climate change and habitat degradation along environmental gradients (Graham et al. 2015). While warm-water bleaching events are increasing (Hughes et al. 2018, Lough et al. 2018), impacts frequently attenuate with depth (Marshall and Baird 2000, Bridge et al. 2013, Muir et al. 2017). Deep-water could offer a potential refuge for coral reef fishes vulnerable to shallow-water habitat loss (e.g. (Jankowski et al. 2015, Bridge et al. 2016, MacDonald et al. 2016)), and fishes with broad depth ranges are considered at lower risk of extinction than species restricted to shallow depths (Graham et al. 2011). Furthermore, recent studies have demonstrated large proportions (up to 85%) of coral-associated fish species occur at or below 20 m depth in some systems (MacDonald et al. 2016). Despite these broad depth ranges and a lack of obvious dispersal barriers, densities of coral-specialists can decline dramatically with depth (Chapter 3), presumably in response to concomitant declines in resource quantity and/or quality (MacDonald et al. 2016). While it is clear that many coral-obligate reef fish species occur at greater depths than currently appreciated, the ecological and physiological costs of deep residence on reefs remain unknown.

The ecological, behavioural, and condition responses of coral-dependent fishes to coral declines in shallow water are well established. Low densities of preferred coral genera are related to increased space use, increased effort in resource protection, and changed social dynamics (Hourigan 1989, Tricas 1989, Wrathall et al. 1992, Righton et al. 1998, Berumen and Pratchett 2006), as well as increased sub-lethal costs (Kokita and Nakazono 2001, Pratchett et al. 2004, Berumen et al. 2005). If similar dynamics occur along depth gradients, this may mitigate the refuge potential of deep reefs. However, due to the difficulty and time limitations of deep-water diving, there is a paucity of detailed ecological data among vulnerable taxa with extensive depth ranges on coral reefs (but see Smallhorn-West et al. 2017). This has lead assessments of extinction threats, and commentary on the potential ability of depth to provide refuge for reef fish, to largely assume intraspecific ecology is static along steep depth gradients (Hawkins et al. 2000, Graham et al. 2011, Darling and Côté 2018). However, this assumption has not been tested. Here I examine changes in the ecology of two corallivorous butterflyfishes (*Chaetodon baronessa* and *C. octofasciatus*) with contrasting levels of dietary specialization along a depth gradient from 0 - 35 m to investigate the behavioural and physiological costs of living at greater depths. Specifically, I tested whether 1) individuals' space use increased with depth; 2) lower resource densities resulted in fewer secured coral resources in deeper territories; 3) decreased resource availability led to behavioural costs related to accessing and securing resources at depth; and 4) individual body condition, energy storage and fecundity declined with depth.

Methods

Study site and focal species

I recorded the spatial parameters, conspecific-neighbour densities, rates of maintenance behaviours, and coral resource densities over 24-weeks of observations within all territories of two obligate coral-feeding butterflyfish species, between <1 m and 35 m depths within a 250 m wide section of Christine's reef in Kimbe Bay, Papua New Guinea. The vertically continuous coral habitat along the entire depth gradient of the focal reef is representative of reefs in the region and presents no physical barriers to movement among depths. I chose two obligate corallivore focal species with equivalent total depth ranges (0 - 40 m), but with contrasting density distributions within depth ranges, and contrasting levels of specialization within their coral-obligate diets. *Chaetodon baronessa* (n = 39 territorial pairs) is termed here a 'Shallow-Specialist' as its distribution is strongly skewed toward shallow water and it has a narrow dietary niche (niche breadth = 0.07), with high selectivity for *Acropora* corals (Chapter 3, Chapter 5). In contrast, *Chaetodon octofasciatus* (n = 21 territorial pairs) is termed a 'Deep-Generalist' as it has a broad dietary niche (niche breadth = 0.23) and occurs infrequently in waters of ≤5 m but is distributed equally from 10 m – 30 m (Chapter 3, Chapter 5).

Territory size

Territorial butterflyfish patrol territory perimeters frequently, using habitual swim paths (Righton et al. 1998). Territorial pairs were identified using individual markings, external tags (Floyd T-bar) and their site fidelity, which was confirmed from many repeat observations over the course of the study. I demarcated territories by observing pairs for multiple 5-15 minute periods (minimum of 3 initial observations), marking swim paths and territorial boundaries with flagging tape. Territories were confirmed via frequent re-visitations over multiple weeks, and the perimeter, minimum and maximum depths of territories were measured in-situ (see supplemental methods).

Within territory resource density and "total secured resources”

I recorded the density of ‘total-coral’ resources and of the highly preferred genus ‘*Acropora*’ within each territory, from 1 m^2 photographed benthic quadrats at ~ 2 m intervals around each perimeter. The benthic component directly under each of 25 randomly allocated points was recorded for each quadrat in Coral Point Count e (CPCe) (Kohler and Gill 2006). Corals were recorded to genus level. I calculated ‘Total Secured Resources’ of total-corals (TSR_T) and *Acropora* corals (TSR_A) within territories by multiplying the mean density of each resource by the area encompassed within a 1m internal border around the perimeter length. For local comparisons, total coral cover and *Acropora* coral cover were also recorded from 60 random points in 4 – 6 replicate transects at depths of <1m, 5m, 10m, 20m, and 30m, on ten reefs throughout Kimbe Bay (MacDonald et al. 2016). I used more intensive benthic sampling on the focal reef from 90 - 120 replicate photo-quadrats per depth (~1 m^2) at <1 m, 5 m, 10 m, 15 m, 20 m, 25 m and 30 m.

Behaviour

I recorded rates of territorial interactions, movement, and pairing within the same focal territories. Observations were recorded simultaneously during 4 - 6 replicate three-minute observation periods for each pair, with focal fish followed at a distance of ~ 2 - 4 m. Movement paths were marked approximately every 0.5 – 1 m, and total distance measured. Pairing status and water depth were recorded every 15 seconds (paired, ≤ 2 m from partner). Observations were not recorded if focal fish showed flight or aggressive display responses. Conspecific density was calculated as the number of directly adjoining territories divided by the length of the focal perimeter.

Body condition

I determined the condition of fish residing at different depths with five commonly used metrics. After collection of behavioural data, fish from most territories were harvested by spear in January 2016 (*C. baronessa* = 35 females, 31 males, *C. octofasciatus* = 16 females and 15 males). A further 10 males and 21 female *C. octofasciatus* were collected in November 2016. All fish were gutted, weighed, and measured. Gonads and livers were removed, weighed and stored in 4% calcium buffered formalin. The five physiological condition metrics were: Total length (TL); Fulton's K ($K = 100 * W_{gutted} / TL^3$); Histosomatic index (HSI) ($HSI = 100 * W_{liver} / W_{gutted}$); Gonadosomatic index (GSI) in females ($GSI = 100 * W_{gonad} / W_{gutted}$); and proportion of vacuolated hepatocyte cells in males.

Hepatocyte vacuolation uses the proportion of hepatic cells with lipid storage vacuoles as a measure of energy storage, where a higher proportion of vacuolated cells equates to greater energy stores and better condition (Pratchett et al. 2004). Livers were dehydrated in a graded ethanol series in the laboratory, embedded in paraffin wax, sectioned to 5µm, and stained with Mayer's haematoxylin and eosin. Sections were digitally photographed at 400x magnification and each frame was overlaid with 50 random stratified points in CPCe. The proportion of points intersecting vacuoles was recorded from three frames from each of three sections per liver, resulting in nine replicate 50-point-counts per fish.

Analyses

Differences in territory sizes among depths were examined using linear models (*lm*) of log(*perimeter*) length against *median-territory-depth (med.ter.depth)*. The density of each coral resource (total-corals, and *Acropora*) was modeled against *med.ter.depth* using binomial comparisons of the number of points identifying 1) *coral* and *non-coral* substrata, and 2) *Acropora* and *non-Acropora* substrata within territories. Models were performed in *glmer*, from the r package *lme4* using *quadrat* as a random factor. TSR_T and TSR_A were modeled against *med.ter.depth* using *lm*. *Conspecific-density* was modeled against *med.ter.depth* using *glm* with a Poisson error-wise family. Rates of territorial *interactions* were modeled against *med.ter.depth* using a Poisson error-wise family in *glmer.* Territory (*ID*), and observation (*Obs*), were included as random factors. The log of *distance* moved, was modeled against *med.ter.depth* in *lmer,* with *ID* and *Obs* included as random factors. Pairing ratios were modeled against *med.ter.depth* in *glmer*, using a binomial comparison of *paired* and *not-paired* observation counts, with *ID* and *Obs* included as random factors. *TL*, *Fulton's K*, *HSI*, and *GSI* were modeled for variation among *med.ter.depth* using *lm*. Variation in hepatocyte vacuolation rates with *med.ter.depth* was tested using a binomial comparison of *vacuolated* and *non-vacuolated* cell counts in *glmer*, with *ID* and *Obs* included as random factors. For models fit in *lmer* and *glmer*; *r.squaredGLMM* was used to obtain pseudo-R-square estimates; *dispersion_glmer* was used to test for over-dispersion; deviance based tests of fit were undertaken; *confint* was used to obtain confidence intervals; and *glht* was used to obtain probability estimates of effects. For *C. octofasciatus*, analyses of body condition metrics first incorporated *collection date* as an interaction term. No interactions were present (no 95% CI crossed zero, all $p > 0.10$), so the term was excluded from final models ($condition.metric_i \sim med.ter.depth$). All analyses were therefore consistent between each species and were undertaken in R version 3.3.2 (R Core Team 2016).

Results

Territory size

Mean territory sizes did not differ between the two species overall (Table 4.1, Fig. 4.1a). However, the hypothesis that territory area would increase with depth was supported for one of the two species: mean territory size increased approximately three-fold along the depth gradient for *C. baronessa* - the shallow-specialist (Fig. 4.1b) but did not change for *C. octofasciatus* - the deep-generalist (Fig. 4.1c).

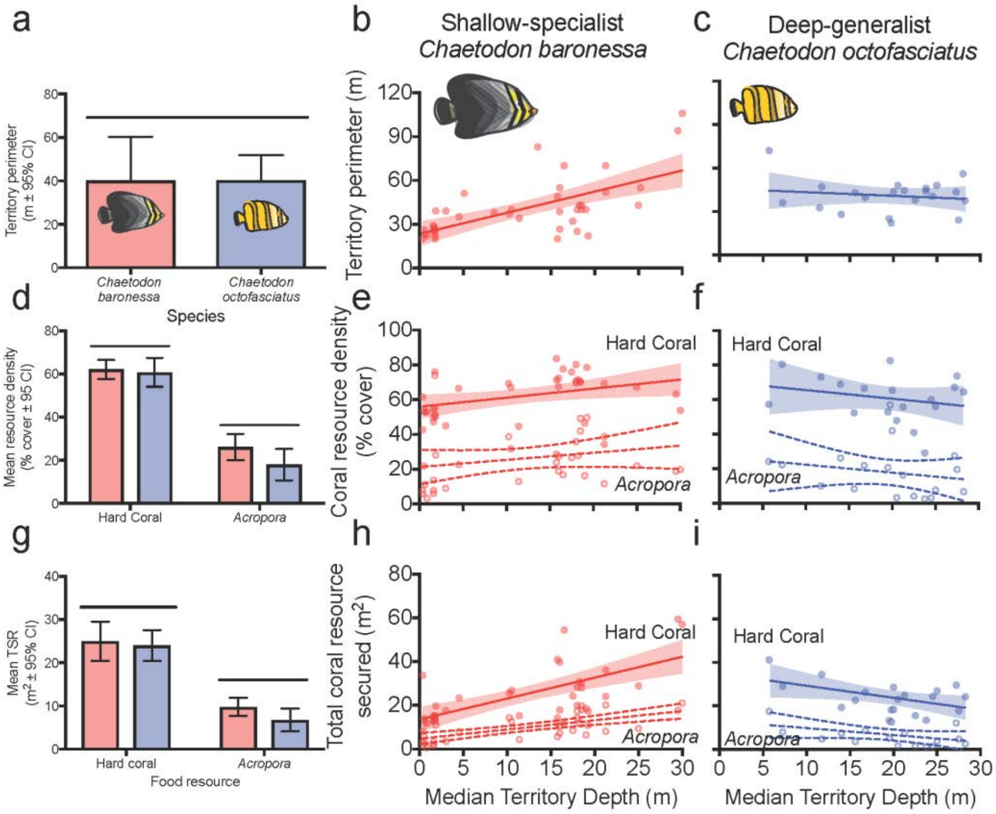

Figure 4.1: (a) Interspecific similarities in territory size between a shallow-specialist (Chaetodon baronessa - red) and deep-generalist (C. octofasciatus - blue) obligate coral-feeding butterflyfish species, and intraspecific variation in territory size along a depth gradient from 0 – 30 m for (b); the shallow-specialist species and (c); the deep-generalist. (d-f) Within-territory resource densities, showing (d) the interspecific similarities, (e) intraspecific variation along the depth gradient for the shallow-specialist, and (f); depth variation for the deep-generalist. (g-i) Total secured resources within territories, showing (g); interspecific similarities, (h); intraspecific variation along the depth gradient for the shallow-specialist, and (i) depth variation for the deep-generalist. Lines above bars in a, d, g, represent statistically similar means. In regression plots, each variable is modeled against the median depth of territories; solid lines and straight dotted lines represent best fits, bands represent 95 % confidence intervals, and each data point represents a territory.

Resource availability

Total hard coral cover throughout the bay did not decline with depth (mean ~ 55% at all depths), but the cover of *Acropora*, the preferred prey of my two focal species declined from ~ 25% at <1 m to ~ 2% at 30 m (supplemental figure S1). Within the focal reef, total hard coral cover peaked at 15 m (~72%) and was lowest at 30m (~ 48%) ($F_{(1,5)} = 10.79$, $p < 0.001$). *Acropora* cover on the focal reef was highest at < 5 m (~ 23 %) and lowest at 30 m (~ 7%) ($F_{(1,5)} = 10.91$, $p < 0.001$).

The hypothesis that within-territory resource densities would decrease with depth was not supported for either species (Table 4.1). Mean densities of both total-coral and *Acropora* resources did not vary between territories of the two species overall (Fig. 4.1d) and did not decline with depth in the territories of either species (Fig. 4.1e & 1f). In fact, the density of total-coral resources increased ~ 15% along the depth gradient for the shallow-specialist (Fig. 4.1e). As a result of increasing territory size and stable or increasing resource densities with depth, TSR_T and TSR_A within territories of the shallow-specialist both increased approximately three-fold along the depth gradient (Fig. 4.1h). In contrast, TSR_T declined by almost half between the shallowest and deepest territories of the deep-generalist species, while TSR_A was consistent along the gradient (Fig. 4.1i).

Neighbour density and maintenance effort

There was no apparent increase in neighbour density or maintenance effort with depth (Table 4.2). For the shallow-specialist, the number of directly neighbouring conspecific territories decreased with depth (Table 4.2, Fig. 4.2a). Correspondingly, mean neighbour densities declined almost five-fold between shallow and deep territories (Fig 2b). The rate of territorial interactions for the shallow-specialist also declined by over two-thirds along the gradient (Fig. 4.2c). Depth explained a small proportion of variation in movement rates of the shallow-specialist, with mean rates declining by approximately one third from the shallowest to deepest territories (Fig. 4.2d). Pairing behaviour in the shallow specialist did not vary with depth. In contrast, there was no depth-related change in neighbour density (Fig. 4.2a), territorial interaction rates (Fig. 4.2b), or movement rates for the deep-generalist (Fig. 4.2c), and pairing rates of the deep-generalist also did not decline with depth (Fig. 4.2d).

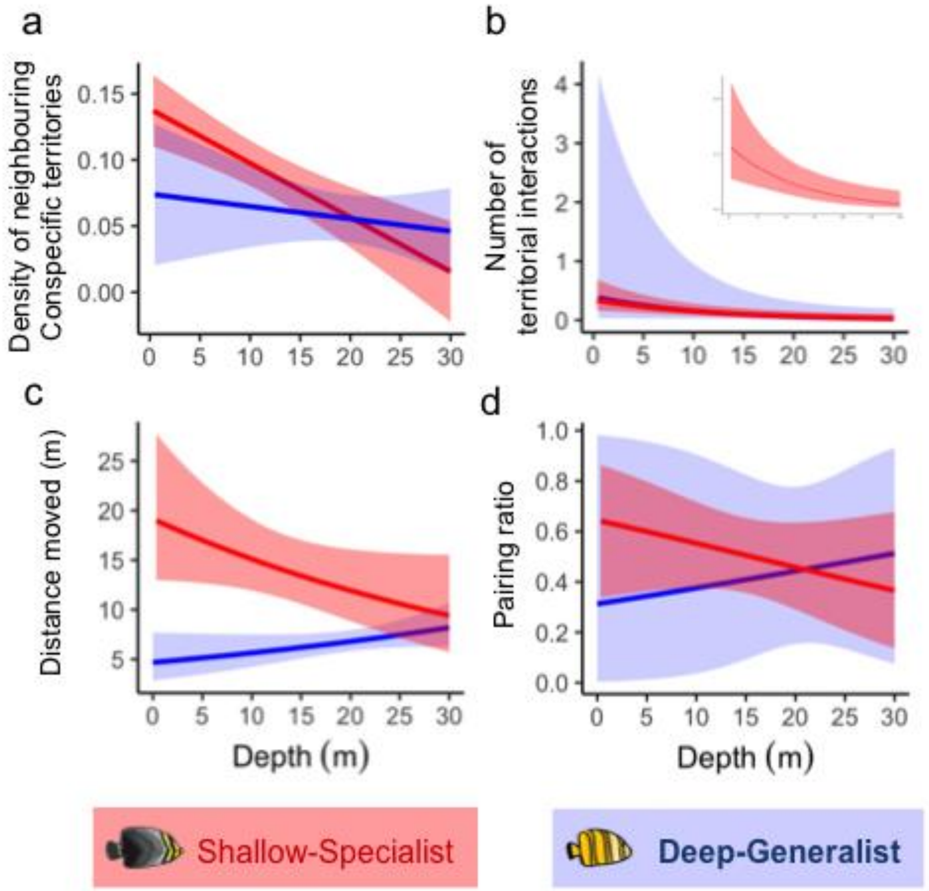

Figure 4.2: Depth related variation in competitor density and territorial maintenance effort. (a) The density of directly neighbouring conspecifics around territory perimeters. (b) The number of territorial interactions (insert shows shallow-specialist only), (c) the distance moved, and (d) mean paring ratios. Solid lines represent the best fit for generalized linear models and bands are 95% confidence intervals

Table 4.1: Result summaries of depth related variation in territory size, within territory densities and total-availability of major coral resources, and the number of directly neighbouring territories.

Species	Metric	Response variable	R2	Estimate ± SE	Intercept ± SE	F(df)	p-value
Chaetodon baronessa (specialist)	Territory size	Perimeter	0.42	1.45 ± 0.14	23.39 ± 4.14	27.09(1, 38)	< 0.001
	Resource Density	Total-coral	0.14	0.52 ± 0.11	55.96 ± 3.37	5.37(1,32)	0.027
		Acropora	0.05	0.41 ± 0.17	21.26 ± 4.90	1.56(1,32)	0.22
	Total Secured Resources (TSR)	Total-coral	0.46	0.96 ± 0.10	13.56 ± 2.78	26.66(1,32)	< 0.001
		Acropora	0.44	0.42 ± 0.09	4.75 ± 1.28	24.76(1,32)	< 0.001
	Neighbour density	conspD	0.40	-0.004 ± 0.0009	0.14 ± 0.01	20.20(1,31)	< 0.001
Chaetodon octofasciatus (generalist)	Territory size	Perimeter	0.02	-0.25 ± 0.39	45.87 ± 8.00	0.43(1, 19)	0.52
	Resource Density	Total-coral	0.26	-0.56 ± 0.24	34.81 ± 4.86	5.50(1,16)	0.032
		Acropora	0.16	-0.32 ± 0.19	12.98 ± 3.79	2.99(1,16)	0.10
	Total Secured Resources (TSR)	Total-coral	0.06	-0.50 ± 0.50	70.52 ± 10.20	1.01(1,16)	0.33
		Acropora	0.04	-0.46 ± 0.54	27.00 ± 11.08	0.74(1,16)	0.40
	Neighbour density	conspD	0.03	-0.0009 ± 0.002	0.07 ± 0.03	0.55(1,19)	0.47

Table 4.2: Result summaries for models of depth related variation in territory maintenance effort.

