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Processes underlying the fine-scale partitioning and niche diversification in a guild of coral reef damselfishes

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Thesis by

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and the College of Science and Engineering, James Cook University

Statement on the contribution of others

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General Abstract

A major goal of ecology is to explain the mechanisms that drive species distributions and ecological partitioning along gradients in the natural environment. The distributions and coexistence of ecologically similar animals may depend on the degree of niche diversification and competitive interactions within and among species. The extent of ecological partitioning in guilds of coral reef fishes was hotly debated in the 1980s, and despite 4 decades of research, the issue remains unresolved. In particular, the link between niche partitioning and agonistic interactions together have received little attention. In the thesis I investigated fine-scale species distributions, resource use (e.g., habitat and food), and competition in a guild of 7 territorial damselfish species in Kimbe Bay, Papua New Guinea. Common generalisations about the ecological function of territorial damselfish and associated interactions with important roving herbivorous fishes were also investigated. Using ecological surveys, laboratory-based analytical methods, observational studies, and manipulative field experiments, this thesis addresses novel questions about the ecology and functional role of territorial damselfish and the resulting community effects.

Competition over resources is recognised to play a primary role in the structure of coral reef fish communities. The distribution of ecologically similar species may depend on the degree to which traditional niche mechanisms operate alongside competitive dynamics. In **Chapter 2** these effects were examined by investigating fine-scale species distributions, microhabitat use, and aggression among territorial damselfishes. I documented patterns of habitat partitioning across the 3 reef zones – reef flat, reef crest, and reef slope – with distinct patterns of distribution within these zones at extremely fine scales (1 − 2 m). Distinct differences between neighbouring species in the microhabitat use selected were also observed. Furthermore, aggression elicited by neighbouring species was significantly higher for all species, compared with non-adjacent species. This chapter revealed a fine level of spatial partitioning among reef zones and microhabitats in this guild of damselfish, which was likely maintained by agonistic interactions among neighbouring species.

While Chapter 2 found that neighbouring damselfish constrain their microhabitat use to facilitate the co-habitation of reef zones, microhabitat selectivity alone was insufficient to explain the distinct zonation and limited distributional overlap. I hypothesised that in this

highly partitioned ecological community, where there are intense agonistic interactions for resources, ecologically neighbouring territorial damselfish may also partition food resources. Other studies had previously quantified diet contributions for the study species, but no isotopic analysis had been conducted for territorial damselfish to date to specifically target pelagic-based food sources. In **Chapter 3** I quantified the trophic niches of the territorial damselfish guild through the use of stable isotopes ($\delta^{13}C$ and $\delta\ ^{15}N$). Adjacent species on the reef flat, reef crest, and reef slope exhibited high to intermediate trophic niche partitioning when examining pelagic versus reef-based dietary sources, with two species previously described as benthic herbivores actually exhibiting pelagic feeding. Findings of Chapter 3 indicate that diet choice reinforces the patterns of spatial partitioning and coexistence among ecologically similar species. In addition, evidence of planktivorous pelagic feeding adds to the growing view that interspecific differences among similar species are lost when categorizing species into broad functional classifications.

In **Chapter 4** the direct and indirect effects of interference competition on resource partitioning were measured. The previous chapters found that microhabitat selectivity and dietary diversification facilitated the co-habitation of reef zones among the territorial damselfish guild. Additionally, evidence suggested that interspecific aggression helped maintain the distributional boundaries between neighbouring species. However, an experimental removal of a dominant competitor was necessary to understand if interference competition is present and if subordinate distributional shifts would occur. I employed an observational experiment and a large-scale removal experiment (220 m^2) to examine the intensity of agonistic interactions among species and the extent to which the most abundant species influenced the distribution and abundance of neighbouring and non-neighbouring species in the guild. The findings indicated that the distinct distribution patterns among the reef crest species were linked to levels of interspecific agonistic behaviour. The competitive release following the removal of a superior competitor resulted in comprehensive direct and indirect effects, with the subordinate neighbour shifting into the newly available space, followed by successive shifts in species responding to the change in the distributions of their immediate neighbours. Through a novel multi-species large-scale experiment, Chapter 4 provides the conclusive evidence that distributions and the coexistence of the territorial damselfish guild are a result of niche diversification and competitive interactions within and among species.