Species	Relationship	Response variable	R^2_{marg}	R^2_{cond}	Estimate	Conf. int. (95%)		z	p
						lower	upper		
Chaetodon baronessa (specialist)	Distance moved	log(*dist*ance)	0.04	0.26	-0.02	-0.04	1.55^{-03}	-1.85	0.098
	Interactions	interactions	0.14	0.22	0.92^	0.87^	0.97^	-3.29	0.001
	Pairing	Cbind(p,np)	<0.00	<0.00	0.49	0.47	0.51	-1.05	0.315
Chaetodon octofasciatus (generalist)	Distance moved	log(*dist*ance)	0.06	0.35	0.02	-0.04	0.04	1.61	0.134
	Interactions	interactions	0.09	0.17	0.91^	0.80^	1.01^	-1.79	0.073
	Pairing	Cbind(p,np)	<0.00	0.31	0.56	0.45	0.56	0.25	0.802

^Estimates and confidence intervals based on log link for the Poisson error family are factorial. In this case, evidence does not support an effect where confidence intervals cross one.

Body condition

No aspect of physiological condition declined significantly with depth in either fish species (Table 4.3, Fig. 4.3). Neither female nor male *C. baronessa* total lengths (TL) declined with depth (Fig. 4.3a). Similarly, neither relative body mass nor hepatosomatic index declined with depth in either sex (Fig. 4.3b, c). The fecundity (GSI) of female *C. baronessa* did not decline with depth (Fig. 4.3d), and neither did energy storage (hepatocyte vacuolation) among males (Fig. 4.3e). However, there was some indication that a small proportion of variation in body mass of male *C. baronessa*, and the fecundity and HSI of females may have depth trends (all; $R^2 < 0.13$, probability = 0.1 <p> 0.05, Table 4.3). For *C. octofasciatus*, neither total lengths, relative body mass, nor hepatosomatic index declined with depth for either sex (Fig. 4.3f-h). The GSI of female *C. octofasciatus* did not decline with depth (Fig. 4.3i), and neither did energy storage among males (Fig. 4.3j).

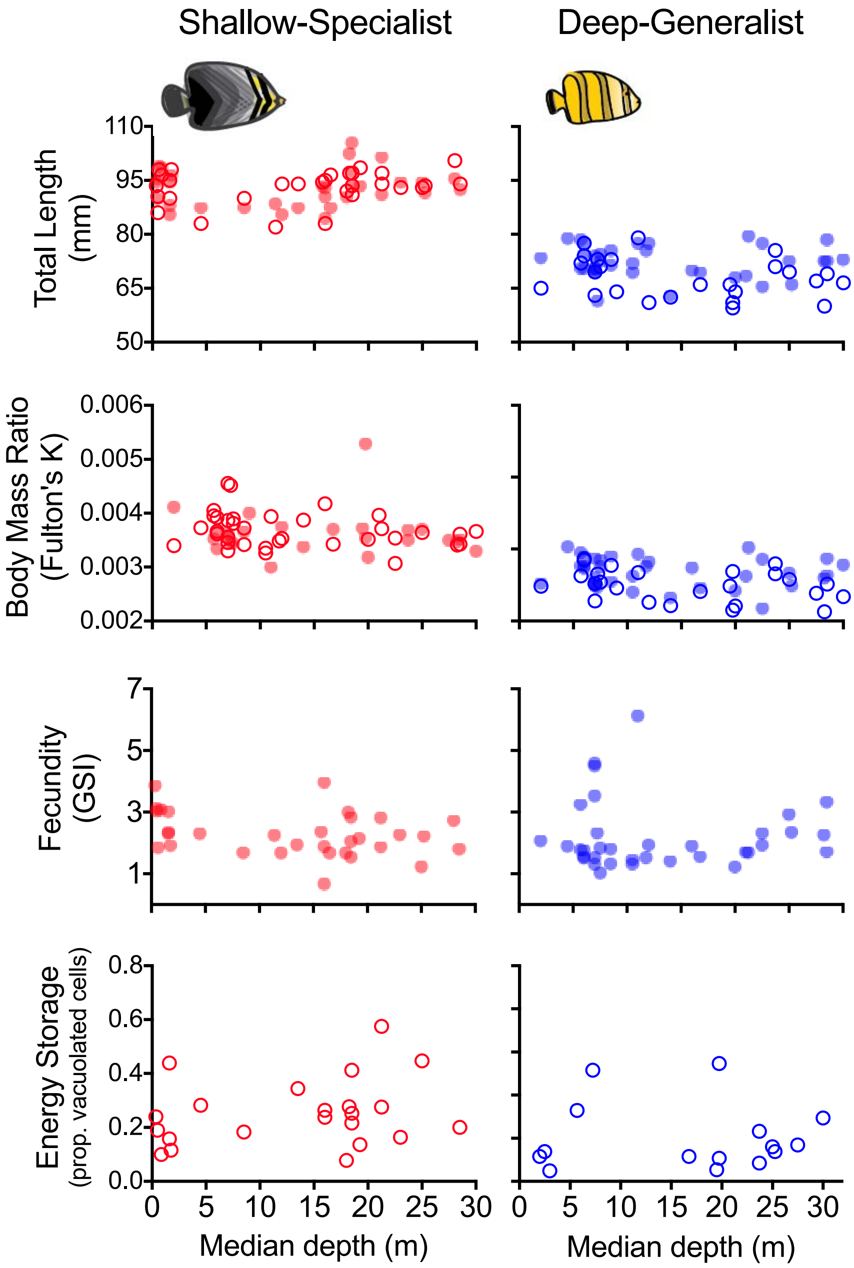

Figure 4.3: Relationships between body condition and depth. Metrics are: (a & f) total length; (b & g) relative body-mass; (c & h) hepatosomatic index (d & i) reproductive potential; (e & j) energy storage. Data points = individual fish. Closed circles = females. Open circles = males.

Table 4.3: Result summaries of depth-related variation in body condition. Italicized P-values show metrics approaching statistical significance.

Species	Condition (metric)	Sex	R^2	Estimate ± SE	Intercept ± SE	Test Statistic	p-value
Chaetodon baronessa (specialist)	Body Length (Total Length)	F	0.02	0.08 ± 0.10	91.34 ± 1.62	F = $0.58_{(1, 30)}$	0.454
		M	0.06	0.13 ± 0.09	91.43 ± 1.50	F = $1.85_{(1, 28)}$	0.184
	Relative Body Mass (Fulton's K)	F	0.04	$-3.46^{-06} \pm 3.23^{-06}$	$3.05^{-03} \pm 5.18^{-05}$	F = $1.14_{(1, 30)}$	0.294
		M	0.12	$-1.11^{-05} \pm 5.67^{-06}$	$3.37^{-03} \pm 9.33^{-05}$	F = $3.81_{1, 28)}$	0.061
	Relative Liver Mass (LSI)	F	0.11	-0.01 ± 3.73^{-03}	1.38 ± 0.06	F = $3.83_{(1, 30)}$	0.060
		M	0.06	-0.01 ± 0.01	1.16 ± 0.10	F = $1.72_{(1,28)}$	0.201
	Fecundity (GSI)	F	0.10	-0.025 ± 0.01	2.56 ± 0.22	F = $3.44_{(1, 30)}$	0.074
	Energy Storage (Hypatocyte vacuolation)	M	-	0.01 ± 0.01	-1.30 ± 0.20	$z = 0.79_{(1, 19)}$	0.429
Chaetodon octofasciatus (generalist)	Body Length (Total Length)	F	3.96^{-07}	$-3.16^{-04} \pm 0.09$	71.90 ± 1.40	F = $1.39^{-0.5}_{(1, 35)}$	0.997
		M	0.08	-1.18 ± 0.13	70.69 ± 2.23	F = $1.93_{(1, 23)}$	0.178
	Relative Body Mass (Fulton's K)	F	0.02	$3.26^{-03} \pm 7.67^{-05}$	$-34.34^{-06} \pm 4.65^{-06}$	F = $0.27_{(1, 35)}$	0.606
		M	7.16^{-04}	$-9.96^{-07} \pm 7.53^{-06}$	$3.26^{-03} \pm 1.37^{-04}$	F = $0.02_{(1, 23)}$	0.899
	Relative Liver Mass (LSI)	F	0.01	$-3.13^{-03} \pm 0.01$	1.03 ± 0.09	F = $0.31_{(1,34)}$	0.581
		M	1.37^{-04}	$-3.45^{-04} \pm 0.01$	1.00 ± 0.11	F = $3.02^{-03}_{(1,23)}$	0.957
	Fecundity (GSI)	F	5.41^{-04}	$-2.96^{-03} \pm 0.02$	2.16 ± 0.35	F = $0.02_{(1, 34)}$	0.893
	Energy Storage (Hypatocyte vacuolation)	M	-	-0.03 ± 0.02	-1.62 ± 0.46	$z = -1.17_{(1, 23)}$	0.243

Discussion

Contrary to expectations, neither the shallow-specialist (*Chaetodon baronessa*), nor the deep-generalist (*C. octofasciatus*) obligate corallivores experienced significant ecological or physiological costs from residing at depths down to 35 m. While the size of *C. baronessa* territories did increase along the depth gradient as expected, there was no decrease in within-territory resource densities; indicative of individuals establishing territories on high quality resource patches. Instead, deeper territories had up to three times the amount of highly preferred resources secured within deeper territories of the shallow-specialist, for apparently little or no cost in terms of defense effort, movement rates, or time paired. In addition, deep residence had little effect on a range physiological condition factors, including fecundity. While the territory sizes of *C. octofasciatus* did not increase at greater depths, and the species did experience some decline in within-territory resource densities, this did not equate to declines in total secured resources (TSR), or to increases in sub-lethal costs. Taken together, my results indicate that living at deeper depths may not confer costs to coral-specialized fishes as previously assumed. Instead, under similar circumstances, even where the density and composition of coral resources decline along the depth gradient, deep-reef habitats may offer substantial refuge potential to populations of reef fishes vulnerable to coral loss in shallow waters.

It has been assumed that frequent territory size increases in response to lower local resource densities, and vise-versa, are a product of in within-territory resource densities declines (Tricas 1989, Wrathall et al. 1992, Berumen and Pratchett 2006), so that TSR remain similar between different levels of surrounding resource availability, or at least TSR does not decline as strongly as surrounding resource densities. However, this has only been tested via manipulative experimentation (e.g. (Tricas 1989)). Here, I show that despite being situated in areas of lower overall resource availability deep territories are established in pockets of comparatively high resource density; or at least the regular swim paths used for feeding around territory perimeters navigate through high-density paths. Lower overall resource availability may therefore influence reduced population densities at deeper depths, but not at the cost of resource access for the fewer individuals utilizing these peripheral habitats.

The fact that deeper residents of the shallow-specialist species had higher TSR than their shallow counterparts suggests that factors other than resource accessibility may drive the strong distributions bias toward shallow water (Chapter 2*).* Rather than a direct response to resource dynamics, spatial-use increases may be a response to the lower conspecific competition observed at greater depths. Spatial increases have previously been linked to decreased competitor density, in addition to food availability (Sutton 1985, Tricas 1989). Therefore, the territories of shallow residents may be spatially constrained by density dynamics, instead of being of optimal size (Hixon 1980). In contrast, lower competitor density and therefore greater space availability at greater depths may reduce the comparative cost of resource access for deep residents.

Cost-benefit models link territory sizes to economic defendability (Mitani and Rodman 1979, Brown 1984), with increased resource access benefits in larger territories being offset by behavioral costs related to higher maintenance and greater vigilance efforts (Hamilton III and Watt 1970, Hixon 1980, Roberts and Ormond 1992). That expectation was not met in this study. Despite shallow-specialist territories being larger at deeper depths, lower conspecific density was related to decreased territorial interactions, trends toward lower patrol efforts, and no changes in paring behaviour. This is important, because increases in all three are related to lower feeding rates. Therefore, residing at distribution peripheries resulted in net benefits rather than costs. My results contrast the few other studies utilizing steep vertical gradients to investigate the energetic costs and ecological drivers of core – periphery range dynamics in animals (Feinsinger et al. 1979, Feldman and McGill 2013). For example, some territorial hummingbird species experience greater net energetic costs with altitude, where flight effort and activity levels increase, and foraging rates decrease; though rates of competitive intrusion remain constant (Feinsinger et al. 1979). While covariation between physiological condition and environmental gradients are commonplace in a multitude of systems (Hjeljord and Histøl 1999, Yoshinori and Shigeru 2000, Sullivan and Miller 2007, Gardner et al. 2009), including among butterflyfishes in shallow reef waters (Kokita and Nakazono 2001, Pratchett et al. 2004, Berumen et al. 2005), I found no evidence here of reduced body condition at depth in either focal species. My results show that the costs and benefits of occurring at range margins are likely to be species- and ecosystem-specific. This highlights the importance of examining different ecological and physiological indices to properly assess costs and refuge potential at range margins.

Conclusion

Investigations including the potential for deep reefs to mediate impacts for species affected by shallow water habitat loss have largely assumed intraspecific ecology and condition is static along a steep environmental gradient (Hawkins et al. 2000, Graham et al. 2011, Darling and Côté 2018). Here, I demonstrate this is not the case for spatial ecology and behavior, which can vary within 30m of depth gradient, and can also differ between species with different levels of depth- and dietary- specialisation. However, the ecological responses did not follow the expectations developed from studies along shallow water resource quality gradients, or from other systems, but surprisingly indicate that deep residence does not confer substantial sub-lethal costs for coral obligate fishes. Overall, I found no evidence that costs of deep residence would mitigate the benefits of potential depth refuges in my study system. If asymmetric habitat disturbances and extinction threats increase in response to rapid and ongoing climate change, marginal habitats may provide potential local-scale refuges. Here I show deep coral habitats on coral reefs are one such potential refuge. Further investigations of this potential among marginal habitats are now imperative.

Chapter 5 - ALTERNATIVE DIETARY STRATEGIES AND ALTERED CARBON PATHWAYS FACILITATE BROAD DEPTH RANGES IN CORAL-OBLIGATE REEF FISHES

Abstract:

Asymmetric habitat degradation and climate-induced range shifts will result in an increasingly large proportion of species' populations living at current range margins where some taxa will benefit from spatial refuges. However, the capacity for persistence at range peripheries will be determined in part by species-specific abilities to mediate costs related to decreases in quantities and quality of key resources. Here, I compare variation in dietary strategies and energy acquisition trade-offs along range-core to range-periphery depth gradients in two obligate corallivores with differing levels of diet specialization, as well as in their mixotrophic prey. I found no changes in feeding effort or total resource availability (total coral cover) toward the deep range peripheries, but availability of the preferred resource (*Acropora* coral) declined. While both fish species selectively targeted *Acropora*, the more specialized species (*Chaetodon baronessa)* exhibited limited feeding plasticity along the depth gradient, and selective feeding effort on the preferred resource increased rather than decreased with depth, being 40 times more than expected at their range periphery. In contrast, the generalist's diet (*C. octofasciatus*) varied greatly with depth-related changes in prey composition. Unexpectedly, the nutritional content of *Acropora* did not decline with depth, with shifts in $\delta^{13}C$ and $\delta^{15}N$ indicating energy offsets from increased coral heterotrophy in deeper water. Mixed modelling revealed a parallel 20% increase in plankton-sourced carbon in the muscle tissue of deep-resident fish. My results indicate that deep ranges in coral-obligate reef fishes, a prerequisite for deep refuge from shallow-water coral-loss, are supported by multiple mechanisms of dietary versatility, but for specialist species this versatility may be at the resource level (corals), rather than among the consumers. For species vulnerable to increasing anthropogenic impacts at range cores, variable and multi-trophic functional responses can act to buffer costs and bolster refuge potentials associated with dwelling at range peripheries (here, deep habitats), even among taxa with differential functional strategies.

Introduction:

Asymmetric habitat declines and range shifts related to rapid environmental change are likely to result in an increasingly larger proportion of species' populations living at current range margins (Cartwright et al. 2004, Thomas et al. 2004, Harris and Pimm 2008, Angert et al. 2011). As environments change, species with viable populations at range margins may show greater resilience, recovery, and long-term persistence potentials (i.e. a refuge effect) (Keppel et al. 2012, Reside et al. 2014). However, range peripheries are commonly associated with natural reductions in the quantity and or quality of resources (Brown 1984, Thomas and Kunin 1999) that often result in costs to consumers (Zammuto and Millar 1985, Badyaev and Ghalambor 2001, Mysterud et al. 2001). Understanding potential trade-offs and compensatory mechanisms of energy acquisition at range peripheries, therefore, will be vital to predicting future trajectories for many species vulnerable to extirpation and extinction.

For energy maximizing species, the ability to persist in marginal habitats, such as range peripheries, is likely to be reliant on flexibility in diets or feeding rates (Flesch and Steidl 2010, Yeager et al. 2014). Consequently, shifts in resource availability in response to disturbances and environmental gradients, tend to result in shifts in consumer communities that favour resource generalists over specialists (Clavel et al. 2011). For example, forest cover reduction in the Brazilian Atlantic Forest has resulted in much greater losses among specialist forest insectivore and fruigivore birds than habitat and diet generalists (Morante-Filho et al. 2015), and high elevation habitats are dominated by dietary generalists among wood-boring beetles, pollinator bees, and butterflies (Pellissier et al. 2012, Rasmann et al. 2014). Where disturbance gradients run parallel to resource production gradients and overlap the core ranges of consumers, individuals and populations at range peripheries may occupy more stable but less productive habitats (Thomas et al. 2004). Comparisons of dietary strategies and trade-offs at range peripheries among species with differential specialization is, therefore, a promising way of studying the ecological mechanisms that drive broad distributions and therefore refuge potential at range margins.

Natural environmental gradients provide powerful systems for testing hypotheses regarding the role of functional strategies in coping with environmental variation at range peripheries (Keppel et al. 2012, MacDonald et al. 2016). Species may have to develop response strategies to overcome two types of resource declines at these margins. First, increased patchiness, decreased resource densities, or resource turnover toward range peripheries may result in fewer preferred resources (Thomas and Kunin 1999). Secondly, even where preferred resources are available at range margins (e.g. in patches), declines in environmental nutrients or energy availability may result in lower productivity in food resources that confer less energy per unit effort to consumers. In either case, versatile generalists often exhibit flexible phenotypic responses to prevailing environmental conditions or resource declines in suboptimal and variable conditions (Kassen 2002) whereas specialists may be maladapted to new resource bases (Sol et al. 2002). Therefore, where distribution, productivity and disturbance gradients all run parallel, specialists will be vulnerable to population declines or extinction due to the dual pressures of habitat disturbance at the range core and resource limitation at the range periphery, resulting in specialist populations showing lower resilience and recovery potential (Deutsch et al. 2008, Williams et al. 2008, Moritz and Agudo 2013).

However, functional strategies observed at the range core do not always hold at range peripheries (Cordell et al. 1998, McGill et al. 2006, Albert et al. 2010, Chevin and Lande 2011). Therefore, species showing specialist diets in the range core may have more flexible diets, or utilize compensatory mechanisms, at the range periphery. Changes in dietary specialization across a species range may result in species possessing greater resilience and post-disturbance recovery potential than predicted from observations of behaviour at the range core (Kawecki 2008). However, investigations of compensatory dietary strategies at range peripheries are rare, particularly among specialized taxa considered vulnerable to habitat degradation.