Chapter 5 broadens the thesis by investigating the common perception that all territorial damselfish negatively influence overall reef function and roving herbivorous fishes. Similar to Chapter 2 where generalisations about the guild's diet were questioned, here I challenged the paradigm that intermediate-sized territorial damselfishes have a negative influence on surgeonfish, parrotfish, and rabbitfish abundance and foraging behaviour. To test this, I conducted experimental removals (220 m^2) of the most abundant territorial damselfish to examine its impact on roving herbivores and the benthic community structure. The overall relative abundance (MaxN) of roving herbivores was not influenced by the removal. No changes in foraging patterns were observed for parrotfish, the family that received the highest rate of agonistic interactions, and rabbitfish. Instead, the removal resulted in a significant decrease in surgeonfish feeding, suggesting the territorial damselfish species altered foraging patterns indirectly through territorial maintenance and not aggression. The results indicate that all territorial damselfishes do not have a negative impact on all roving herbivores and instead may enhance surgeonfish foraging indirectly through the removal of sediment. The generalisation that territorial damselfish reduce foraging rates of roving herbivores may not be applicable in all systems or for all species.

In summary, this thesis investigated the mechanisms that drive species distributions and ecological partitioning along gradients in the natural environment as a precursor to the long-term ecological changes on coral reefs. It first established fine-scale partitioning in a guild of competing fishes on a high-diversity coral reef. Second, the research showed that microhabitat selectivity and dietary diversification facilitates the co-habitation of reef zones, and that interspecific aggression maintains the distributional boundaries between neighbouring species. In order to demonstrate how competitive interactions and resource partitioning influence species coexistence in a complex ecosystem a large-scale field experiment was conducted. The results demonstrate that when exploring coexistence in reef fish communities, the more traditional niche mechanisms operate alongside direct and indirect competitive dynamics, and within highly diverse systems these ecological processes are magnified. Moreover, the thesis highlights the importance of challenging common generalisations and paradigms. By examining the functional role of territorial damselfishes this research provides evidence of novel dietary diversification and demonstrates the complexity of territorial damselfish and roving herbivore interactions.

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Chapter 1

General Introduction

1.1 Resource partitioning in a changing climate

Partitioning of space and other critical resources facilitates the coexistence of ecologically similar species in natural communities (MacArthur 1958, Schoener 1974, Connell 1978). When a resource - a substance or factor that is used by an organism that contributes to its growth, maintenance, or reproduction (Tilman 1982) - is limited, competition among individuals is expected. Interactions among ecologically similar species, often congenerics, can directly influence their local distribution and can result in ecological separation among habitats or along environment gradients (Connell 1983, Schoener 1983, Hixon and Johnson 2009). As a species occupies or utilises a limited resource a direct or indirect competitor may be displaced. Some of the most conspicuous patterns of apparent ecological partitioning occur along steep physical gradients such as altitude, latitude, and depth (Hawkins 1999, Jankowski et al. 2015). While resources can be derived from continuous external sources like sunlight, wind, or rainfall, many are provided by the local habitat. Similar species may use or occupy different resources along environmental gradients to minimize competition. In addition, dominant species may exclude others from preferred positions and eliminate non-versatile subordinate species in the process. However, differences in species distributions along ecological gradients may also arise as each species independently becomes adapted to different local biotic and abiotic conditions (Connell 1978, Ross 1986, Gaston 1996, Hawkins 1999, Lomolino et al. 2010). In this case, differences may reflect evolved species-specific differences in habitat and food preferences and the degrees of specialization.

Biodiversity is in decline due to nonrandom species turnover, typically characterized by the loss of specialist species (Cardinale et al. 2012, Ellis et al. 2013). Recently, niche partitioning has been viewed as one of the key factors in promoting the diversification of animals as anthropogenic threats increase (Cavender-Bares et al. 2009, Ndiribe et al. 2013, Gajdzik et al. 2016). Thus, investigating resource use (e.g., habitat and food) and describing species in the context of broad functionality have received considerable attention (Pratchett et al. 2011, Chong-Seng et al. 2012, Kok et al. 2016, Hughes et al. 2017, Richardson et al. 2018). Traditionally, in complex ecosystems (e.g., tropical forests and coral reefs), each species is known to occupy a functional niche in which it is the most effective competitor (Whittaker et al. 1973). Habitat loss as a consequence of impacts associated with climate change may influence population processes directly or indirectly by altering interactions for resources. Either way, a species may be forced to expand or compress its functional niche. In recent times, to gain generality and predictive power, species have been modelled or grouped by family with regards to ecological function (e.g., herbivore, carnivore, or omnivore). However, evidence suggests that interspecific differences among similar species are obscured when categorizing species into broad functional groups (Brandl and Bellwood 2014, Tebbett et al. 2017a). Despite this, the functional role of multi-species competitive networks have received little attention.

1.2 Limiting competition through niche diversification and ecological versatility

The overall concept of a *niche* has been debated over many decades, with the definition shifting over time and interpreted differently among fields. Grinnell (1924) described it first as a behavioural response of a species to a given set of ecological variables within its habitat. Elton and others (1927) further defined the functional concept of a niche as the status of an animal in its community and its place in the biotic environment, particularly its relation to interactions between its predator and prey. Presently, the ecological niche of a species is widely described as the volume that is occupied in an n-dimensional space within an ecosystem (Hutchinson 1957, Whittaker et al. 1973, Devictor et al. 2010). Hutchinson’s (1957) work inspired ecologists to develop models of coexisting species within a community and led to the concepts of *niche breadth* (variety of resources and resource parameters used by a species), *niche partitioning* (resource differentiation by coexisting species), and *niche overlap* (overlap of resources used by different species).

A species’ *ecological versatility*, defined as the degree to which organisms can fully exploit the available resources in their local environment (MacNally 1995), builds on the concept of a niche and further increases ways to characterize how populations are regulated and structured (Robertson 1995, Berkström et al. 2012). The availability of habitat and food resources can be unstable and influence exploitation, thus facilitating the coexistence of ecologically similar species (Schoener 1974). Adaptations to abiotic conditions and biotic interactions allow some species to be more specialized for a narrow range of resources, whereas other species become more versatile in their resource exploitation, utilizing a broad range of resources (MacNally 1995, Brown 2014). These species, generally referred to as specialists and generalists, represent opposite ends of the resource versatility continuum (Morris 1996). When these species occur together specialists often outcompete generalists for a preferred resource (Connell 1978). This directly influences the local abundance and distribution of associated and congeneric species (Schoener 1974, Cappuccino 1995, Gotelli and Graves 1996, McPeek 1996, Hixon and Johnson 2009). Ecological versatility has been well documented in a variety of different ecosystems and research has predominantly supported Brown's (1984) *ecological specialisation hypothesis* (Inkinen 1994, Gotelli and Graves, Pyron 1999, Hughes 2000, Bean et al. 2002, Berkström et al. 2012). Most studies have focused on terrestrial systems (Bock and Ricklefs 1983, Gaston 1996, Morris 1996, Gaston and Spicer 2001), but there is an increasing attention in marine systems (Munday and Jones 1998, Jones et al. 2002, Jones et al. 2004, Graham 2007, Pratchett et al. 2008, Hobbs et al. 2010, Berkstrom et al. 2012).