Coral reefs offer an ideal system for assessing ecological changes along environmental and resource gradients. Steep gradients in light energy, decreased photosynthetic ability, and rapid turnover in the composition of coral communities with depth are likely to result in declines in the quantity and quality of resources available to coral consumers (Crossland et al. 1980, Crossland 1987, Anthony et al. 2002, Einbinder et al. 2009, Roberts et al. 2015). Moreover, although coral reefs are increasingly affected by anthropogenic climate change (Bellwood et al. 2004, Hughes et al. 2018), many stressors attenuate with depth (e.g. (Marshall and Baird 2000, Bridge et al. 2016, Muir et al. 2017)). Butterflyfishes, one of the most abundant coral reef fish families, offer an ideal model group to assess dietary variation and plasticity responses to environmental and resource gradients among contrasting functional strategies (Nowicki et al. 2013). Butterflyfish occupy a broad spectrum of dietary specialization on corals and their feeding bouts are conspicuous, so it is possible to record proportional feeding effort on different resource types at the core and periphery of their ranges (Cole and Pratchett 2013, Pratchett 2013). More specialized coral feeders also have stronger asymmetrical distribution biases toward shallow water than generalists (MacDonald et al. 2016, Chapter 2, Chapter 3) and are known to be vulnerable to population declines due to coral loss (Pratchett et al. 2006, Wilson et al. 2006). Therefore, specialist corallivorous butterflyfishes are both vulnerable to anthropogenic coral loss, and gradients in their species distribution, environmental productivity, and disturbance exposure are likely to decline in parallel along a depth gradient. Recent studies have shown that even the most specialized corallivore butterflyfishes can occur over broader depth ranges than previously thought, occurring to at least 40 m depth (Chapter 2). Consequently, dietary flexibility along a depth gradient may facilitate the persistence of refuge populations in deep water following disturbance, thereby mediating local extinction. However, it is unknown whether the dietary strategies of coral-obligate fish observed in shallow waters are maintained along the extensive depth gradients most likely to confer increased resilience.

Here, I examine whether flexible diets or feeding rates along a depth gradient could drive broad depth distributions, and therefore increased resilience potential, for two obligate coral feeders with common deep depth ranges but divergent dietary and depth specialization. I examine two obligate corallivore species with contrasting ecological niches and dietary breadths: a coral-resource specialist with a shallow-biased depth distribution (*shallow-specialist, Chaetodon baronessa*), and a coral-resource generalist with a depth-generalist distribution (*deep-generalist, C. octofasciatus*). Specifically I investigated whether: 1) Depth patterns occur in overall resource quantity and feeding effort, 2) Changing resource composition along the depth gradient results in dietary flexibility, 3) A reduction of feeding effort, on and selectivity for, preferred resources occurs at depth, and 4) compensatory mechanisms of energy provision in corals, and energy acquisition in their consumers may occur at the deep range periphery.

Methods:

Study site and species

The study took place in Kimbe Bay, Papua New Guinea between May and December, 2015. The vertically continuous coral habitats along the entire depth gradient of the reefs in the region present no physical barriers to species distributions. I examined two butterflyfish species, *C. baronessa* and *C. octofasciatus,* both of which are obligate coral-feeders but with differing levels of dietary specialization (Pratchett 2013, Madduppa et al. 2014). While both species occur across a relatively broad depth range of >30 m, individuals from both species maintain territories with discrete and relatively narrow depth ranges (mean depth range of both species ~7 (± 0.5 SE) m: Chapter 4), enabling examination of variation in dietary and feeding ecology among depths. The feeding ecology of the two species is well-documented in shallow water: (Pratchett 2013, Madduppa et al. 2014) *C. baronessa,* a dietary specialist, strongly selects corals of the genus *Acropora*. In contrast, *C. octofasciatus* feeds on a much broader range of other coral taxa (Ghaffar et al. 2006), but does also selectively feed on

Acropora (Madduppa et al. 2014). The abundance of both species also varies along the depth gradient (Chapter 3): *C. baronessa* is most abundant in shallow water (< 5 m) and declines with increasing depth, while *C. octofasciatus* is least abundant in water < 5m, and most abundant at 25 m.

Data collection

Depth patterns in overall resource quantity and feeding effort

To examine broad-scale spatial patterns in potential coral prey across Kimbe Bay, I quantified the abundance of all hard corals and of the preferred genus *Acropora* (as % cover) from photo-quadrats at 5 depths (<1 m, 5 m, 10 m, 20 m, and 30 m) on 10 reefs across Kimbe Bay (see Chapter 2 for complete methods). In order to quantify overall feeding effort, I recorded bite rates of individuals from both fish species pooled across all hard coral types on 6 reefs (Vanessa's, South Ema, and Otto reefs, Christine's reef, Kimbe Island, and Tuare Island; *C. baronessa* total n = 344*, C. octofasciatus* total n = 107). 'Feeding Observations Protocol' - Focal fish were followed for 3 minutes at a distance of ~ 2-3 m by scuba divers, and the total number of bites, the coral genus targeted by each bite and the minimum and maximum depth of the observation period were recorded. Some feeding obervations were replicated among identified fish pairs. Most of these replicate observations were non-sequential in time and possible pseudo-replication among this subset of observations was accounted for in formal analyses, as outlined in the *Data analysis* section below.

Depth related variation in resource composition and feeding flexibility

In order to assess variation in resource composition along the depth gradient I recorded the availability of 9 key targeted-coral-prey taxa (reviewed in (Pratchett 2013); *Acropora, Galaxia, Fungia, Pavona, Montipora, Porites, Pocillopora, Echinopora,* and *Platygyra)* from 90 - 120 replicate photo-quadrats in each of 6 depth bins at 0-5 m, 5-10 m, 10-15 m, 15-20 m, 20-25 m and 25-30 m on one reef (Christine's Reef). I used Coral Point Count with Excel extensions (Kohler and Gill 2006) to record the benthic component under each of six random points within each quadrat, (≥ min 540 points per depth). In order to assess feeding variation along the depth gradient I used the same 'Feeding Observations Protocol' above to record the proportion of bites taken from each of 37 coral genera (See supplemental table 1) at random depths on Christine’s reef, Kimbe Island, and Tuare Island (*C. baronessa* n = 276*, C. octofasciatus* n = 90*)*.

The level of selective feeding effort on the 9 key coral prey genera by both species was calculated across all depths and within each 5m depth bin depth on the focal reef. I used Manly resource selection ratios (Manly et al. 2002), calculated using the formula:

$$\hat{w}_i = o_i / a_i$$

where $\hat{w}_i$ is the resource selection ratio for coral prey genera *i*, o_i is the proportion of prey genera *i* used, and a_i is the proportion of prey genera *i* available. Selection indices above 1.0 indicate preference; values less than 1.0 indicate avoidance. Selectivity was confirmed by comparing observed and expected bite frequencies on each prey genera, for each fish species and depth combination, using chi-squared tests.

Feeding observations

I recorded the bite rates of individuals from both fish species on 37 coral genera (See supplemental table 4.1) at random positions along the depth gradient on three reefs (Christine’s reef, Kimbe Island, and Tuare Island) (*C. baronessa* n = 276*, C. octofasciatus* n = 90*)*. I also made additional counts of non-genus specific bite rates (ie. Total bites pooled across all hard coral types) on 6 reefs (those above, and Vanessa’s, South Ema, and Otto reefs) (*C. baronessa* total n = 344*, C. octofasciatus* total n = 107*)*. Individual fishes were followed for 3 minutes at a distance of ~ 2-3 m by scuba divers, and the total number of bites, the coral genus targeted by each bite and the minimum and maximum depth of the observation period were recorded. Observations were abandoned if the focal fishes showed signs of distress due to diver presence (i.e. erratic burst swimming or defensive displays). Some feeding observations were replicated among identified fish pairs. Most of these replicate observations were non-sequential in time and possible pseudo-replication among this subset of observations was accounted for in formal analyses, see below. All other replicate observations were independent.

Trophic carbon pathways of corals and fish

Potential depth related shifts in the trophic position and carbon pathways supporting coral prey were analyzed using bulk stable isotope analysis (SIA_B) of tissue samples from 6 shallow (0 - 5 m) and 4 deep (30 - 40 m) *Acropora* colonies. Decalcified, dried, and homogenized non-lipid extracted samples were combusted and analyzed for $\delta^{13}C$ and $\delta^{15}N$ isotope values on a Costech elemental analyzer coupled to a ThermoFinnigan Delta-V gas source isotope-ratio-monitoring mass spectrometer (EA-IRMS) at the Advanced Analytical Centre, James Cook University, Australia. Stable isotope results are reported using standard delta (δ) notation in parts per thousand (‰) relative to standards Vienna Pee Dee Belemnite for carbon and atmospheric N_2 for nitrogen. Reproducibility of lab standards was ± 0.1 ‰ and ± 0.2 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

To examine the food-web baseline carbon sources supporting corals and coral-feeding butterflyfishes, I used a compound-specific isotope analysis of amino acids (SIA_{cs}) of *Chaetodon baronessa* white muscle tissue (n = 5 fish per depth) and lipid-extracted coral tissue (n = 6 colonies per depth) from shallow (0 - 5 m) and deep reefs (30 - 40 m). Upper and lower depth boundaries were determined for all sampled fish during previous territorial observations (Chapter 4). Territories of shallow fish were wholly in ≤ 5 m water depth, deep fish were wholly ≥ 20 m (max = 40 m) depths. The total lengths (TL) of fish did not differ between depths (*C. baronessa;* $TL_{shallow}$ = 93.9 mm, TL_{deep} = 94.6, t = 0.24, df = 7.15, p = 0.82). All fish and coral-tissue samples were dried, homogenized, and acid hydrolyzed prior to derivatization to trifluoroacetyl/isopropyl esters as detailed in McMahon et al. (2018). Derivatized amino acids were analyzed on a Thermo Trace Ultra gas chromatograph coupled to a Finnegan MAT Delta^{Plus} XL EA-IRMS at the University of California, Santa Cruz. Standardization of runs was achieved using intermittent pulses of a CO_2 reference gas of known isotopic value and internal nor-Leucine standards. All SIA_{cs} samples were analyzed in triplicate along with amino acids standards of known isotopic composition

(Sigma-Aldrich Co.). The estimate of full protocol reproducibility was ± 0.7‰.

Data Analysis

All analyses were undertaken in R (R Core Team 2016), unless otherwise specified. Acceptable dispersion parameters and homogeneity of variance in residuals were met for each model presented. All reported models were also tested against potential candidate models with other transformations or distributions where appropriate, using the Akaike information criterion with corrections for small sample sizes (AICc) in the *MuMIn* package (Barton 2016). In all cases, the presented model had the lowest AICc score (≥ 2 points difference).

Potential depth related variation in total bite rates within fish species was analyzed using negative binomial general linear mixed effect models (glmm). *Total bites* per observation was modelled against the median observation *depth* in *lme4* (Bates et al. 2014). *Reef* and known *individual* fish were included as nested random effects. Depth related variation in the mean proportion of bites on key coral prey genera were analysed among discrete 5m *depth* bins (min and max depth of observations completely within predetermined 5 m depth bins) for each species using glmms on square-root transformed proportional *bite* data and Gaussian distributions (AICc < for binomial models), with *individual* fish as a random effect. Pairwise comparisons of differences between depths were tested using Tukey's adjusted paired t-tests with the *glht* function in *multcomp* (Hothorn et al. 2017).

Depth patterns in dietary niche and coral prey composition

Dietary niche breadth was calculated within each depth bin and across all depths for each species using a basic measure of richness (n of genera) and a standardized Levins' index using *pop.diet* in *RInSp* (Zaccarelli et al. 2013). Niche dietary overlap and variance were calculated across all depths for each species, and among 5 m depth bins within species, using the Pianka-modification of the MacArthur-Levin's niche overlap index as per Krebs (Krebs 1999) in *EcoSimR* (Gotelli et al. 2015). Niche overlap among depths was calculated on the total number of bites per coral genera within each depth bin for each species.

Depth patterns in the carbon pathways of corals and fish.

Differences in bulk δ^{13}C and δ^{15}N values in between shallow and deep coral colonies were tested using Welch's t-tests. To quantify the relative contribution of carbon sources to shallow and deep populations of the dietary specialist butterflyfish *Chaetodon baronessa*, I used an amino acid carbon isotope fingerprinting approach within a fully Bayesian mixing model (sensu (Ward et al. 2010). I used δ^{13}C values from five essential amino acids (threonine, isoleucine, valine, phenylalanine, and leucine), to identify unique isotopic signatures for three potentially important source end-members to fish diets; (i) local shallow and deep-resident *Acropora* coral colonies, (ii) water column phytoplankton, (iii) microbially reprocessed detritus (McMahon et al. 2016) (Supplemental Table X). Separate mixing models were used for shallow and deep butterflyfishes via the *siarsolomcmcv4* function within *SIAR* (Parnell et al. 2010) (mean model variance = 7 ± 4%). To facilitate comparisons of amino acid "fingerprints" across systems and environmental conditions, all essential amino acid δ^{13}C values were normalized to the mean values within each individual (sensu (Larsen et al. 2013); see supplemental material). I used a small non-zero trophic discrimination factor (minimal trophic fractionation) of 0.1 ± 0.1‰ (McMahon et al. 2010). I tested for statistical significance in depth related differences in proportional carbon-source contributions in fish samples using a glmm of a randomized dataset comprised of 1000 values for each individual based on means and standard deviations produced by *SIAR* results, and with *individual* fish used as random variable.

Results:

Depth patterns in overall resource quantity and feeding effort

Availability of the highly preferred dietary coral genus *Acropora* declined with depth throughout Kimbe Bay, more than halving between the shallowest 5 m (17.0 ± 1.9 SE %) and 30 m (8.3 ± 1.8 %) ($z = -3.25$, $p = 0.006$) (Fig. 5.1a). Despite these *Acropora* declines, the availability of all potential coral food sources to coral-feeding fishes (total hard coral cover) was relatively high at all depths throughout the bay ($F_{1,3} = 2.74$, $p = 0.20$), and ranged from 49 - 62 % mean cover (Fig. 5.1a). Correspondingly, overall feeding rates on all hard coral types did not decline with depth in either fish species. (*C. baronessa*, $z = 0.64$, $p = 0.52$; *C. octofasciatus*, $z = 1.15$, $p = 0.25$) (Fig. 5.1 b,c).

Depth related variation in resource composition and feeding flexibility

Changes in available coral resource types

Total hard coral cover on the focal reef used for the detailed feeding ecology component of this study was high throughout the gradient, but increased from 54.9 (± 2.1) % at 0 - 5 m to a peak of 72.5 (± 2.4) % at 10 – 15 m ($t = 4.84$, $p < 0.001$), before declining to a low of 39.3 (± 2.6) % at 25-30 m ($t = -7.58$, $p < 0.001$) (Fig. 5.2a). *Acropora* cover (Fig. 5.2b) declined monotonically ($F_{5,674} = 10.91$, $p < 0.001$), decreasing four fold from 22.3 (± 2.0) % at 0 - 5 m to 5.3 (± 1.5) % at 25 – 30m ($t = -6.35$, $p < 0.001$) (Fig. 5.2a). The distribution of other highly targeted coral genera also varied with depth (Fig. 5.2a). The cover of *Porites* corals closely followed that of total hard corals and doubled from 14.6 (± 1.3) % cover at 0 - 5 m to 30.8 (± 2.6) % at 10 – 15 m ($t = 5.97$, $p < 0.001$), then declined by a third to a low of 10.5 (± 1.1) % at 25 – 30 m ($t = -6.25$, $p < 0.001$). The cover of *Montipora* was much lower than *Porites* and *Acropora* and peaked at 10 m (10.0 ± 0.6 %), where it was approximately three times higher than at other depths (2.6 – 3.4 %; all comparisons $p < 0.01$). Cover of *Echinopora* corals was comparatively low overall and was lower at 0 - 5 m (0.7 ± 0.3 %) than at all other depths (3.2 – 5.6 %; all comparisons $p < 0.01$) except 10 - 15 m (2.3 ± 0.6 %; $t = 2.50$, $p = 0.13$) (Fig. 5.2a).

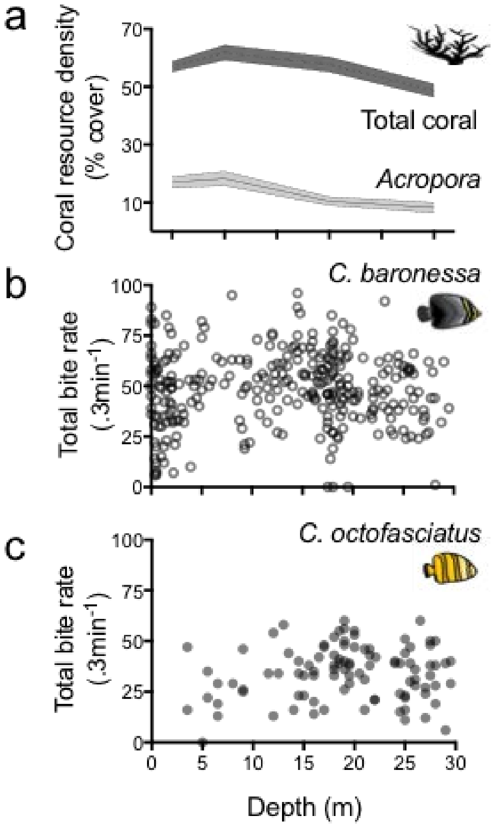

Figure 5.1: (a) The mean cover (± 95% CI) of total hard coral and Acropora coral resources along a depth gradient from 0 to 30 m in Kimbe Bay, PNG, and; Total feeding effort on all corals along the same depth gradient for (b) the 'shallow-specialist' butterflyfish Cheatodon baronessa (grey fish) and (c) the 'deep-generalist' butterflyfish C. octofasciatus (yellow fish). Each data point represents the total number of bites observed during a three-minute feeding observation. Data points are semi-translucent and darker areas represent overlapping data points.

Depth related changes in corallivore diets

The shallow-specialist, *C. baronessa*, had a highly specialized overall dietary niche breadth, and specialization remained high along the gradient (Fig. 5.2 c,e). The overall niche breadth was 0.07, and the species fed on a total of 18 coral genera across the depth gradient. Niche overlap among all depths was 0.95, and neither niche breadth ($F_{1,4}$ = 0.467, p = 0.53) nor the total number of dietary genera ($F_{1,4}$ = 0.233, p = 0.65) increased with depth. There was a small increasing trend in niche breadth between 5-10 m (0.1) and 20-25 m (0.9) (Fig 2e). However, niche breadth was highest in the shallowest depth (0.21), where the most dietary genera (15) were also utilized. The lowest overlap in the dietary niche of the shallow-specialist population was 0.86 and occurred between 0-5 m and 25-30 m depths.

In contrast, the deep-generalist, *C. octofasciatus,* had a broad overall dietary niche (niche breadth = 0.23, 36 genera), low niche overlap between depths (0.36), and an increasing breadth of utilized genera from 7 genera at 0-5 m to 25 genera at 25-30 m ($F_{1,4}$ = 8.41, p = 0.044, R^2 = 0.597) (Fig. 5.2 d,f). The dietary niche realized by the deep-generalist did not broaden significantly with increasing depth ($F_{1,4}$ = 1.41, p = 0.30, R^2 = 0.597). Instead, a general increase occurred between 5 m (0.12) and 30 m (0.26) but was punctuated by 65 - 75 % decrease in niche at 15 - 20 m (0.07) compared to other depths (Fig. 5.2f). There was high variation in dietary overlap between depths for the deep generalist (0.229 – 0.895), though there was no clear depth related patterns in this variation.