When resources are limited, theory holds that species coexist by partitioning resources via *exploitative competition*, depletion of a common resource, or *interference competition*, aggressive interactions that prevent access to a resource (Case and Gilpin 1974, Schoener 1983). While competition theory is largely based on exploitative competition among sympatric species (Amarasekare 2002), interference competition is the main mechanism leading to interspecific differences in patterns of distribution or use of resources. There is ample empirical evidence that interference competition influences the abundance or distribution of subordinate species for insects (Kunte 2008), birds (Pimm et al. 1985), mammals (Brown 1971), and fishes (Robertson and Gaines 1986, Munday et al. 2001, McCormick and Weaver 2012). In nature, interference competition is linked to interspecific territoriality and aggressive interactions among species that regularly come into contact, with the most aggressive species gaining priority access to resources (Grether et al. 2013). Species in the community that do not openly share a resource or compete may be indirectly linked by species that lie between them on a resource axis. Hence, when interference competition between two species results in a partitioning of resources, this may have indirect consequences for other species distributed along the same resource gradient (Case and Gilpin 1974, Grether et al. 2013).

1.3 Coexistence of coral reef fishes

Coral reefs harbour exceptional diversity and a primary goals of reef fish ecology is to understand the mechanisms that allow similar species to coexist. Ecological partitioning is recognized to be a core mechanism structuring coral reef fish assemblages, but its role is controversial (Bonin et al. 2015). Early studies stressed intense interspecific competition for living space as the main driver behind niche partitioning (Smith and Tyler 1972, 1973, Smith 1978). However, the apparent instability of reef communities sparked an early and founding debate on species coexistence. Sale (1976, 1977, 1978, 1980) stressed that a high degree of overlap in ecological niches and stochastic recruitment events sustains species co-existence. This *lottery hypothesis* argued that space is the limiting resource and that species with similar niche requirements and competitive abilities could coexist through chance colonization of vacant space after a random gain or loss occurs. Other studies suggested that predation maintains populations below carrying capacity and limits the need for intense competition (Talbot et al. 1978). The *neutral model* furthered the debate by accepting that a lottery for space at recruitment exists but proposed that biodiversity is maintained by chance variations in demographic and evolutionary rates (Bell 2000, Hubbell 2001). This theory was subsequently classified into competition models based on stabilizing mechanisms (*niche theory*) and fitness equivalence (*neutral theory*) to explain the coexistence of competing species (Adler et al. 2007, Bode et al. 2012). Studies suggest that aspects of both niche and neutral processes can change through ontogeny within a species and may operate in many communities simultaneously (Schmitt and Holbrook 1999, Munday et al. 2001, Gravel et al. 2006, Pereira et al. 2015). However, the ongoing debate on the mechanisms of coexistence has been largely pursued in the absence of detailed information on the extent of habitat partitioning or knowledge of species-level interactions (Gravel et al. 2011, Connolly et al. 2014).

1.4 Resource use and competition in reef fishes

Habitat partitioning

In coral reefs, habitat encompasses the physical and biological characteristics of the substratum (i.e., benthic cover, complexity, or the degree of siltation), and can be divided into distinct zones (e.g., reef flat, reef crest, and reef slope) that are physically and ecologically connected (Jones 1991). Environmental features, such as depth, light, and aspect, also add to these characteristics to increase the diversity of available habitat. The wide range of ecological niches within reefs maintains one of the most biodiverse species assemblages known (Sale 1980). However, further ecological separation among similar species has occurred due to declining resource availability (Connell 1978, Ross 1986, Gaston 1996, Lomolino et al. 2010, Brown 2014). Species that overlap in resource use partition the available habitat in ways that will minimize interspecific competition and increase their fitness success. Thus, habitat partitioning has been widely documented among coral reef fish families across multiple regions (Doherty 1983, Robertson and Gaines 1986, Wainwright 1988, Shpigel and Fishelson 1989, reviewed by Williams 1991). Most investigators have concentrated on studying space-shelter partitioning, including the location of the space, type and dimensions of shelter used, and the duration of use (Fishelson 1980). However, many studies measure the *fundamental niche* (Nyström 2006, Johansson et al. 2013), the potential volume a species could theoretically occupy if only morphological or physical attributes were expressed, and not the *realized niche* (but see Fox and Bellwood 2013, Brandl and Bellwood 2014), the actual volume a species could occupy when affected by biotic and abiotic factors (Hutchinson 1957, Whittaker et al. 1973, Devictor et al. 2010). Studies that combine patterns of habitat selectivity and interspecific interactions can together help define the mechanistic drivers underlying the (often distinct) boundaries between species along important ecological gradients.