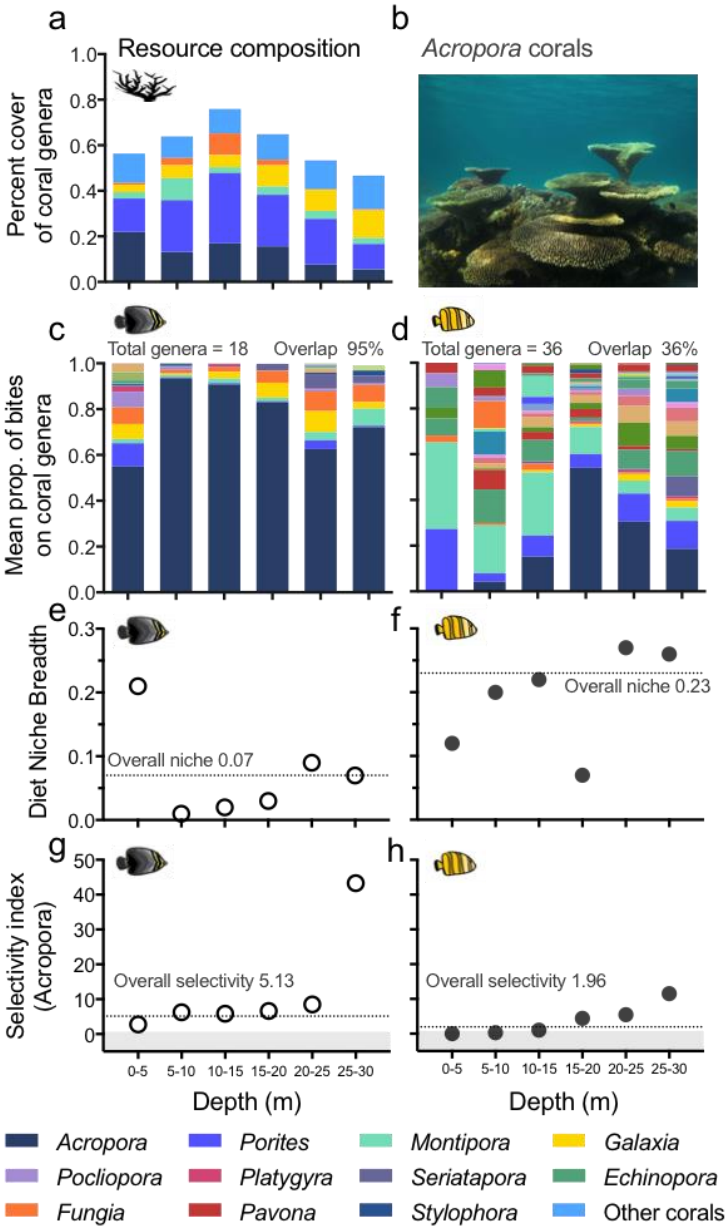

Figure 5.2: Depth-related variation in resource availability (a), and diet (c-f) and selectivity (g, h) of a shallow-specialist (grey fish) and deep-generalist (yellow fish) corallivore, along a coral reef depth gradient. (a) The percent cover of primary coral genera within each 5 m depth-bin on the focal reef (total bar height = total cover). (b) A stand of Acropora colonies, the preferred dietary coral of many butterflyfish species including *Chaetodon baronessa*. (c & d) The proportional number of bites on primary dietary coral genera. (e & f) The breadth of dietary niche. (g & h) Dietary selection for the preferred coral genus Acropora. Dotted lines in e & h indicate overall metrics across all depths. In g & h, values < 1 (greyed-out area) indicate avoidance of Acropora, and values > 1 indicate positive selection for the genus. Photo credit: C. MacDonald.

Depth related variation in the utilization and selectivity of preferred resources

Proportional foraging on the preferred coral resource, *Acropora*, was higher overall than on any other coral genus for both fish species and did not decrease uniformly with depth among either species (Fig. 5.2 c,d). However, some non-linear differences among depths were evident. *C. baronessa* fed predominantly on *Acropora* within each depth (75 % of all bites) (Fig. 5.2c, Supplemental figure 1), but utilized the genus approximately 1.5 - 2 time less in the shallowest depth (0 - 5 m, ~ 45% of bites) compared to deeper depths (all comparisons, $p < 0.05$), with no significant difference among depths deeper than 5 m (all comparisons, $p > 0.10$). *C. octofasciatus* took less than half as many bites from *Acropora* overall (31 % of all bites) and fed on *Acropora* more than any other coral genera at depths deeper than 15 m (Fig. 5.2 d, Supplemental figure 1). This species did not feed on *Acropora* at 0 - 5 m and took a higher proportion of bites on *Acropora* at 15 - 20 m (55 %) than at 5 - 10 m ($z = -2.90$, $p = 0.039$), but not at other depths (all comparisons, $p > 0.10$).

Overall, both fish species fed on *Acropora* colonies more than expected given *Acropora* availability (Table 5.1, Fig. 5.2 g,h). However, the level of selective feeding increased, rather than decreased with depth in both species. The strength of *C. baronessa*'s selection for *Acropora* increased linearly between 0 - 5 m (selectivity ratio = 2.77) and 20 - 25 m (selectivity ratio = 8.48) ($F_{1,3} = 12.79$, $p = 0.034$, $R^2 = 0.75$), then more than quadrupled between 20 - 25 m and 25 - 30 m, where the proportion of bites targeting *Acropora* was 43 times more than its proportional cover (selectivity ratio; 43.3) (Fig. 5.2g, Table 5.1). The level of selective feeding on *Acropora* by *C. octofasciatus* also increased linearly with depth ($F_{1,4} = 24.72$, $p = 0.007$, $R^2 = 0.83$). However, the species avoided feeding on *Acropora* colonies between 0 - 10 m, fed on them in proportion to availability at 10 - 15 m, and selectively fed on them at depths deeper than 15m (all depths; $p < 0.001$) (Fig. 5.2h).

Compensatory mechanisms of energy acquisition

There was no evidence to support decreased energy availability in the tissue of deep-reef corals. However, there were indications of compensatory energy acquisition in deep *Acropora* corals and in the deep residents of the shallow-specialist corallivore (Fig. 3). The total lipid content (energy availability) in *Acropora* coral tissue was not related to depth ($z = -0.42$, $p = 0.67$) (Fig. 5.3a). Tissue from deep-reef *Acropora* colonies had lower bulk $\delta^{13}C$ values than shallow-reef *Acropora* ($t = 10.16$, $p = 0.001$) (Fig. 5.3b), as did the compound specific $\delta^{13}C$ of essential Amino Acids within *Acropora* tissues (Fig. 5.3c). Taken together, the SIA_b and SIA_{cs} results strongly suggest altered carbon pathways occurred in deep-reef *Acropora*s. Corresponding increases in bulk $\delta^{15}N$ values with depth ($t = -12.52$, $p < 0.001$) also indicated a higher coral trophic position at deeper depths (Fig 3b).

Compound specific $\delta^{13}C$ of essential Amino Acids within *C. baronessa* muscle tissue were also lower among deep-reef residents (Fig 3c). Mixed-modelling of SIA_{cs} carbon contributions to *C. baronessa* muscle tissue further supported differentiation in the dietary carbon pathways of shallow-reef and deep-reef butterflyfish populations (Fig 3d). As expected, coral was the dominant carbon source supporting *C. baronessa* overall (79 ± 13%). However, the relative contribution of coral-sourced carbon to the food web supporting *C. baronessa* decreased between the shallow-reef and deep-reef (Deep 90 ± 2% (SD); Shallow: 67 ± 5%). In contrast, the corresponding contribution of water column-derived planktonic carbon increased substantially among deep-resident fish (Deep: 27 ± 4%; Shallow: 7 ± 2%) (Fig. 5.3d).

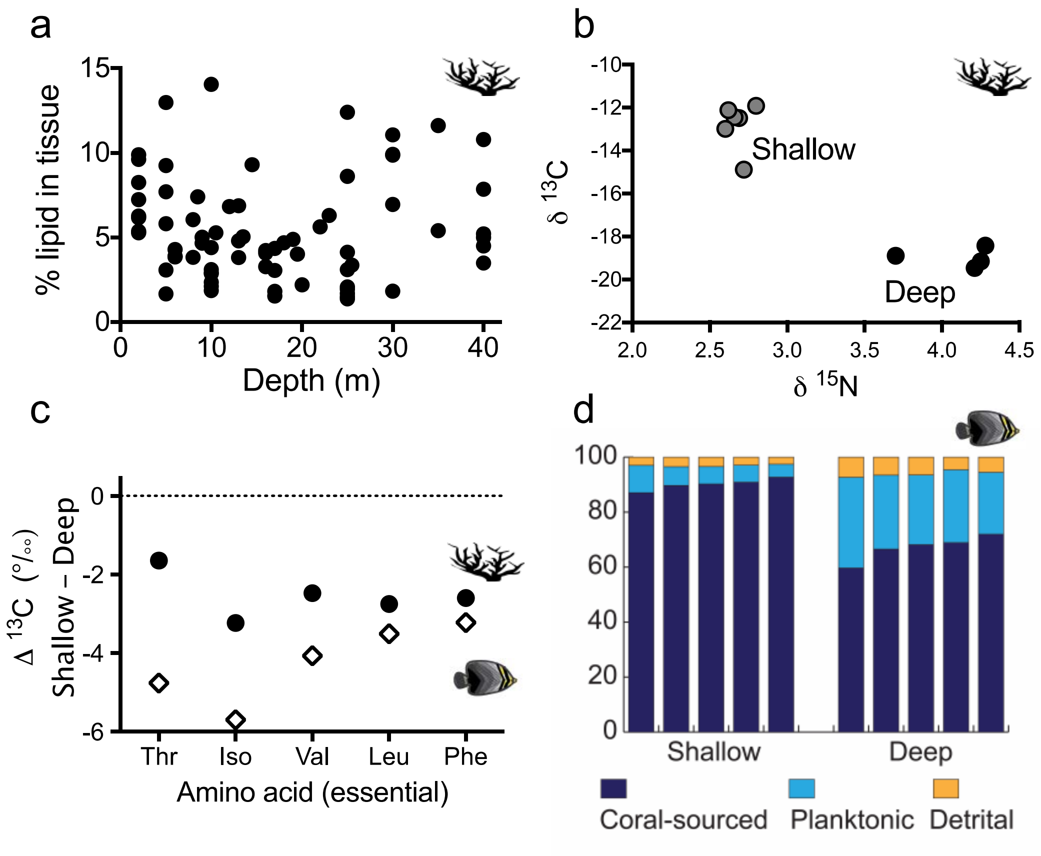

Figure 5.3: (a) The proportional lipid content of *Acropora* tissue along a depth gradient from 0 – 40 m. (b) Differences in isotopic space between shallow (grey) and deep (black) *Acropora* corals. (c) Altered carbon pathway signals in the essential amino acids of *Acropora* colonies (dots) and *Chaetodon baronessa* individuals (diamonds) on the deep reef. Note the greater change among the later. (d) Relative contribution of local coral, water column-derived plankton, and microbially reprocessed detritus to *Chaetodon baronessa* residents in shallow-reef (0 – 5 m) and deep-reef (20 – 40 m) depths. In d, each bar represents an individual fish.

Table 5.1: Dietary niche breadth and overlap between 5 m depth bins for two *Chaetodon* species between 0 m and 30 m. (0 = no dietary overlap, 1 = full dietary overlap.

Sp.	Depth (m)	No. obs	No. bites	Niche overlap						Prey selectivity ratios and evidence for selection							
				All	0-5	5-10	10-15	15-20	20-25	*Acro.*	*p*	*Mont.*	*p*	*Porit.*	*p*	*Echin.*	*p*
C. baronessa	All depths	159	3309	0.952						5.13	***	0.55	***	0.14	***	0.78	*
	0-5	48	946	-	1					2.77	***	0.77	NS	0.70	***	3.50	***
	5-10	10	314	-	0.933	1				6.27	***	0.11	***	0.02	***	0.39	*
	10-15	18	451	-	0.923	0.992	1			5.83	***	0.81	NS	0.02	***	0.74	NS
	15-20	58	1101	-	0.925	0.996	0.991	1		6.60	***	0.45	***	0.01	***	0.56	***
	20-25	11	368	-	0.925	0.996	0.988	0.998	1	8.48	***	2.00	NS	0.34	***	0.73	NS
	25-30	14	129	-	0.860	0.928	0.940	0.925	0.947	43.3	***	2.62	***	0.06	***	0.40	**
C. octofasciatus	All depths	79	2395	0.360						1.96	***	2.97	***	0.42	***	1.08	NS
	0-5	3	63	-	1					0.00	***	13.63	***	1.95	NS	7.27	NS
	5-10	11	151	-	0.726	1				0.29	***	2.22	***	0.17	***	0.90	NS
	10-15	13	272	-	0.804	0.841	1			1.02	NS	10.69	***	0.31	***	1.43	NS
	15-20	18	768	-	0.229	0.278	0.568	1		4.43	***	3.31	***	0.27	***	0.57	NS
	20-25	13	417	-	0.376	0.332	0.567	0.893	1	5.46	***	1.59	NS	0.62	**	0.95	NS
	25-30	21	724	-	0.468	0.438	0.597	0.728	0.895	11.5	***		**	1.15	NS	0.50	**

Obs = observation, *Acro.* = *Acropora, Mont.* = *Montipora, Porit.* = *Porites, Echin.* = *Echinopora.* NS = Non-significant.

Discussion

Specialist resource strategies are characterized by the targeting of a limited set of resources that are expertly exploited (Clavel et al. 2011). However, this strategy produces trade-offs in habitat utilization along spatial and temporal changes in resource quality (Caley and Munday 2003) that frequently result in attrition (Wilson et al. 2006) and occasionally extirpation (Munday 2004). Specialist species with distributions that overlap disturbance exposure, such coral-resource specialists on shallow-water coral reefs, are particularly vulnerable to anthropogenic forcing of climate changes and habitat losses (Wilson et al. 2006, Graham et al. 2011). While range peripheries are theoretically well positioned as potential refuges in some systems, the costs associated with resource turnover and declining resource quantity and quality along production gradients are expected to limit this potential for resource specialists, but not as strongly for generalists. I hypothesized that there would be reductions in the availability and nutritive quality of preferred corals, so individuals could only persist in deeper water if they had flexible diets or feeding rates. Conversely, my results demonstrate that contrasting ‘specialist’ and ‘generalist’ feeding strategies, as well as compensatory energy acquisition by deep-reef corals and fish supported broad depth distributions of coral-obligate butterflyfish species. Here I show that both generalist and specialist dietary strategies can facilitate broad ranges within a single feeding guild of coral feeding butterflyfishes that is considered among the most reef-fish most vulnerable groups to extinction (Graham et al. 2011). Therefore, the costs of deep-reef residence may not be as high among this group as previously thought.

The dietary strategies employed by *C. octofasciatus* and *C. baronessa* in shallow water largely translated along the depth gradient. The specialist remained specialized, while the generalist became more generalist with depth. Surprisingly the relative feeding effort (selectivity) targeted toward *Acropora* increased with depth for both species. For the specialist species, this is likely related to a continued reliance on the prey genus, yet for the generalist species, this may be related to competitor relief at deeper depths as the dominant specialist *C. baronessa* (Blowes et al. 2013) declines substantially in abundance along the depth gradient (Chapter 3). While such a study has not previously been undertaken for coral reef fishes, the generality of these results is supported by similar patterns along environmental and resource gradients demonstrated separately in other taxon groups. For example, the generalist strategy is apparent in the dietary niche of the Eurasian Otter, which increases with both increasing latitude (Clavero et al. 2003) and altitude (Remonti et al. 2009). Similarly, the increased magnitude of resource selectivity where availability of selected resources is low also occurs among Ferruginous Pygmy-Owls along elevational gradients (Flesch and Steidl 2010).

Our results here also suggest similar depth related patterns may occur among dietary and microhabitat resource use strategies among coral reef fishes. Microhabitat versatility and selectivity among strongly coral-associated, but planktivorous, reef fishes also increase with depth more among species that are habitat generalists in shallow-water, than with specialists (MacDonald et al. 2018). Further, selectivity for spatially complex coral habitats increases with depth among both habitat generalist and specialist species (Jankowski et al. 2015, MacDonald et al. 2018).

The lack of lipid decline in prey corals was surprising as experimental shading has previously resulted in between 30% and 90% reductions in lipid storage (Anthony and Fabricius 2000). However, in that study lipid declines were lowest for species demonstrating high rates of heterotrophic feeding under shaded conditions. Based on the enhanced signal of coral heterotrophy with depth here, I propose that compensatory coral heterotrophy with depth is the mechanism also offsetting lipid stores and, therefore, indirectly supplementing energy availability to deep coral consumers.

Our study supports previous observations of increased heterotrophic feeding effort in photosynthetic corals at depth but represents the first evidence of increased metabolic uptake of heterotrophic energy sources at depth, that I am aware of. Previous investigations of coral stable isotopes along depth gradients found decreased bulk $\delta^{13}C$ values at depth, comparable with the shallow and deep $\delta^{13}C$ values in my study (Alamaru et al. 2009, Einbinder et al. 2009). However those studies either did not find a 'trophic enrichment' signal in $\delta^{15}N$ (Alamaru et al. 2009), or did not measure $\delta^{15}N$ at all (Einbinder et al. 2009). Controlled feeding experiments have demonstrated some increased feeding effort on plankton under greater depth conditions at higher than ambient plankton concentrations, though, responses varied between geographic locations and were not conclusive (Palardy et al. 2005, Palardy et al. 2008)

I have previously demonstrated that neither body condition nor reproductive potential declines with depth in either of my focal study species (Chapter 4). Taken together with the results here, these surprising findings suggest increased coral heterotrophy and/or substitute feeding on plankton may buffer individual fish from depth related declines in the availability of preferred corals, and may constitute an argument for investigating significantly altered energy pathways on deep reefs (Bradley et al. 2015). I argue that the broad depth range of these species is explained by a combination of more intensified feeding on less available preferred corals (specialist strategy), diet flexibility (generalist strategy), and a potential ability to exploit non-coral sources of nutrition. On the other hand, depth-related dietary versatility in prey corals, rather than in their consumers may be key to extending deep limits of depth ranges for reef fish with specialist coral resource strategies. These interconnected mechanisms of dietary versatility along a depth gradient indicate depth may be a viable refuge for many coral-obligate reefs fishes provided anthropogenic disturbances attenuate significantly with depth.

Overall, the increasing vulnerability of taxa to anthropogenic impacts at range cores and consequential range displacements, particularly among resource specialists, has increased the necessity to assess potential spatial refuges, many of which will occur at current range margins (Keppel et al. 2012). My data show variable and multi-trophic functional responses can act to buffer costs and bolster refuge potentials associated with dwelling at range peripheries (here, deep reef habitats), even among taxa with contrasting functional strategies.

Chapter 6 - EVALUATION OF A DEPTH REFUGE FOR A CORAL REEF FISH: AN OBSERVATIONAL AND EXPERIMENTAL APPROACH

Abstract

Increasing coral losses on a global scale represent a great threat to highly specialized coral-obligate reef fishes. Deeper reef habitats have been hypothesized to be potential refuges from shallow disturbances. However, the susceptibility of deep populations to coral losses and the capacity of individuals to migrate downslope to exploit less susceptible habitats has rarely been tested. Here, I used a shallow water outbreak of the coral-feeding seastar *Acanthaster planci* and a deep water butterflyfish removal experiment to evaluate differential impacts on shallow and deep populations of the coral-obligate reef fish *Chaetodon baronessa,* and their ability to move to deeper locations. *C. baronessa* declined by an order of magnitude in shallow water (<10m) following a 75% decline in their preferred food corals (genus *Acropora*) between 2013 and 2015. However, neither *Acropora* corals nor *C. baronessa* declined at depths of 15-20m, or 25-30m over the same period and post-disturbance *Acropora* and fish densities were higher at these deeper depths than in shallow water. Further, a tagging and competitor removal experiment demonstrated that adult individuals can migrate to healthier coral habitats in deeper waters when shallow water resources decline. *C. baronessa* may be pre-disposed to this potential to 'migrate to refuge' because of individual ontogenetic migrations; recruits and juveniles here preferentially occupied shallow-water habitats (<10m), but adults can occupy depths ≥ 40 m. Our data support that hypothesis that deeper-reef habitats can provide a local-scale spatial refuge for coral-obligate reef fishes when coral losses are asymmetric along depth gradients.

Introduction

Habitat degradation is a major contributor to global biodiversity loss (Brooks et al. 2002, Hoekstra et al. 2005), particularly among specialist species (Munday 2004, Devictor et al. 2008, Clavel et al. 2011). Rapid environmental change and heightened habitat losses will therefore increase the importance of refugia and refuges in maintaining biodiversity (Ashcroft 2010, Keppel et al. 2012). By definition, refugia maintain species over evolutionary timescales (e.g. Tzedakis et al. 2002), while refuges can increase resilience and act as important precursors to refugia by buffering populations or individuals from habitat losses over smaller spatial and temporal scales (Sedell et al. 1990, Lancaster and Belyea 1997, Ashcroft 2010, Keppel et al. 2012). Refuges can operate in-situ, where spatially heterogenous habitat degradation leaves a portion of a population’s habitat unaffected, reducing population loss, or ex-situ, where individuals migrate away from degraded habitats and colonize empty or underutilised habitats, thus mediating species’ extinction risks (Brown and Kodric-Brown 1977, Hanski et al. 1997).

Local-scale spatial refuge effects may be likely where disturbances operate on individual habitat units or within habitat patches, or where disturbances attenuate rapidly along steep environmental gradients. (Chase and Leibold 2003). In these cases, if species responses to asymmetric habitat losses are not assessed over their entire range, the severity of impacts may be unintentionally misrepresented. In addition, where species losses and subsequent recovery are recorded in part of a range (Halford et al. 2004, Gilmour et al. 2013), individual migration or dispersal in and out of patches of localized disturbance may be a key mechanism supporting recovery and longer-term persistence (sensu Hanski et al. 1997, Hanski 1998), particularly in highly connected systems (Thomas and Kunin 1999). For species with broadcasting reproductive strategies (e.g. trees with aerial seeds or aquatic organisms with pelagic larval phases), resilience against spatially restricted habitat degradation may be further enhanced if establishment of propagules and recruits is distributed across ranges incorporating both disturbed and undisturbed habitats (Hanski 1998, Nathan and Muller-Landau 2000, Jones et al. 2007, Grober-Dunsmore et al. 2009, Teller et al. 2015). In contrast resilience may be limited if propagules and recruits only arrive on frequently disturbed habitats. Moreover, successful settlement of undisturbed habitat patches following migration or dispersal may also be mediated by competition and prior occupancy effects (Almany 2004).

Coral reefs are increasingly degraded by anthropogenic climate change, tropical storm events and predation by the coral feeding sea-star, *Acanthaster planci* (Bellwood et al. 2004, McClanahan et al. 2004, De'ath et al. 2012, De’ath et al. 2012, Hughes et al. 2018). Up to 75% of coral-reef fish species rely on live coral habitats for food, shelter or settlement (Jones et al. 2004) and in shallow waters coral-obligate species suffer large abundance declines following coral habitat losses (Munday 2004, Jones et al. 2004, Pratchett 2006, Wilson et al. 2006). However, highly divergent responses often occur at smaller spatial scales (e.g. (Nyström and Folke 2001, Graham et al. 2015, Roche et al. 2018)) and in some cases localised reef-fish declines may be related to individuals moving to unaffected habitat patches (Walsh 1983, Letourneur et al. 1993, Coker et al. 2012).

Where disturbance events such as warm-water coral bleaching result in broad-scale habitat degradation, horizontal post-settlement movement of individual reef fishes may be confined within disturbance boundaries (Berkelmans et al. 2004, Pratchett et al. 2008, Hughes et al. 2017). However, depth-related attenuation of major coral-habitat degradation drivers (within tens of meters of water depth in many cases) (Walsh 1983, Hughes et al. 2010, Bridge et al. 2013, Muir et al. 2017, Baird et al. 2018) may allow: 1) some deeper-reef fish populations to avoid habitat degradation, or 2) some individuals normally resident in shallow-waters to migrate downward away from degraded habitats. For example, large storm-swell events and related habitat degradation can cause individual fishes and whole assemblages to shift into deeper waters on both temporary and longer-term bases (Walsh 1983, Letournier et al. 1993, Aspillaga et al. 2016). However, the potential for deeper reefs to provide a spatial refuge for coral-obligate reef fish populations and the capacity of individual fishes to shift downslope in response ongoing habitat degradation have rarely been tested.

In this chapter I utilize natural habitat degradation in shallow water and a competitor removal experiment on deep reefs to examine whether: 1) differential impacts and outcomes occur among shallow and deep populations of the highly specialized coral-obligate reef fish *Chaetodon baronessa*, following a localized outbreak of the coral consuming crown-of-thorns sea-star *Acanthaster planci* (COTS), 2) individuals occupying degrading shallow-water habitats can migrate downslope to re-establish on unaffected habitat patches at deeper depths, and 3) whether this capacity is influenced by the presence of conspecifics. I further use observations of natural settlement patterns to assess whether 4) *C. baronessa's* capacity to utilize potential depth refuges is enhanced by a broad depth distribution of recently settled juveniles and recruits.

Methods

Study site and study organism

The study took place in Kimbe Bay, Papua New Guinea, using the coral-obligate fish species *Chaetodon baronessa*. *C. baronessa* preferentially feeds on *Acropora* corals, which account for ~75% of their diet (Chapter 5). In Kimbe Bay adult *C. baronessa* distributions are strongly skewed toward shallow water (Chapter 3) but deeper-water residents do not demonstrate sublethal costs (Chapter 4). In shallow-waters, *C. baronessa* abundances commonly decline in response habitat degradation attributed to COTS predation (Emslie et al. 2011), coral bleaching (Pratchett et al. 2006) and a combination of stressors (Emslie et al. 2011). Up to 80% of abundance has been lost in some studies (Pratchett et al. 2006), with extirpation recorded in the shallow waters of one reef (Emslie et al. 2011). *C. baronessa* distributions typically correlate with cover of live coral their preferred *Acropora* prey corals (Pratchett & Berumen 2008). In Kimbe Bay, *C. baronessa* densities broadly correlate with the cover of complex coral habitats (Chapter 2).

Pre- and Post- disturbance depth distributions

The densities of *C. baronessa* were recorded from replicate transects at 4 depths between 0 – 10m on Kimbe Island, at 6 depths between 0 – 30 m in 2013 and again at 8 depths between 0 – 30 m in 2015 (see Table 1 for sampling design). The percent cover of *Acropora* coral colonies was recorded at the same depths at all time periods. In shallow water (≤ 10 m), cover was recorded from point intercept transects as part of a long-term monitoring program, with 50 points recorded per transect. Below 10m, cover was recorded from 9 random points from each of 40 replicate photo-quadrats (~ 1 m^2) per depth (10 per transect) using Coral Point Count with excel extensions (CPCe) (Kohler and Gill 2006). COTS were also counted at 6 depths between 0 – 30 m in 2013 and again at 8 depths between 0 – 30 m in 2015, as per the sampling for *C. baronessa.*

Table 6.1: Sampling design for depth distributions of COTS, *Acropora*, and *Chaetodon baronessa* on Kimbe Island.

Depth (m)					**2013**		**2015**	
	n	L*W (m)	n	L*W (m)	n	L*W (m)	n	L*W (m)
0	4	50x4	4	50x4	4	50x4	4	50x4
2	4	50x4	4	50x4	4	50x4	4	50x4
6	4	50x4	4	50x4	4	50x4	4	50x4
10	4	50x4	4	50x4	4	50x4	4	50x4
15	-	-	-	-	-	-	4	50x4
20	-	-	-	-	4	30x4*	4	50x4
25	-	-	-	-	-	-	4	50x4
30	-	-	-	-	3	30x4*	4	50x4

*video transect

Vertical migration experiment

The possibility of downward migration of *C. baronessa* away from degrading habitat was tested using a fish tagging and conspecific competitor removal experiment on Christine's reef in Kimbe Bay. As on Kimbe Island, high numbers of COTS were predating on the shallow water corals of Christine's reef during the experimental period. The experiment consisted of two treatment plots (P1 & P2), and one control plot (C1). All plots extended spatially from the edge of the reef flat (< 3 m back from the crest and < 1 m water depth) down the reef slope to 30 m depth. Plots were ~ 50 m wide and were separated horizontally by buffer zones of ~ 15 m – 30 m. The control plot was separated from the treatment plots by a natural sand slope of ~ 15 m width that housed very few corals and no butterflyfish. In January 2016, 11 - 12 adult *C. baronessa* resident in < 5 m water depth were tagged within each of the treatment and control plots. The fish were tagged with a combination of external T-bar tags (Sensu (Berumen and Almany 2009)), and sub-cutaneous elastomer injections. All untagged *C. baronessa* were removed from between 0m and 30m depths in treatment plots, as well as in buffer zones between plots. The control plot had no fish removed from within the plot and no fish were removed from the inner reef flat adjacent to any plot or buffer zone. Plots were re-surveyed at 1 week (T1) and 9 months (T2) after initial removal and tagging (i.e. January and October 2016). Two divers swam an ascending zig-zag pattern from 30 m to 0 m twice at each time period within the experimental plots and buffer zones and the depths of all located tagged fish were recorded. The proportional cover of total hard corals and *Acropora* corals were recorded in the experimental and control plots at T1 and T2. The benthic component under each of 9 random points was counted from within 50 replicate photo-quadrats (~ 1 m^2) per plot in both shallow (< 1 - 5 m) and deep water (15 - 20 m) in each plot, using CPCe. Benthic data from below 10m in the control plot were not retained. However, *Acropora* cover was as dense, if not denser, in this plot compared to the deeper-water areas of the experimental plots (Pers. Obs.). The mean depth-range for *C. baronessa* was determined before the removal experiment by recording the minimum and maximum depth of 39 territories within the study area, as per methods in **Chapter 4**.

Settlement Depth of Recruits and Juveniles

The settlement depth and settlement habitat of *C. baronessa* recruits (< 3 cm length) and juveniles (3-5 cm length) were surveyed using a zigzag search pattern covering all depths from 30 m to 0 m on four reefs.

Analysis

All models were fit in R and checked for adherence to model assumptions, goodness of fit and dispersion rules. Where multiple model fits were possible, best-fit models were selected using AICc selection criteria. The availability of *Acropora* colonies and *C. baronessa* abundance were pooled into three depth bins (≤10m, 15-20m, 25-30m). Between-depth differences in each group were analyzed within the pre- (2010-2013) and post- (2015) disturbance periods. Differences between pre- and post-disturbance periods were also analyzed within each depth bin. Changes in *C. baronessa* abundance was analyzed using a Generalized linear model with a poisson error family in 'lme4' and percent *Acropora* cover was analyzed with a beta-binomial model using 'glmmADMB'. In order to test pairwise between-year differences in *C. baronessa* abundance and *Acropora* cover I used the 'glht' function in the CAR package, with tukey's post hoc adjustments. I tested for reductions in the availability of shallow water coral resources between T1 and T2 within each treatment and control plot using general linear models on proportional cover data with a quasibinomial error family within 'lme4' (model: proportional resource cover ~ time). Differences in coral resource availability between shallow and deep water at T2 were tested using the same protocol (model: proportional resource cover ~ depth).

Results

Pre- and Post- disturbance depth distributions

COTS density

Mean COTS densities reached 4 (± 1.14 SE) per 200m^{-2} (n = 16) in the shallow waters (<10m) of the focal reef (Kimbe Island) in 2013 and declined to 1.38 (± 0.56) per 200m^{-2} in 2015 (n = 16), as coral cover declined. Only one COT was observed at depths below 10m during the study period.

Acropora cover

Acropora cover in shallow water (<10m) declined from 5.81% (±1.13% SE) in 2013 to 1.38% (±0.51%) in 2015, ($p < 0.001$). However, there were no *Acropora* declines in deeper waters, at 15-20m ($p = 0.60$), or at 25-30m ($p = 0.63$). Moreover, *Acropora* cover in 2015 was higher at depths ≥15 m than at ≤10 m (0-10m ~15-20m, $p < 0.001$; 0-10m ~25-30m, $p = 0.044$) (Fig. 6.1a).

Fish abundance

The mean abundance of *C. baronessa* in shallow water (≤10m) on Kimbe Island did not vary significantly between 2010 and 2013 (Table 6.2, 2010 = 0.75 indv.200^{-2}m ± 0.28 SE, 2011= 1.0 ± 0.29, 2013 = 1.25 ± 0.35), but then decreased by an order of magnitude between 2013, and post-disturbance in 2015 (0.125 ± 0.09) ($p = 0.003$) (Table 6.6.2, Fig. 6.1b). However, there was no significant change in abundance between pre and post disturbance (2013 vs 2015) at either 15-20 m (pre = 1.25 ± 1.24, post =1.68 ± 0.46) or 25-30 m depths (pre = 0.42, post = 0.875 ± 0.04, Table 6.2). Post-disturbance abundance of *C. baronessa* was also significantly lower in water ≤10m (0.125 ± 0.09), than at 15-20m (1.675 indv.200^{-2} m ± 0.46, $p = 0.001$) and at 25-30m (0.875 indv.200^{-2} m ± 0.35, $p = 0.015$), whereas pre-disturbance abundance did not differ significantly between depths in the year previous to the disturbance (2013; 0-10m ~ 15-20m, $p = 0.\ 996$; 0-10m ~ 25-30m, $p = 0.437$).

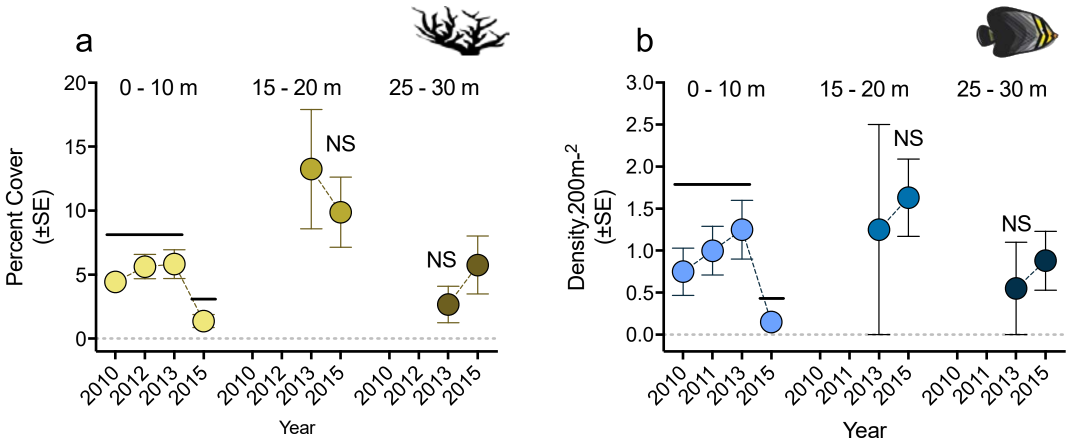

Figure 6.1: (a) The Shallow water declines and deeper resilience in (a) the cover of *Acropora* corals and (b) the abundance of *Chaetodon baronessa* between 2010 and 2015. Kimbe island, Papua New Guinea.

Table 6.2: Summary table for between-year comparisons of *C. baronessa* abundances and *Acropora* cover at Kimbe Island, Papua New Guinea. Bold values denote significance, confirmed with non-overlapping 95% CI.

Depth Bin	Organism	Year comparison	Z value	Pr(>|z|)
0-10 m	C. baronessa	2010 - 2011	0.753	0.868
		2010 - 2013	1.399	0.482
		2010 - 2015	-2.346	0.080
		2011 - 2013	0.665	0.904
		2011 - 2015	-2.773	0.026
		2013 - 2015	-3.105	0.009
	Acropora	2010 - 2011	1.53	0.368
		2010 - 2013	1.76	0.253
		2010 - 2015	-4.88	<0.001
		2011 - 2013	0.18	0.997
		2011 - 2015	-4.35	<0.001
		2013 - 2015	-4.33	<0.001
15-20 m	C. baronessa	2013 - 2015	0.39	0.696
	Acropora	2013 - 2015	-0.58	0.560
25-30 m	C. baronessa	2013 - 2015	0.52	0.598
	Acropora	2013 - 2015	0.51	0.610

Vertical Migration Experiment

Natural depth range of C. baronessa

The depth-range of *C. baronessa* territories varied from 0.3 m to 15 m, with a mean of 5.78 (± 0.61 SE) m. The distribution of territory depth-ranges was non-normal, however, with the depth-range of many territories being less than 5m in breadth (Shapiro-Wilks test: w = 0.91, p = 0.003). Depth range of < 5m were almost ubiquitous among shallow water individuals.

Coral cover

The cover of all hard corals and of *Acropora* specifically decreased in the shallow waters (> 5m) of all three experimental plots between T1 and T2 (Fig. 6.2). Mean total coral cover decreased from 42.04 (± 8.45 95% CI) %, to 34.41 (± 5.93) % in P1 (t = 0.146, p = 0.146) (Fig. 6.2a), from 54.69 (± 7.42) % to 40.35 (± 6.14) % in P2 (t = 2.835, p = 0.006) (Fig 6.2b), and 63.02 (± 8.38) % to 37.57 (± 7.28) % in C1 (t = 4.256, p <0.001) (Fig. 6.2c). During the experimental period the shallow water cover of *Acropora* corals declined by more than half. In P1, *Acropora* cover declined from 17.60 (± 6.33) % to 7.95 (± 4. 03) % (t = 2.50, p = 0.014) (Fig. 6.2a), in P2 cover declined from 24.79 % (± 8.90) to 6.37 (± 3.97) % (t = 3.45, p <0.001) (Fig 6.2b) and in CP it also declined from 20.32 (± 8.01) % to 7.28 (± 4.80) % (t = 2.62, p = 0.010) (Fig 6.2c).

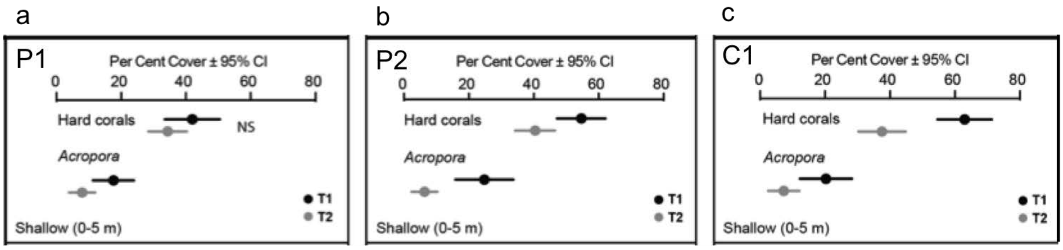

Figure 6.2: Concurrent declines in the mean cover of all hard corals and preferred *Acropora* corals in shallow water between the commencement (T1) and conclusion (T2) of the experimental period in experimental plots (a) P1, (b) P2, and a control plot (c) C1. Error bars are 95% confidence intervals.

At the conclusion of the experiment both total coral cover and *Acropora* cover were higher in deeper water (15 – 20 m), than in shallow water (0 – 5 m) (Fig. 6.3). In deeper water, total coral cover in P1 (67. 10 % ± 6.77) was ~ 50% greater than in shallow water (t = -6.61, p < 0.001) (Fig. 6.3b) and in P2 (62.27 % ± 9.15) was approximately a third higher than in shallow water (t = -5.57, p <0.001) (Fig. 6.3b). Final mean *Acropora* cover in deeper water was more than 50 % greater in deeper water than shallow water in both P1 (t = -3.856, p < 0.001), and P2 (t = -2.00, p = 0.049) (Fig. 6.3). Mean deeper water *Acropora* cover was 24.21 (± 6.73) % in P1 (Fig. 6.3a) and 14.82 (± 5.94) % in P2 (Fig. 6.3b).

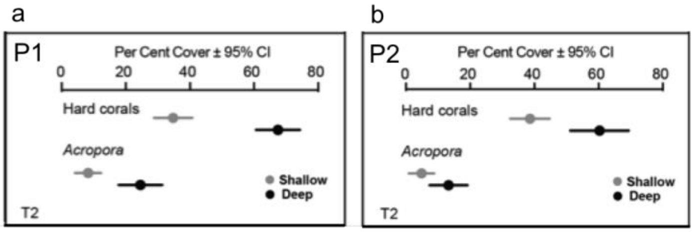

Figure 6.3: Increased mean cover of coral types in deep (15-20 m) water compared to shallow water (0=5m) at the conclusion of a nine-month experimental period in the experimental plots (a) P1, (b) P2. Error bars are 95% confidence intervals.

Fish Migration

One week after commencement of the experiment (T1) all tagged fish were present in the three experimental plots and one pair from P1 had moved from <1 m depth to a large tabular *Acropora* colony at 18 m (Fig. 6.4). At T2, the migratory pair in P1 was still present at ~18m and one pair from P2 had migrated to a depth of 17-21 m, again to a large tabular *Acropora* colony. No fish from C1 were located below the initial tagging depth limit of 5m in any surveys. Retention of tagged fish through untill T2 was higher in the removal plots (10 fish located in each of P1 and P2) than in the control plot (6 fish located).