Trophic diversity

In addition to habitat availability, animals are inherently dependent on food and will maximize access to dietary resources. In the early stages of theoretical resource partitioning on coral reefs, food was considered the resource least likely to be limiting (Sale 1977, 1978, 1980, Smith 1978), but further observations have shown that food availability on coral reefs considerably influences species spatial patterns (Low 1971, Ebersole 1977, Jones 1986). Successive studies have provided evidence of the partitioning of food resources among coral reef fishes (Ross 1986, Wainwright 1988, Pimentel and Joyeux 2010, Nithirojpakdee et al. 2012, Wollrab et al. 2013). Stomach content analysis (gut content) has been a widely used technique for accessing the diet of fishes (Hyslop 1980). However, stomach content data are a snapshot that reflects the most recent meals and may not represent the overall diet. In addition, accurate prey identification is difficult due to digestion rates and the cryptic nature of consumed prey (Cresson et al. 2014). Stable isotopes are increasingly used in ecology to study diet and trophic niche analysis as they reflect tissue assimilation from prey and are not hindered by stomach content analysis biases (pomacentrids reviewed by Frédérich et al.

2016). Stable isotopes of a consumer are concurrently integrated from various prey tissues at a rate slower than digestion (Matley et al. 2016). Thus, stable isotope analysis provides a measure of the diet contributions over longer periods of time (Post 2002). Although stable isotope analysis does not provide high-resolution dietary information, it can be used to estimate contribution of dietary sources (Jackson et al. 2011, Parnell et al. 2012). The ratio of carbon (δ13C) is commonly used because it indicates food sources or habitat (i.e., limited enrichment between predator and prey; Michener and Schell 1994), while the ratio of nitrogen (δ15N) indicates trophic level (i.e., consistent enrichment between predator and prey; Minigawa and Wada 1984). Moreover, stable isotope analysis can be used to assess the trophic niche width and overlap among populations or species at similar spatial and temporal scales (Bearhop et al. 2004, Frédérich et al. 2009). While studies of habitat partitioning have generated a substantial amount of evidence, the diet or trophic niche of reef fishes have received much less attention at this scale (but see, Ceccarelli 2007, Frédérich et al. 2009, Gajdzik et al. 2016).

Direct and indirect competition

The ecological role of competition within coral reef fish communities is critical in understanding how these two main types of resources (habitat and food) are partitioned (Sale 1980, Jones 1991, Jones and McCormick 2002, Hixon 2011, Bonin et al. 2015). The high diversity of fish in coral reef systems offers a natural laboratory for developing competition theory. Studies of *intraspecific competition* (same species) provided evidence on the local distribution (Robertson and Gaines 1986, Clarke 1989), demographic rates (Jones 1987a, 1987b), and resource use of coral reef fishes (Munday and Jones 1998, Schmitt and Holbrook 2000, Holbrook and Schmitt 2002). Alternatively, *interspecific competition* (different species) evidence within reef systems was not originally thought to be as prevalent due to early studies failing to detect any associations (Jones 1991). The underlying assumption of intense competition for space was later challenged, and for many years the idea that reef fish communities were limited by recruitment prevailed in the literature (Doherty 1983, Doherty and Fowler 1994). Nevertheless, researchers have continued to address basic ecological interactions such as competition and predation (see reviews by Hixon 1991, Jones 1991, Hixon and Webster 2002, Jones and McCormick 2002, Forrester 2015, Hixon 2015). Several decades of research have generated a substantial amount of evidence that limited available habitat can result in competitive interactions, which in turn influences the structure of communities (e.g., Robertson 1996, Holbrook and Schmitt 2002, Forrester et al. 2006, Boström-Einarsson et al. 2014). Further, interactions among interspecific competitors plays an important role in reef fish spatial distributions (McCormick and Weaver 2012). However, the majority of evidence for mobile reef fish species has involved measuring pairwise interactions experimentally and not expanded competitive networks within a community (see reviews by Forrester 2015, Hixon 2015, Bonin et al. 2015). Few studies have documented competitive interaction networks between multiple species with similar resource requirements.