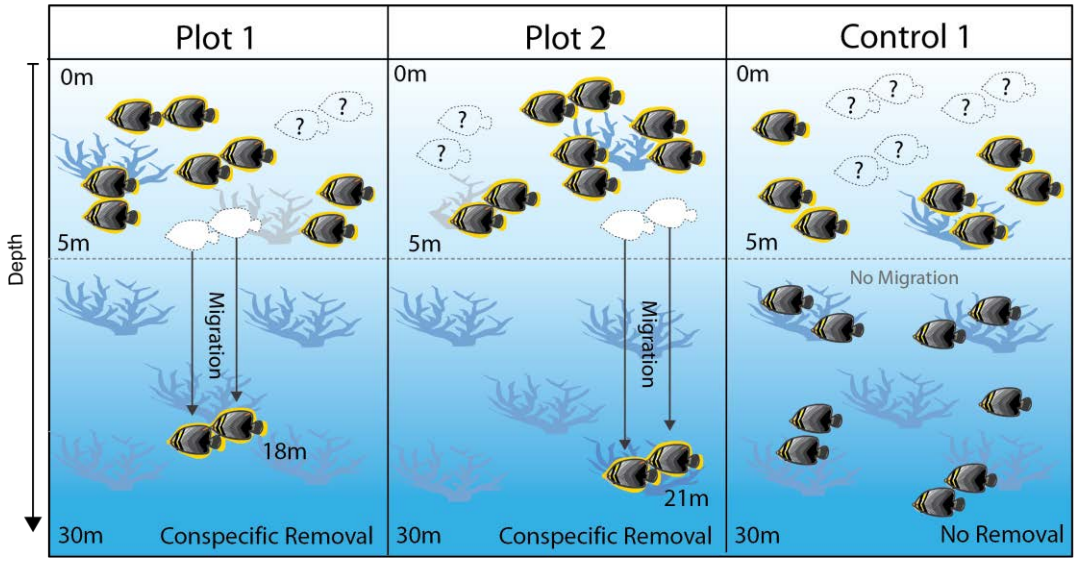

Figure 6.4: Schematic of experimental set-up and results showing evidence of downward vertical migration by *Chaetodon baronessa* in a natural habitat degradation and competitor removal experiment. The two replicate treatment plots (Plot 1 & Plot 2) had all conspecifics removed from between 5 m and 30m, and the one control plot had no competitors removed. Fish with yellow highlights indicate tagged fish; 12-13 in each plot. Outlines with '?' indicate tagged fish that were not relocated 9 months after the start of the experiment. Cut-outs indicate fish that migrated downward to deeper habitats.

Settlement Depth

All *C. baronessa* recruits (0-3cm) were located on either *Acropora* colonies at depths shallower than 11m (mean = 4.59 ± 0.50 m, n = 23). All juveniles (3-5cm) were associated with the same coral habitats and were located only in depths shallower than 10m (mean = 4.44 ± 0.62 m, n = 19).

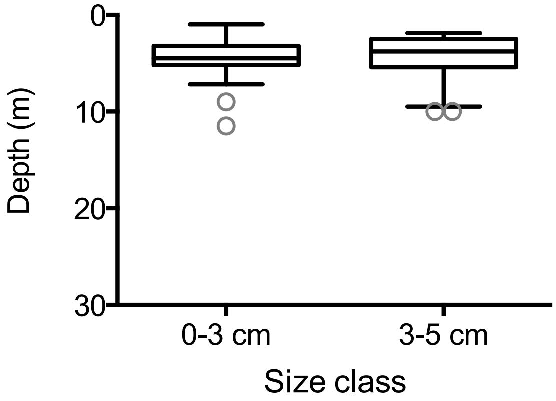

Figure 6.5: Settlement depth of *Chaetodon baronessa* recruits and juveniles.

Discussion

The cover of *Acropora* corals and the abundances of *C. baronessa* were stable in the shallow waters around Kimbe island between 2010 and 2013. In response to the COTs outbreak on Kimbe Island in 2014, high losses of shallow water *Acropora* coral habitats resulted in corresponding abundance declines of the obligate corallivore *C. baronessa*. However, neither *Acropora* nor *C. baronessa* declined in deeper water between the years immediately before (2013) and following (2015) the disturbance. Further, post-disturbance densities were higher in deeper waters than in shallow water. These results support the hypothesis that vertically asymmetric pressures on coral habitats can, in certain situations, result in differential outcomes for coral-reef fishes resident at shallow and deep depths. In response to a shallow-disturbance and adult-removal experiment at Christine’s Reef, a small number of tagged fish migrated from declining coral resources at <5m depth to a greater abundance of *Acropora* corals at ~20m. However, this only occurred in experimental plots where deep habitats were ecologically released via conspecific removal. Moreover, a greater proportion of the tagged shallow-water fish were missing at the conclusion of the experiment in the control plot, where deep habitats were not released via the removal of conspecifics. Whilst this was only a small-scale experiment, the results support the potential for individual reef fishes inhabiting degraded shallow-water habitats to emigrate downward to establish on deeper-reef habitats. It also suggests prior occupancy and competition effects may limit this potential for many individuals. Finally, all observed sub-adult *C. baronessa* were located on *Acropora* colonies in depths shallower than 10m. Therefore, the capacity to benefit from potential depth refuges may be restricted in some species if the availability of shallow settlement habitats are severely reduced and settlement depths are inflexible.

Acropora corals are frequently the preferred shelters (Bonin et al. 2009, Messmer et al. 2011, Boström-Einarsson et al. 2013) and food sources (Pratchett 2013, Chapter 5) of strongly coral-associated fishes but are also among the most vulnerable to degradation from a range of disturbances (Marshall and Baird 2000). Correspondingly, near collapses of coral-obligate populations are not uncommon responses to *Acropora* declines in shallow waters (e.g. Pratchett et al. 2006, Emslie et al. 2011). In chapters 2 and 3 I demonstrated that many coral-obligate and coral-associated species utilize extensive depth-ranges that incorporate deeper coral habitats. Here, I show both corals and coral-obligate reef fish can, in some circumstances, benefit from a refuge effect on deeper reefs. A number of recent studies have demonstrated that coral losses due to coral bleaching can also attenuate significantly with depth in multiple regions and across multiple taxa (Muir et al. 2017, Baird et al. 2018, Frade et al. 2018). These results suggest that assessments of species responses to habitat losses may misrepresent total impacts on metapopulations if they do not cover the full depth ranges of coral habitats and their fish associates. Though significant spatial variability occurs among reef-habitat degradation events and this may not always hold true and further, more comprehensive, assessments will be required to confirm the validity of these results across different disturbance events, reef systems and reef-fish species.

Even severe degradation of shallow-water coral-reef habitats has, in some cases, given way to impressive recovery trajectories at some time after disturbance events (Halford et al. 2004, Gilmour et al. 2013, Graham et al. 2015), though not always (Norström et al. 2009). Recolonization and depth effects have been implicated as drivers in some recovery trajectories (Walsh 1983, Gilmour et al. 2013, Graham et al. 2015), though the mechanisms through which depth has a positive influence has not yet been fully clarified (Graham et al. 2015). Here, I demonstrate that motile coral-obligate reef fishes do have the potential to migrate away from degrading habitats and that this capacity may be affected by conspecific densities. In broader ecological systems, migration in and out of degraded habitats is expected to enhance overall metapopulation stability by distributing abundance more evenly among patches, according to their varying carrying capacities (Sæther et al. 1999, Kindvall and Petersson 2000). Therefore, individual migration between habitat patches with declining and recovering resource availability along depth gradients may play a role in longer term resilience of reefs, via both resistance to, and recovery from, shallow-water habitat degradation (sensu Kuussaari et al. 1996, Hanski et al. 2002, Schneider et al. 2003). This has been demonstrated in at least one other example of coral-reef fish utilizing depth-migration as a temporary refuge from shallow-water habitat degradation (Walsh 1983). In that instance, almost the entire initial shallow-water assemblage migrated to deeper habitat (within 13m of depth, but up to 50 linear meters) after a large storm-swell event and much of the assemblage returned to shallow habitats within 6 months after the disturbance.

The propensity for individuals to undertake among-patch migrations may be enhanced by prior migration propensities among individuals or within populations (sensu Ronce et al. 2001, Massot et al. 2002). The disconnect between limited shallow-water sub-adult distributions and broader depth distributions of many adults (up to 40m depth, Chapters 2 and 3) in Kimbe Bay suggests that *C. baronessa* may be pre-disposed to take advantage of downslope ‘migrations to refuge’. The actual ability to migrate downslope may, however, be limited by competition and prior occupancy effects (Almany 2003). Here individuals migrated to deep-water corals only where habitats were ‘ecologically released’ (sensu Wilson 1959, Allaby 1998) via competitor removal and not where superior resources were protected within the territories of established occupants. The probable lack of competitive ability among shallow-water residents to occupy better quality resources at depth in this control situation may be exasperated by declines in physiological condition among individuals subjected to protracted declines in key coral resources (Pratchett et al. 2004). Migration-limiting effects of prior residency and competition in deeper-reefs will be important in controlling refuge access for shallow-water individuals. However, the refuge potential of deeper-habitats for metapopulations may not be affected unless lower prior-resident densities on deeper-reef habitats (sensu Chapter 4) maintain deeper subpopulations below actual carrying capacities. Additionally, predation pressure, in the form of predator density, often increases with depth on coral reefs and this may partially account for low densities on deeper reefs.

The shallow distribution of sub-adults in Kimbe Bay corresponds to peak densities of both their preferred *Acropora* prey and adult conspecifics along the depth gradient (Chapter 3 & 5). Coral feeding reef-fish species, including *C. baronessa*, often display highly concordant distributions among adults and juveniles (Pratchett et al. 2008, Clark and Russ 2012), and strong coral reliance appears to constrain settlement to essential prey resources and on microhabitats occupied by adult conspecifics (Pratchett et al. 2008). If these are the primary dynamics influencing settlement preferences, then future sub-adult settlement may shift to deeper depths to follow densities of resources and established conspecifics. This flexibility in depth-use would enhance the refuge potential. However, larval reef fish can also demonstrate strong pre-settlement depth stratification e.g. (Leis 1991, Srinivasan 2003, Huebert et al. 2011). If the shallow-water pre-adult depth preferences observed here are pre-determined by pre-settlement larval behaviour, disproportionate losses of shallow-water habitats are likely to result in juveniles settling to areas of lower food resources and higher rates of predation (Srinivasan et al. 2003), leading to lower survival rates into adulthood, therefore lower total fecundity and reduced future resilience.

The limited depth distribution of C. baronessa sub-adults may also have been partially related to the depth distribution of their predators and relative 'predation release' in shallow water. Whilst not recorded here, the distribution of meso-predators are more abundant at deeper depths on red-sea reefs (Brokovich et al. 2008)_and their abundances peak at depths of 20-30m both on submerged reefs of the Great Barrier Reef (Cooper et al. in review) and on reefs of the Florida Keys (Goldstein et al. 2017). Goldstein et al. (2017) further found that body condition and 'risky' behaviours both covaried with depth (inversely to meso-predator abundances). It should be noted that depth-related differences were confounded by geographic position in that study, with shallow and deep sites separated by a major oceanographic feature. In contrast, in chapter 4 here, there were no depth-related changes in multiple behaviour metrics related to predator vigilance or in body condition metrics of adult coralivores. However, densities of early post-settlement juveniles and new recruits of C. baronessa were strongly concentrated in shallow waters. This suggests that if predation is a factor controlling butterflyfish depth distributions it is likely to be strongest during the settlement or early post-settlement phases. Finally, it should be noted, that other obligate-coralivore species within the same genus (C. octofasciatus and C. lunulatus) have broad early-settlement depth distributions that are centered in, or include, the lower portion of the 0-30 m depth gradient (C. MacDonald, unpublished data).

Conclusion

Rapidly changing environments, increased habitat losses, and species displacements threaten extinction in a growing number of species globally. Coral reef ecosystems are a highly diverse and charismatic example where the loss of keystone taxa threatens to cascade into broad-scale losses across multiple taxa and trophic levels, especially among coral obligate species. A number of recent investigations have determined that depth can in some cases mediate negative environmental impacts, reduce coral losses and therefore provide spatial refuge for a broad range of taxa (Bridge et al. 2013, Smith et al. 2014, Muir et al. 2107, Baird et al. 2018, Frade et al. 2018), and a similar refuge effect has been hypothesized for reef fishes. However, the susceptibility of fish populations to coral losses on deeper reefs and the capacity of individuals to migrate downslope to exploit these potential refuge habitats has only been tested once, over three decades ago (Walsh 1983). My investigation here, whilst limited in its scope, provides some perfunctory support for the hypothesis that vertically asymmetric pressures on coral habitats can result in differential outcomes for coral-reef fishes resident at shallow and deep depths. My results further suggest that coral-obligate individuals inhabiting degraded shallow-water habitats may have the propensity to emigrate downward where suitable deeper-reef habitats are available. A disconnect between shallow-water preferences in sub-adult distributions and broader depth distributions in adults suggest *C. baronessa* may be pre-disposed to downward-migrations due to a propensity to undertake ontogenetic or density dependent migrations. Previous investigations have demonstrated that deeper residence does not confer substantial ecological or physiological costs to my focal species *C. baronessa* (Chapters 4-6). Therefore, whilst deeper water will not be a panacea to rapidly increasing environmental stressors, I provide direct evidence that some coral-obligate reef fishes vulnerable to habitat loss in shallow water can plausibly benefit from depth refuges.

Chapter 7 - GENERAL DISCUSSION

In this thesis I undertook a comprehensive ecological assessment of the drivers, costs, and benefits of broad depth distributions and deep-residence in coral reef fishes, across a wide depth range from the surface to upper mesophotic depths (< 40 m) in Kimbe Bay, PNG. I assessed five major ecological requirements that deep-reef habitats and coral reef fishes will need to meet if deep-reefs have a chance to provide refuges from increasing habitat losses in shallow water.

In **chapter 2**, I quantified the depth distributions of reef fishes and determined whether many species have ‘broad or deep depth distributions’ that might render them resilient to shallow water disturbances. I found a quarter of the 123 focal fish species were distributed across 0-30 m, and 12% were distributed from 0-40 m. I also found that coral habitat was broadly available throughout the depth gradient and that 85% fish species strongly associated with complex coral habitats occurred at 20m or deeper. Clear-water, offshore reefs supported deeper distributions than on near-shore reefs. In general, I found that the major fish assemblage split occurred between 5 m and 10 m depths, and up to 25% of fish species were limited to the shallowest 5m, where disturbance of coral habitats has historically been the greatest. Hence, a significant component of the fish fauna likely has no refuge in depth.

In **chapter 3**, I investigated whether 'ecologically vulnerable species are limited to shallow waters'. I found that butterflyfish species with low local abundance also had the narrowest depth ranges, but that these were also among the least coral-specialised species in the family. Counter to expectations from the literature, I also found that highly specialized coral feeders were the most abundant species and had the broadest depth distributions. Therefore, no coral specialist fish experienced a depth-related double or triple jeopardy (based on any combination of resource specialization, abundance and depth-distribution). Few species had limited shallow depth distributions and these were non-coral benthic feeders or planktivores with lower risks associated to coral losses. I did find, however, that despite having the broadest depth distributions, the most specialized corallivores had great proportions of their populations utilizing shallow-reef habitats. This suggested costs may be higher for individuals utilizing deep periphery reef habitats.

In **chapter 4**, I examined for two coral-obligate focal species (a specialist, *Chaetodon baronessa*, and a generalist, *Chaetodon octofasciatus*) whether 'deep-reef residents can efficiently secure resources without suffering sub-lethal costs'. As predicted, I found that the density of preferred resources declined with depth and that territories of the more-specialised coral feeder increased with depth in response. However, the density of preferred resources did not decline with depth within territories, suggesting that deep resident individuals were selecting occupying high quality resource patches. This resulted in deep resident individuals having greater total secured resources compared to their shallow-reef counterparts, which was an unexpected result. I further found that competitor densities and competitor interactions decreased with depth, whereas foraging distances, and time spent pairing did not. In addition, all four commonly used body-condition metrics, including the gonad-somatic index - a proxy for reproductive output, were stable along the depth gradient for both the specialist and generalist corallivore species. Therefore, small populations of even highly specialized coral-feeding fishes can utilize deep-reef habitats with little to know ecological or physiological costs.

In **chapter 5**, I investigated potential compensatory mechanisms that support the low-cost deep-reef residence demonstrated in chapters 2 – 4. I tested whether ‘depth related resource changes are met by dietary plasticity or other compensatory mechanisms’ among a dietary specialist corallivore species (C. baronessa) with a numeric preference for shallow-reef habitats and more deeply distributed dietary generalist corallivore (C. octofasciatus). I found that neither overall resource availability nor feeding effort declined along the depth gradient. As expected, feeding plasticity at a coral genus level was high for the dietary generalist, but not for the dietary specialist, which feed on its preferred resource over 40 times more than expected given is availability at deeper depths. Surprisingly, the energy content of coral tissues did not decline with depth and both bulk and compound specific SIA supported an argument for increased coral heterotrophy at deeper depths. A similar increase in plankton-sourced carbon was recorded in deep resident ‘corallivores’. These results suggest that multiple mechanisms of energy compensation may buffer declining energy and changed resource compositions on deep reefs. Such mechanisms appear operate among varying functional strategies, as well as across multiple trophic levels.

Finally, in **chapter 6**, I used natural and removal experiments to test whether ‘deeper reef assemblages are more resilient to coral loss, and individuals from degrading shallow water environments can benefit from healthy deep-reef habitats’. I found that at least some combinations of disturbance can result in differential impacts and outcomes for obligate coral-associated reef fishes in shallow and deep reefs. Some individuals also show the propensity to migrate to deeper-water, which ultimately provided spatial refuge to deep-reef residents, sheltering them from a collapse of their key resource.

In **Box 7.1**, I have compiled the evidence for and against the potential role of deep reefs as a refuge for coral reef fishes. Of these 24 points, 17 positively support a potential for deep refuges, and 7 demonstrate some potential cost or limiting factor for successful utilization of deep-peripheral habitats for at least some section of the assessed reef fish community. Among these 7 potential costs, two identify groups of species that appear currently to have distributions limited to shallow water. Approximately 25% of all assessed species and 15% of assessed species with strong coral habitat associations were limited to shallow water. These species will not benefit from any potential deep refuge effect unless they undertake future downward range shifts. This is clearly feasible, as demonstrated for an obligate corallivore species in chapter 6. A tendency for rare species to also have narrow depth distributions puts some species at risk where their distributions are limited to shallow waters. Species with this combination of traits do potentially suffer a depth-related double jeopardy. This risk may be offset in part by having broad or non-specialist diets that make them less susceptible to coral losses, at least as adults (Jones et al. 2004, Wilson et al. 2006). The densities of highly coral-specialized species did, however, tend to be concentrated in shallow waters, both in trait group and species levels of assessment. This is likely due to depth-related changes in habitat composition that reduce the availability of preferred resources at greater depths. Largely inflexible dietary specialization along the depth gradient among specialists is another potentially limiting factor, as was the increase in space use by specialists resident at greater depths. However, in this study actual costs were not borne out for either of these potential limiting factors. Dietary inflexibility in the focal specialist coral consumer was offset by depth related flexibility in their coral prey, and lower competition at depth meant larger territories did not result in usual increases in maintenance costs.

Certain limitations of the work in this thesis must also be recognised. Firstly, the geographic location is limited to a clear-water, low latitude reef system that likely has low human populations and limited local-scale stressors compared to many of the most threatened reef locations globally. Papua New Guinea is also situated in the species-rich Coral Triangle and a much larger pool of coral and fish species compete for space than in less specious regions such as the Caribbean. Long-term competition for space is likely to increase adaptation to marginal environments, such as low light at deeper depths. This, in combination with the steep local bathymetry and clear warm waters, mean complex, habitat forming corals extend deeper in Kimbe Bay than the shelf-bottoms of many reef systems globally. Therefore, whilst I conclude that deep reefs may provide a strong refuge potential for regional scale recovery, the transferability of these results to some systems may be limited. By nature, refuges do not have to operate ubiquitously on a global scale. However, further ecologically comprehensive cost-benefit investigations of the depth-refuge potential for reef fishes do need to be carried out to identify areas with refuge potential in other regions. For example, in the GBR, the depth-refuge potential has been scarcely investigated, and in other regions studies have focussed on depth-distributions only or have primarily had a strong emphasis on corals (but see the good work of Goldstein et al. (2016a, 2016b, 2017)). In addition, chapter two of this thesis introduces the importance of the interaction of multiple gradients in mediating refuge potential, the interactions between light penetration and ocean temperature latitude mean future studies would preferably extend the type of ecological assessments carried out here across multiple locations along latitudinal and cross-shelf gradients.

The tractability of the studies here also necessitated limitations in some of the study design. Future studies will ideally begin to incorporate time series data to: 1) better assess longer-term shifts in depth distributions within whole assemblages, in response to habitat degradation events such as warm-water coral bleaching. 2) asses the longer-term stability of primary the ecological patterns and processes identified here. In addition, (3) because of low replication and the limited spatial extent of the studies in chapter six, these results should be treated as tests of plausibility, rather than comprehensive assessments of depth migration among individuals.

A final limitation that warrants highlighting is the role of predation pressure on natural distributions of adult and larval fish and the potential for predation pressure to covary with depth. Whilst no predation attempts were recorded during the many months of observations conducted here, witnessing predation events in person is rare on coral reefs. In addition, predators are considered more abundant at greater depths (Brokovich et al. 2008). For example, meso-predators are more abundant at deeper depths on red-sea reefs (Brokovich et al. 2008)_and their abundances peak at depths of 20-30m both on submerged reefs of the Great Barrier Reef (Cooper et al. in review) and on reefs of the Florida Keys (Goldstein et al. 2017). Goldstein et al. (2017) further found that body condition and 'risky' behaviours both covaried with depth (inversely to mesopredator abundances). In contrast, in chapter 4 here, there were no depth-related changes in multiple behaviour metrics related to predator vigilance or in body condition metrics of adult coralivores. However, densities of early post-settlement juveniles and new recruits were strongly concentrated in shallow waters. This suggests that id predation is a factor controlling butterflyfish depth distributions it is likely to be during the settlement or early post-settlement phases.

Overall, the broad implication of the research presented in this thesis is that while areas of deep coral habitat (e.g. Kimbe Bay) are not likely to be a panacea, they do show many characteristics that suggest they could be potentially important refuges for regional persistence of reef fish species vulnerable to coral losses. However, this refuge potential will only be realised if some regions of deep-reef habitats remain stable. Recent data have shown that deep reefs may not be as stable as previously thought (Colin 2018, Frade et al. 2018, Rocha et al. 2018), though many assessments do demonstrate significant attenuation of degradation with depth (Muir et al. 2017, Frade et al. 2018, Baird et al. 2018). There is no doubt that human impacts on coral reefs will gradually extend to deeper reefs unless comprehensive action is taken. Coral reefs are clearly heading for an uncertain future and this thesis offers hope that the demise of many species is not inevitable.

Box 7.1: Evidence supporting refuge potential for reef fishes at deep peripheral coral reef habitats.

	Contributing factor	Rationale	Support for refuge potential?	Thesis chapter
1	Overall coral resource base is stable over broad depth gradient	Reef fish have strong associations and positive density correlations with live coral habitats, therefore availability of deep habitat is crucial	Positive	Chapter 2
2	A quarter of assessed species limited to shallow waters	Species naturally limited to shallow waters are unlikely to benefit from a depth refuge unless capable of range shifting	Negative	Chapter 2
3	High proportion of species have deep or broad distributions	Species with naturally broad or deep distributions are likely to be buffered from some effects of differential coral loss among depths	Positive	Chapter 2
4	Coral associated species generally have broad depth distributions	Coral associated species are more likely to decline following loss of coral habitats in shallow water	Positive	Chapter 2
5	Approximately 15 % of coral associated species are limited to shallow water	Coral associated species limited to shallow waters likely to be the most vulnerable to loss of coral habitats in shallow water	Negative	Chapter 2
6	Species with low abundance have narrow depth ranges	Species showing combinations of risk factors (i.e. Low abundance and narrow depth ranges) have naturally higher extinction risks	Negative	Chapter 3
7	Species with high coral-specialisation have high local abundance	Species showing combinations of risk factors (i.e. High coral reliance and low abundance) have naturally higher extinction risks	Positive	Chapter 3
8	Species with high coral-specialisation have broad depth ranges	Species showing combinations of risk factors (i.e. High coral reliance and narrow distributions) have naturally higher extinction risks	Positive	Chapter 3
9	High abundance and/or low coral specialisation offset shallow depth range risks	Species showing combinations of multiple risk factors have naturally higher extinction risks	Positive	Chapter 3
10	Increased specialisation increases population skew toward shallow-water	Highly coral specialised species with shallow distributions are likely to have greater declines following shallow water coral loss	Negative	Chapter 3
11	Preferred dietary coral resources decline in density with greater depth	Resource limitation at range margins may negatively affect individual and population level viability	Negative	Chapter 4
12	Preferred resource density within territories does not decline with depth	Individuals at range margins may inhabit resource patches that have similar quality to those in the range core	Positive	Chapter 4

Box 7.1 Cont’d: Evidence supporting refuge potential for reef fishes at deep peripheral coral reef habitats.

	Contributing factor	Rationale	Support for refuge potential?	Thesis chapter
13	Territory size increases with depth	Individuals at range margins may have to increase space use to access similar resource densities as at their species' range core	Negative	Chapter 4
14	Total resources secured within territories of deep residents increases with depth	Individuals at range margins may inhabit resource patches that have similar quality to those in the range core	Positive	Chapter 4
15	Competitor density and competitive interactions decrease with depth	Competitor release allows greater access to sparse resources and reduced interactions decreases energy demands and possible injury	Positive	Chapter 4
16	Foraging distances do not increase with depth	Lower resource availability at range peripheries can increase energetic costs of accessing sufficient resources for energy maximising species	Positive	Chapter 4
17	Body condition does not decline with depth	Reduced body condition is a key indicator of stressed individuals in suboptimal environments	Positive	Chapter 4
18	Reproductive output does not decline with depth	Long term population maintenance will be limited if individuals at range peripheries have low reproductive output	Positive	Chapter 4
19	Feeding rates do not decrease with depth	Lower resource availability at range peripheries can increase energetic costs of accessing sufficient resources for energy maximising species	Positive	Chapter 5
20	Nutritional quality of preferred resources does not decline with depth	Abiotic resource gradients can limit biotic resource quality at range peripheries even where resources are available in patches	Positive	Chapter 5
21	Trophic and dietary shifts offset potential resource limitations at deep depths	Functional changes along environmental gradients may work to offset resource declines	Positive	Chapter 5
22	Higher dietary specialisation is related to decreased plasticity along depth gradients	Inability for functional plasticity along resource gradients increases risk of exposure to costs related to resource declines	Negative	Chapter 5
23	Differential depth impacts and outcomes from disturbance	The real test or refuges is if peripheral habitats and populations are actually more stable over periods of disturbance/coral loss	Positive	Chapter 6
24	Downward vertical migration is possible	Refuges ideally operate at a population level. One way this can play out is individuals migrating to take up high quality resource patches on range peripheries when they become available	Positive	Chapter 6

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SUPPLEMENTAL MATERIAL: CHAPTER 2

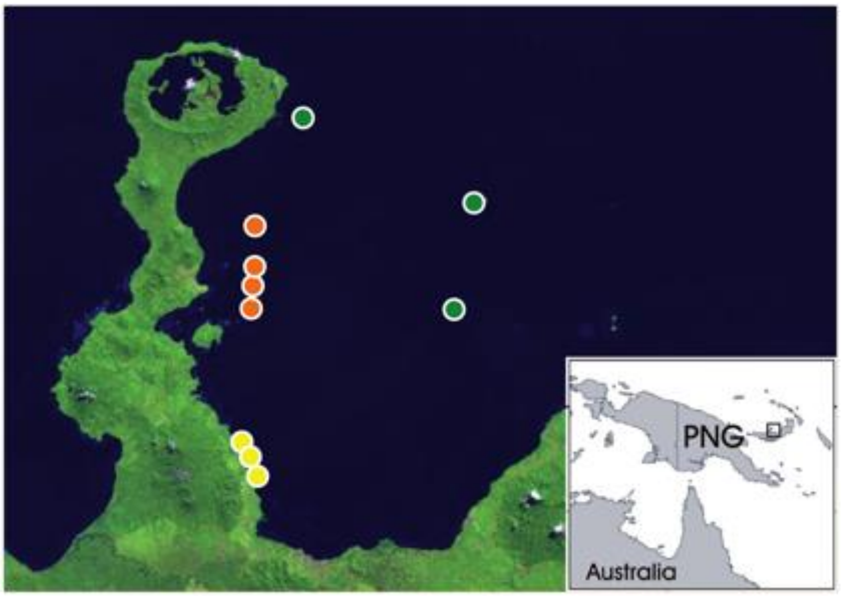


Figure S2.1: Study location (Kimbe Bay, Papua New Guinea), and the ten study sites organized by three bay positions. Yellow circles indicate inshore reefs, orange circles indicate mid-bay reefs and green circles indicate offshore reefs.

Table S2.1: Total number of transects at each combination of depth and bay position.

Depth	Bay Position		
	Inner	Mid	Outer
<1m	17	22	15
6m	18	24	15
10m	15	21	14
20m	16	21	15
30m	16	21	15
40m	-	-	7

Table S2.2: Summary table of Tukey's post-hoc comparisons supporting similarity of reef fish densities between shallow inshore and deep offshore sites.

	Mid 20m		Outer 20m	
	t	p value	t	p value
Inner 1m	3.311	0.1103	2.168	0.6832
Inner 5m	0.82	0.9999	-0.125	1
Inner 10m	2.774	0.2986	1.756	0.9025

SUPPLEMENTAL MATERIAL: CHAPTER 3

Table S3.1: Dietary specialisation indices used for regression models.

Species	Dietary specialisation index (X^2)
Chaetodon baronessa	4.79
Chaetodon lunulatus	4.38
Chaetodon pelewensis	4.11
Chaetodon kleinii	3.91
Chaetodon vagabundus	3.78
Chaetodon rainfordi	3.47
Chaetodon rafflesi	3.32
Chaetodon semeion	2.90

Specialisation indices from Pratchett 2007.

Table S3.2: Sampling occurrences and frequencies for the trait groups and species used in HOF models, and the dietary specialisation index used to rank the four focal species in order with increasingly generalist diets.

Species/ Trait group	Transects	Occurrences	Frequency	H' dietary diversity index *
Obligate coral feeders	253	167	0.66	-
Facultative Coral feeders	253	90	0.36	-
Non-coral invertebrate feeders	253	97	0.38	-
Chaetodon baronessa	253	69	0.27	0.32
Chaetodon lunulatus	253	80	0.32	0.43
Chaetodon ornatissimus	253	39	0.15	0.50
Chaetodon octofasciatus	253	32	0.13	0.80

*Index used to rank dietary specialisation among the four focal butterflyfish species, based on dietary coral genera, from a global review. Higher numbers represent greater breadth in dietary coral sources. Reference: (Pratchett 2013).

Supplemental Methods note:

The hierarchical logistic regression models fit in ‘eHOF’ are also known as Huisman, Olff, Fresco (HOF) models, which are based on realized niches and use statistical information criteria to test responses to environmental gradients (i.e. Depth) against seven predetermined ecologically-meaningful distribution shapes (model types I-VII). This facilitates easier identification of spatial preferences along environmental gradients, because; (1) distribution patterns along gradients are not always monotonic (Rahbek 1995, 1997); but (2) unconstrained model fits (i.e. General Additive Models) can be difficult to interpret in ecologically meaningful ways (Huisman et al. 1993). The seven model types are outlined in Supplemental Box 3.1.

Supplemental Box 3.1: The seven ecologically driven model response types for Huisman, Olff, Fresco (HOF) models.

(I) No response (intercept-only model);

(II) A monotonic increase or decrease along the gradient;

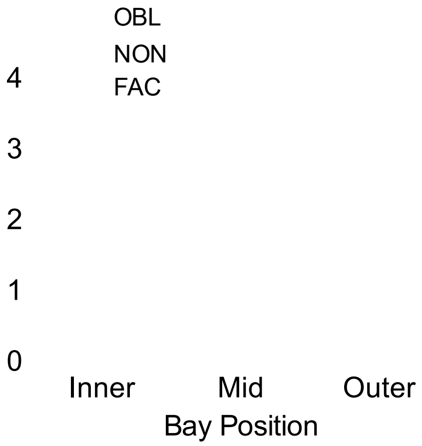
(III) A sigmoidal response, the species or group is suppressed up until a threshold in the gradient at which point it increases rapidly, and/or the species increases along the gradient but reaches a plateau at a particular threshold;

(IV) A symmetrical hump response, the species or group has an optimum position in the center of the gradient;

(V) A skewed hump response, the optimal condition occurs at an asymmetrical position along the gradient;

(VI) A bimodal symmetric response;

(VII) A bimodal skewed response.



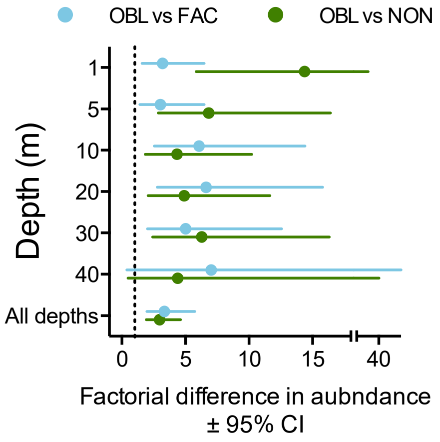


Figure S3.1: Caterpillar plot of effects and confidence intervals (CI) from pairwise comparisons of diet group abundance at each depth. The dotted line represents no difference between diet groups (i.e. No difference = a factor of 1), and obligate coral feeders are significantly more abundant in comparisons where the CI does not cross the line. Error bars in all plots are 95% confidence intervals. OBL = obligate coral feeders, FAC = facultative coral feeders, NON = non-coral benthic invertebrate feeders.

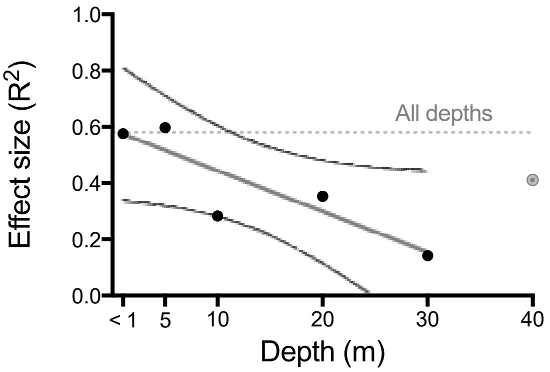


Figure S3.2: Decline in effect size of abundance – specialisation relationships with increasing depth among Chaetodontidae species in Kimbe Bay, PNG. 40m is greyed out, as only one species with specialisation data available was present at 40m. The dotted line corresponds for the effect size of the relationship with data pooled across all depths.

SUPPLEMENTAL MATERIAL: CHAPTER 4

Supplemental methods:

Territories were photographed in swathes, from above, with one-meter scale, horizontal (*x*) and vertical (*y*), and perimeter (p) markers in place. Effort was made to maintain, as best as possible, equal distances from, and perpendicular angles to the substratum. Conglomerate images of territories were constructed by stitching individual photos together using overlapping common visual reference points (i.e. coral heads, and linear markers). Initial stiches were then adjusted slightly where necessary so that the x, y, and p lengths matched in-situ measurements. Areas were estimated using spatial analysis tools in Photoshop CS. Area measurements were untenable in very shallow water (i.e. reef flats) due to lack of distance from substrate for ‘aerial’ photography, and also with very large territories at deep depths because of poor resolution of visual reference points. Due to these limiting factors, and because perimeters are ecologically relevant spatial measures for butterflyfish territories (butterflyfish utilize the perimeters the majority of the time and rarely use internal areas (Righton et al. 1996, personal observation), I used perimeter length as the sole metric for territory size in our analyses. I also confirmed that perimeter and area were related among 30 *C. baronessa* ($R^2 = 0.82$, $F_{1,28} = 123.6$, $p < 0.001$) (Supplemental Figure S2a) and 11 *C. octofasciatus* ($R^2 = 0.60$, $F_{1,9} = 13.02$, $p = 0.006$) (Supplemental Figure S2b) territories for which I had confidence in both size metrics. The number of contiguous neighbouring conspecific territories was also recorded for each territory measured.

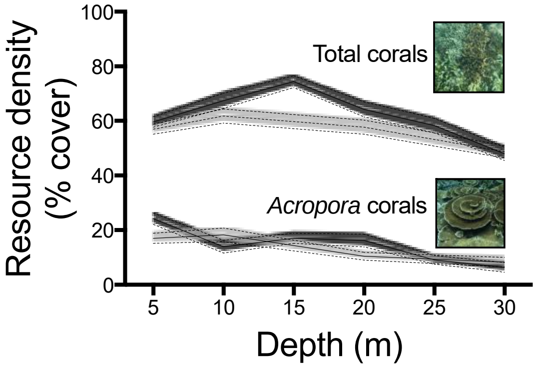


Figure S4.1: Density of total-coral and Acropora coral resources within the focal reef (dark grey), and bay wide (light grey), within Kimbe bay, PNG.

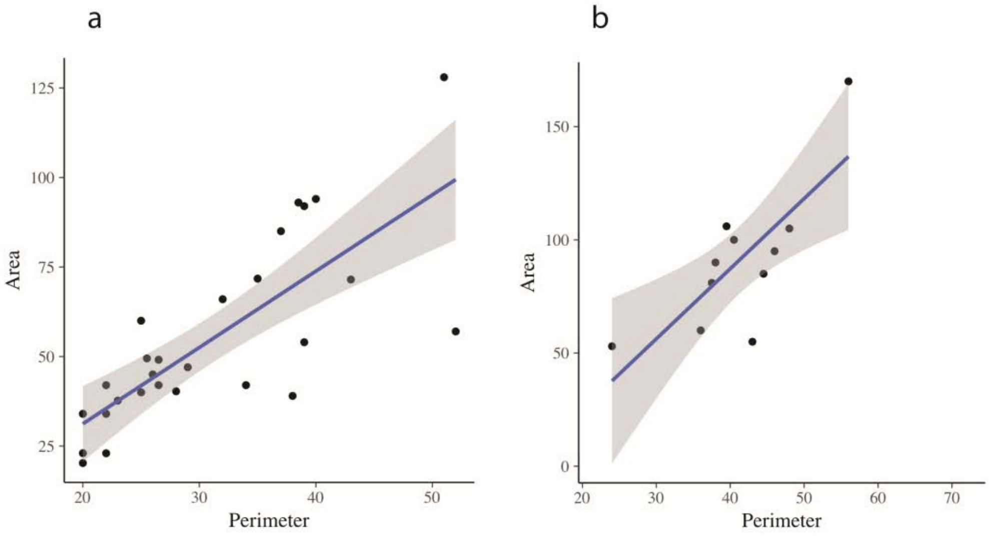


Figure S4.2: Relationships between territorial perimeter and area for two species of obligate corallivore Chaetodontidae species, Kimbe bay, PNG. a) *Chaetodon baronessa*. b) *Chaetodon octofasciatus*.