Niche diversification within the marine environment has attracted increasing attention due to the associated threats of climate change (Hawkins et al. 2000, Graham 2007, Pratchett et al. 2008, Hobbs et al. 2011). Understanding how species respond to natural gradients (i.e. abiotic conditions and species richness) through large experimental comparisons can provide vital information on species variation and how they may adapt to changing ecosystems (Longo et al. 2014). On one extreme, if a species is highly specialized and occupies a finite niche the risk of local extinction increases due to high ecological specialisation (Harcourt et al. 2002, Davies et al. 2004). Species interactions are a function of abiotic conditions, biodiversity, genetic structures, and other factors, all of which are likely to vary across large temporal and spatial scales (Pennings and Silliman 2005). Therefore, it is important to assess whether a species can and will diversify its niche parameters based on the available resources and neighbouring associated species. In addition, similar knock-on or indirect effects of subordinate competitors within trophic levels may also be present after the collapse of a primary competitor and have received much less attention (Navarrete et al. 2000, Gosnell and Gaines 2012).

Competitive interactions between unrelated taxa

Roving herbivorous fishes play an important role on coral reefs in reducing algal biomass and preventing alternative algal dominated stable states (Mumby et al. 2006, Hughes et al. 2007, Francini-Filho et al. 2010). Hence, they are considered important in maintaining healthy coral cover and promoting ecosystem resilience (Burkepile and Hay 2008, Hamilton et al. 2014, O'Leary and McClanahan 2016). The most important roving herbivores, in a broad use of the term, appear to be surgeonfish (Acanthuridae), parrotfish (Labridae: Scarini), and rabbitfish (Siganidae) in terms of algal biomass consumption or removal (Lewis and Wainwright 1985, Francini-Filho et al. 2010). However, these taxa do not have exclusive access to algal covered reef habitat. Territorial farming damselfish often influence the structure of algal communities though the deterrence of larger roving herbivores (reviewed by

Hata and Ceccarelli 2016). The aggressive territorial defence may lead to an increase in turf algae, a desired food source of roving herbivores (Hixon and Brostoff 1983, Russ 1987, Hixon 1996, Ceccarelli et al. 2005a). However, the generalisation that territorial damselfish reduce foraging rates of roving herbivores may not be applicable in all systems or for all species. Despite this, the functionality of territorial damselfish and roving herbivores and interactions between these groups remains to be fully resolved. Studies that combine the foraging patterns of roving herbivores and agonistic interactions within a healthy community can together help define the mechanistic drivers that underlie reef habitat structure and resilience.

1.5 Aims

The overall aim of this thesis was to investigate the mechanisms that drive species distributions and ecological partitioning along gradients in the natural environment as a precursor to the long-term ecological changes expected on coral reefs. As a model system I selected a guild of 7 territorial damselfish species in Kimbe Bay, Papua New Guinea. Territorial damselfish (Pomacentridae) provide ideal models for understanding the outcomes of niche diversification and competition. For most species, ecological parameters, or the measurable niche properties whose value is a determinant of the ecosystem characteristics, can be effectively obtained due to their highly site attached habits, territorial behaviours, and lack of concern for observer presence (Ceccarelli et al. 2005, Ceccarelli 2007). Furthermore, patterns of distribution and partitioning of space along the natural reef profile gradient – the reef flat, reef crest, and reef slope, have been well documented (Robertson and Lassig 1980, Sale 1980, Waldner and Robertson 1980, Meekan et al. 1995). A distinctive pattern of zonal distribution along this steep physical gradient provides an experimentally tractable system for isolating the direct and indirect effects of any one species on neighbouring species along the resource gradient. Lastly, territorial damselfish play an integral role in the structure of coral reefs through their abundance and role as small-bodied consumers (Hata and Kato 2004, Ceccarelli et al. 2005a, Jones et al. 2006). The modification of algae through farming behaviour and territorial defence is thought to play an important role on the benthic community structure and have a major influence on roving herbivores (Wellington 1982, Hixon and Brostoff 1983, Ceccarelli et al. 2005a, Ceccarelli 2007, Barneche et al. 2009). Using ecological surveys, laboratory-based analytical methods, observational studies, and manipulative field experiments, this thesis addresses novel questions about the ecology and functional role of intermediate-sized territorial damselfish and the resulting community effects. This thesis represents a significant advance in our understanding of the ecology of territorial damselfish and how the guilds' functional roles may change as live coral reef habitat is lost.