SUPPLEMENTAL MATERIAL: CHAPTER 5

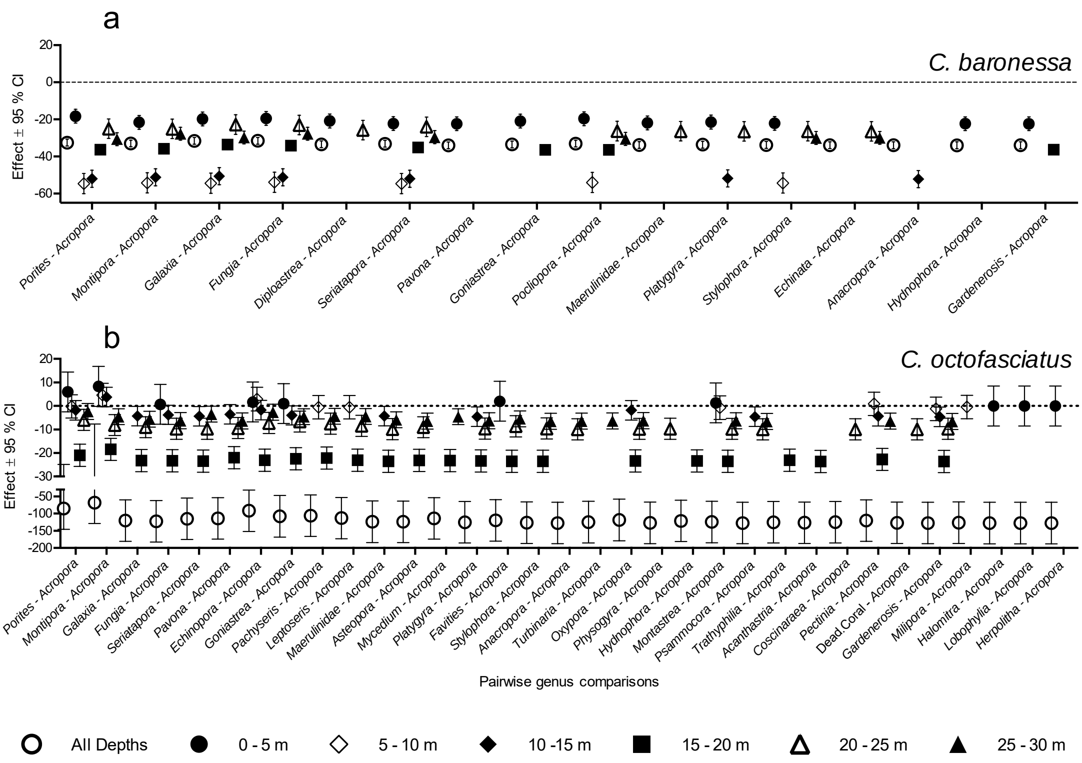


Figure S5.1: Caterpillar plots of effect sizes and 95% confidence intervals (CIs) for Tukey’s adjusted pairwise comparisons between the proportion of bites taken from commonly preferred *Acropora* corals and from all other coral genera fed on by two obligate coral feeding butterflyfish species, *Chaetodon baronessa* (a) and *C. octofasciatus* (b), along a depth gradient. Pairwise comparisons where CIs do not cross 0 indicate significantly different proportions of bites were taken from each of the paired coral genera ($\alpha_{adjusted} = 0.05$). Negative effect sizes indicate that the *Acropora* genus was fed on more frequently. Open circles indicate comparisons made across bites from all depths; other symbols indicate comparisons made between bites observed within 5 m depth bins along a gradient from 0 – 30 m. Note: Not all genera were fed on at each depth, nor by each fish species.

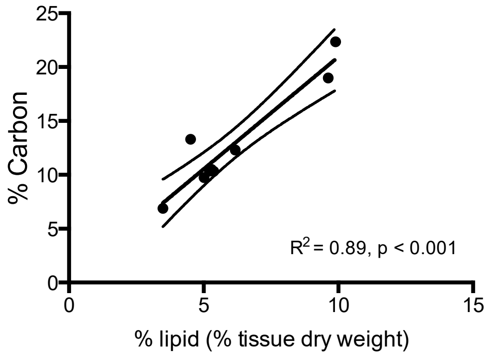


Figure S5.2: A strong relationship between lipid content and carbon content in randomly selected paired *Acropora* subsamples reinforces the robustness of lipid measures.

Table S5.1: Normalized $\delta^{13}C$ values (mean ‰ ± SD) of source end-members (mean of five essential amino acid $\delta^{13}C$ values subtracted from individual essential amino acid $\delta^{13}C$ values for each sample) used as the molecular-isotopic training data set in the mixing model of relative contribution of primary producers to fish carbon (superscript reference: a) McMahon et al. 2016); b) this study. N = 24 for plankton, macroalgae, and detritus, N = 6 for coral.

End Member	Threonine	Isoleucine	Valine	Leucine	Phenylalanine
Plankton[a]	10.0 ± 1.2	2.8 ± 0.8	-2.3 ± 1.0	-5.8 ± 0.6	-4.7 ± 0.6
Macroalgae[a]	7.5 ± 1.0	0.9 ± 0.8	-0.7 ± 0.5	-4.2 ± 0.8	-3.5 ± 0.8
Coral_Shallow[b]	11.7 ± 0.8	5.4 ± 0.5	-5.1 ± 0.5	-6.4 ± 0.7	-5.5 ± 0.6
Coral_Deep[b]	12.5 ± 0.9	4.7 ± 0.7	-5.1 ± 0.4	-6.6 ± 0.6	-5.6 ± 0.6
Detritus[a]	10.4 ± 1.2	-0.6 ± 0.7	-1.6 ± 0.7	-3.2 ± 0.9	-5.1 ± 0.8

Table S5.2: Differences in raw $\delta^{13}C$ values of essential amino acids between shallow and deep samples.

Acropora									
Shallow		Deep		Proportional $\delta^{13}C$ shift	Shallow		Deep		Proportional $\delta^{13}C$ shift
$\delta^{13}C$ (‰)	± SE	$\delta^{13}C$ (‰)	± SE		$\delta^{13}C$ (‰)	± SE	$\delta^{13}C$ (‰)	± SE	
-0.899	0.406	-2.544	0.491	0.647	0.066	0.528	-4.694	0.237	1.014
-7.172	0.273	-10.405	0.370	0.311	-6.014	0.217	-11.716	0.281	0.487
-17.695	0.276	-20.172	0.191	0.123	-16.153	0.142	-20.222	0.218	0.201
-18.928	0.187	-21.683	0.250	0.127	-19.156	0.223	-22.666	0.210	0.155
-18.063	0.336	-20.665	0.240	0.126	-18.081	0.251	-21.306	0.349	0.151

Table S5.3: The proportion of bites on different coral taxa by two obligate coral-feeding butterflyfish species within depth bins along a gradient from 0 – 30 m.

Coral taxa	*Chaetodon baronessa*							*Chaetodon octofasciatus*						
	Depth bin (m)							Depth bin (m)						
	All depths	0-5	5-10	10-15	15-20	20-25	25-30	All Depths	0-5	5-10	10-15	15-20	20-25	25-30
Acropora	0.75	0.57	0.94	0.91	0.83	0.62	0.72	0.31	-	0.04	0.18	0.55	0.31	0.19
Galaxia	0.06	0.06	0.01	0.03	0.06	0.08	0.02	0.02	-	-	<0.01	0.01	0.03	0.03
Fungia	0.06	0.08	0.02	0.02	0.05	0.09	0.09	0.01	0.03	-	0.03	0.01	0.01	0.01
Seriatapora	0.02	0	0	0.01	0.03	0.07	0.03	0.03	-	-	0.01	<0.01	0.01	0.09
Montipora	0.03	0.02	0.01	0.02	0.02	0.04	0.09	0.15	0.4	0.42	0.4	0.12	0.06	0.06
Pocliopora	0.02	0.06	0.02	-	<0.01	0.01	0.01	-	-	-	-	-	-	-
Diploastrea	0.01	0.04	-	-	-	0.02	-	-	-	-	-	-	-	-
Stylophora	0.01	0.01	0.01	-	-	0.01	0.02	<0.01	-	-	-	<0.01	0.01	<0.01
Porites	0.03	0.08	<0.01	0.01	<0.01	0.04	0.01	0.10	0.29	0.03	0.11	0.06	0.12	0.13
Maerulina	0.01	0.01	-	-	-	0.01	-	0.01	-	-	0.01	<0.01	<0.01	0.02
Platygyra	0.01	0.02	-	0.01	-	<0.01	-	0.01	-	-	<0.01	0.01	0.01	0.01
Echinata	<0.01	-	-	-	-	<0.01	0.03	-	-	-	-	-	-	-
Goniastrea	0.01	0.04	-	-	<0.01	-	-	0.05	0.05	-	<0.01	0.03	0.1	0.06
Pavona	<0.01	<0.01	-	-	-	-	-	0.02	-	-	0.01	0.04	0.02	0.01
Favities	-	-	-	-	-	-	-	0.02	0.1	-	-	<0.01	0.04	0.03
Anacropora	<0.01	-	-	<0.01	-	-	-	0	-	-	-	-	0	<0.01
Echinopora	-	-	-	-	-	-	-	0.09	0.08	0.26	0.12	0.01	0.08	0.12
Turbinaria	-	-	-	-	-	-	-	0	-	-	-	-	-	0.01
Mycedium	-	-	-	-	-	-	-	0.02	-	-	-	0.01	-	0.06
Pachyseris	-	-	-	-	-	-	-	0.05	-	0.05	-	0.04	0.07	0.06
Asteopora	-	-	-	-	-	-	-	0.01	-	-	-	0.01	0.03	<0.01
Oxyopora	-	-	-	-	-	-	-	0.02	-	-	0.11	0.01	<0.01	0.01
Leptoseris	-	-	-	-	-	-	-	0.03	-	0.01	-	0.01	0.05	0.06
Physogyra	-	-	-	-	-	-	-	<0.01	-	-	-	-	0.01	-
Hydnophora	<0.01	<0.01	-	-	-	-	-	<0.01	-	-	-	0.01	-	-
Montastrea	-	-	-	-	-	-	-	0.01	0.06	0.03	-	<0.01	<0.01	0.01
Psammocora	-	-	-	-	-	-	-	<0.01	-	-	<0.01	-	<0.01	-
Trathyphilia	-	-	-	-	-	-	-	0.01	-	-	-	0.01	-	-
Acanthastria	-	-	-	-	-	-	-	0.01	-	-	-	0.02	-	-
Coscinaraea	-	-	-	-	-	-	-	<0.01	-	-	-	-	0.02	-
Pectinia	-	-	-	-	-	-	-	0.02	-	0.15	0.01	0.02	-	0.01
Gardenerosis	<0.01	<0.01	-	-	<0.01	-	-	<0.01	-	-	-	-	0.01	-
Milipora	-	-	-	-	-	-	-	<0.01	-	0.02	-	-	-	-
Halomitra	-	-	-	-	-	-	-	<0.01	<0.01	-	-	-	-	-
Lobophylia	-	-	-	-	-	-	-	<0.01	<0.01	-	-	-	-	-
Herpolitha	-	-	-	-	-	-	-	0.003	0.02	-	-	-	-	-
Other encrusting	-	-	-	-	-	-	-	<0.01	-	-	-	0.01	<0.01	0.01
Other branching	-	-	-	-	-	-	-	<0.01	-	-	-	-	-	-
Other massive	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Other laminar	<0.01	<0.01	-	-	-	-	-	-	-	-	-	-	-	-
Dead coral	-	-	-	-	-	-	-	<0.01	-	-	-	0.01	-	-

Table X. Mean (‰ ± SD) essential amino acid $\delta^{13}C$ values of three source end-members (n = 24 individuals for each source end-member) characteristic of potential carbon sources fuelling coral and butterflyfish (Literature data from McMahon et al. 2016). Each essential amino acid $\delta^{13}C$ value was normalized to the mean of all essential amino acid $\delta^{13}C$ values within each individual to facilitate comparisons of amino cid “fingerprints” across systems and environmental conditions (sensu Larsen et al. 2015). Thr = Threonine, Iso = Isoleucine, Val = Valine, Leu = Leucine, Phe = Phenylalanine.

End-member	Thr	Iso	Val	Leu	Phe
Plankton	10.0 ± 1.2	2.8 ± 0.8	-2.3 ± 1.0	-5.8 ± 0.6	-4.7 ± 0.6
Coral	11.7 ± 1.0	5.7 ± 1.2	-6.4 ± 0.6	-7.1 ± 1.1	-3.9 ± 1.3
Detritus	10.4 ± 1.2	-0.6 ± 0.7	-1.6 ± 0.7	-3.2 ± 0.9	-5.1 ± 0.8

Table Y. Essential amino acid δ^{13}C values (‰) of individual *Acropora spp.* colonies (n = 6 colonies per depth) and individual *Chaetodon baronessa* (n = 5 individuals per depth) form 5m and 40m water depth in Kimbe Bay, Papua New Guinea. Each essential amino acid δ^{13}C value was normalized to the mean of all essential amino acid δ^{13}C values within each individual to facilitate comparisons of amino acid “fingerprints” across systems and environmental conditions (sensu Larsen et al. 2015). Thr = Threonine, Iso = Isoleucine, Val = Valine, Leu = Leucine, Phe = Phenylalanine.

Consumer			Thr	Iso	Val	Leu	Phe
Acropora	Shallow	AS1	11.3	6.1	-5.3	-7.1	-5.0
		AS2	10.8	5.4	-4.7	-6.0	-5.5
		AS3	12.5	4.4	-5.4	-6.1	-5.4
		AS4	12.6	5.5	-6.0	-5.8	-6.3
		AS5	11.1	5.5	-4.7	-5.8	-6.0
		AS6	11.6	5.3	-4.7	-7.4	-4.8
	Deep	AD1	12.0	5.5	-4.7	-6.6	-6.3
		AD2	11.9	5.0	-5.3	-5.9	-5.6
		AD3	11.5	4.3	-4.6	-6.4	-4.8
		AD4	13.0	5.0	-5.2	-6.6	-6.2
		AD5	13.1	3.5	-4.8	-6.4	-5.4
		AD6	13.9	4.7	-5.8	-7.7	-5.2
Chaetodon baronessa	Shallow	CbS1	11.7	6.0	-4.4	-7.1	-6.3
		CbS2	12.4	6.0	-4.6	-7.5	-6.3
		CbS3	12.6	5.5	-4.2	-7.6	-6.4
		CbS4	10.7	6.1	-3.5	-7.1	-6.1
		CbS5	12.2	5.6	-4.7	-7.1	-6.0
	Deep	CbD1	11.5	3.5	-4.4	-6.5	-4.1
		CbD2	11.0	4.9	-4.4	-6.2	-5.3
		CbD3	11.4	4.5	-4.2	-6.4	-5.3
		CbD4	11.1	4.8	-4.1	-6.8	-5.0
		CbD5	12.2	4.3	-3.4	-6.8	-6.3

End-Member Justification:

To examine the relative contribution of carbon source end-members to corals and coral-feeding butterflyfishes, we used an amino acid carbon isotope fingerprinting approach (McMahon et al. 2015, 2016) within a fully Bayesian stable isotope mixing model (sensu Ward et al. 2010) using the *SIAR* package (Parnell et al. 2010; R development core team 2013, ver. 3.0.2). We used three data files to parameterize our mixing model: 1) consumer data consisting of $\delta^{13}C$ values for five essential amino acids (threonine, isoleucine, valine, leucine, phenylalanine) for individual coral or butterflyfish (separate models), 2) source end-member essential amino acid $\delta^{13}C$ fingerprints (see description below), and 3) Trophic discrimination factors for the five essential amino acids (0.1 ± 0.1; McMahon et al. 2010). In SIAR, we ran 500,000 iterations with an initial discard of the first 50,000 iterations as burn-in. By using $\delta^{13}C_{EAA}$ values within the Bayesian isotope mixing model, we avoid the major issue that plagues poorly resolved dual isotope approaches in multi-end-member systems (Fry 2013; Brett 2014): underdetermined mixing, and complications of variable and poorly characterized trophic fractionation (Bond and Diamond 2011).

We characterized unique amino acids isotope fingerprints (multi-variate patterns in relative $\delta^{13}C$ among essential amino acids) for three potentially important source end-members to *Acropora* and *Chaetodon baronessa*: autotrophic coral carbon (zooxanthellae-proxy), herbivorous zooplankton carbon (water column phytoplankton proxy), and detritivorous sea cucumber carbon (microbially-reprocessed detritus proxy). The source end-member data (Table X) pulled from a relevant subset of molecular-isotopic training data sets from McMahon et al. (2016) (see justification for using literature data below). McMahon et al. (2016) collected staghorn coral, *Acropora pharaonis*, that is targeted by coral-eating butterflyfish (e.g., Berumen and Pratchett 2008) to represent carbon fixed by autotrophic zooxanthellae. The essential amino acid $\delta^{13}C$ fingerprints of these corals aligned with the essential amino acid $\delta^{13}C$ fingerprints of pure cultures of *Symbiodinium* sp. from Woods Hole Oceanographic Institution, indicating that these corals rely almost exclusively on autotrophically fixed carbon with little to no heterotrophic feeding. As such, we used these corals as proxies for autotrophic coral end-members in our mixing model. McMahon et al. (2016) collected pelagic calanoid copepods that feed on water column phytoplankton as proxies for water column phytoplankton carbon. They did not use phytoplankton directly because the fast turnover rate of phytoplankton means that their isotope signatures are just a snapshot of the water column baseline signature. Instead, they analyzed zooplankton, which integrate dietary carbon signals over longer time scales more relevant to the turnover rates of butterflyfish. Furthermore, given that essential amino acids show virtually no isotope discrimination between diet and consumer (McMahon et al. 2010), the essential amino acid $\delta^{13}C$ values of pelagic copepods provided a faithful proxy for pelagic phytoplankton. As expected, the essential amino acid $\delta^{13}C$ fingerprints of these coral reef plankton aligned with the fingerprints of water column phytoplankton from the Larsen et al. (2013) dataset. Given the challenges in isolating the detrital end-member, McMahon et al. (2016) selected the detritivorous black sea cucumber, *Holothuria atra*, as a proxy for microbially reprocessed detritus (Moriarty 1982; Uthicke 1999). These detritus-proxy fingerprints aligned with heterotrophic bacteria from the Larsen et al. (2013) dataset. Together, these source end-member essential amino acid $\delta^{13}C$ fingerprints provide a robust data set to reconstruct the relative contribution of source end-members to coral and butterflyfish production.

We focused our analyses on only essential amino acids (threonine, isoleucine, valine, leucine, and phenylalanine) for two reasons: 1) The essential amino acid $\delta^{13}C$ fingerprints represent the sum of the isotopic fractionations associated with individual biosynthetic pathways and associated branch points for each essential amino acid (Hayes 2001; Scott et al. 2006), generating phylogenetically diagnostic amino acid fingerprints of different source end-members (Larsen et al. 2009, 2013). Because essential amino acids have very long and complex biosynthetic pathways (typically >10 independent enzymatic steps), they provide the best potential for lineage-specific isotope effects (*Lehninger 1975; Stephanopoulos et al. 1998*). 2) Essential amino acid $\delta^{13}C$ patterns of source end-members are preserved, essentially unchanged, across trophic transfers (14, McMahon et al. 2010). This is because, while plants, algae, and bacteria can synthesize essential amino acids *de novo,* metazoans have lost the necessary enzymatic capabilities and must acquire essential amino acids directly from their diet with minimal fractionation (Reeds 2000).

In order to compare the essential amino acid fingerprints of our three source end-member groups collected from literature data to the corals and butterflyfish in this study, we examined essential amino acid δ^{13}C values that were normalized to the mean of all five essential AAs for each sample. As expected, there is strong experimental and field-based evidence that primary producer essential amino acid δ^{13}C fingerprints are faithful and robust across large environmental gradients in growing conditions and carbon sources that can affect bulk δ^{13}C values (Larsen et al. 2009, 2013, 2015). This is because the underlying biochemical mechanisms generating unique internally normalized essential amino acid δ^{13}C fingerprints are driven by major evolutionary diversity in the central synthesis and metabolism of amino acids. For example, Larsen et al. (2013) examined the extent to which normalized essential amino acid δ^{13}C fingerprints were affected by environmental conditions by looking at seagrass (*Posidonia oceanica*) and giant kelp communities (*Macrocystis pyrifera*) across a variety of oceanographic and growth conditions (see Larsen et al. 2013 Table S1 for details). For both species, the range in bulk δ^{13}C values was five- to ten-times greater (2.6‰ and 5.2‰, respectively) than it was for normalized essential amino acids δ^{13}C (0.4‰ to 0.6‰, respectively). By normalizing the individual $\delta^{13}C_{EAA}$ values to the mean, Larsen et al. (2013) showed that natural variability in δ^{13}C values of individual amino acids is effectively removed, creating diagnostic fingerprints that were independent of environmental conditions. Larsen et al. (2015) further confirmed this concept with the first directly controlled physiological studies of fidelity in normalized essential amino acid δ^{13}C fingerprints. This study grew the laboratory-cultured marine diatom, *Thalassiosira weissflogii*, under a wide range of conditions: light, salinity, temperature, and pH. This study showed that normalized essential amino acid δ^{13}C values remained unmodified despite very large changes in bulk and raw amino acid δ^{13}C values (>10‰), molar percent abundances of individual amino acids, and total cellular carbon to nitrogen ratios. Together, Larsen et al. (2013, 2015) provide strong evidence that normalized essential amino acid $\delta^{13}C$ fingerprints are diagnostic of the primary producer source rather than the myriad factors affecting bulk $\delta^{13}C$ values, such as carbon availability, growth conditions, and oceanographic conditions. As such, we are confident that the normalized essential amino acid $\delta^{13}C$ fingerprints of literature source end-members are robust, faithful proxies of the identity of major carbon sources relevant in this study, regardless of the exact location and growing conditions of the end-members.