The four data chapters that comprise this thesis are self-contained publications, which address four main objectives:

1. Examine the role of aggression in maintaining fine-scale differences of distribution and microhabitat use.
2. Investigate if trophic diversity and niche partitioning drives coexistence and spatial partitioning in high-diversity systems.
3. Test whether interference competition directly or indirectly influences the ecological versatility of subordinate competitors.
4. Explore the influence of territorial damselfish on roving herbivores and the benthic community structure.

The extent of ecological partitioning in guilds of coral reef fishes has been a matter of debate, but the roles of habitat selectivity and agonistic interactions have received little attention. **Chapter 2** investigates the fine-scale species distributions, microhabitat use, and aggression in a guild of 7 territorial damselfish species at Kimbe Bay, Papua New Guinea. I documented patterns of habitat partitioning across an environmental gradient – the reef flat, reef crest, and reef slope – and observed distinct patterns of distribution within these zones at extremely fine scales (1 − 2 m). I then employed a 'bottle' experiment to examine the influence of aggressive interactions in maintaining the distribution patterns. The chapter discusses how traditional niche mechanisms operate alongside competitive dynamics and addresses coexistence in reef fish communities. Here, I provide the necessary background to further explore the fine level of spatial partitioning among reef zones and microhabitats in this guild of fishes.

In **Chapter 3** I evaluate how food resources are used and whether neighbouring species diets differ to explore the niche diversification in this high-diversity system. Territorial damselfish on coral reefs are usually considered to be herbivores that defend conspicuous algal mats from other food competitors. However, this guild contains numerous smaller bodied intermediate species whose functional role and dietary diversification is poorly understood. Thus, I investigated the relationships between diet and spatial distribution of the 7 territorial damselfishes. Examination of isotope ratios of carbon and nitrogen delineate three distinct feeding strategies, analogous to previous literature, within this group and quantify high to intermediate trophic niche partitioning. The outcomes of this study suggest territorial damselfish generalizations and commonly described functional roles may not be applicable in all systems or for all species. This study adds to a growing view that important interspecific differences are lost when categorizing species into broad functional classifications.

Few studies have documented direct and indirect effects of competition over time within a multi-species competitive network. In **Chapter 4** I address this by investigating the consequences of interference competition between two competing species and the resulting indirect effects for other species distributed along the same resource gradient. The distinctive pattern of zonal distribution documented previously provided an experimentally tractable system for isolating the direct and indirect effects of any one species on all others over time. Additionally, by examining how species recover after a selective removal this study addresses how and whether competitive interactions of residents and recruitment interact. Through large-scale (22 m x 10 m) experimental removals of the most abundant species I follow the abundance and distribution of all territorial damselfish species for 6 months at an ecologically relevant resolution of 25 cm. This study provides a comprehensive example of competitive release and illustrates how indirect effects on the distribution of other neighbouring species are triggered. As such, the study shows that the distinct distribution patterns are linked to levels of interspecific agonistic behaviour, and this adds to the growing body of work outlining how reef fish communities are affected by disturbances.

Chapter 5 explores the influence of territorial damselfishes on coral reef community dynamics and overall reef function through the agonistic interactions towards 3 roving herbivorous families: surgeonfish, parrotfish, and rabbitfish. I used video observations of roving herbivores during a removal of a territorial damselfish to record how abundance and foraging behaviour is affected by a competitive release. In addition, I further quantified the impacts to the benthos to assess how the removal of a common territorial damselfish may alter the substratum. This study provides context to the important role of territorial damselfish on reef function and adds to the growing view that the interactions between these families of fishes is complex. This study suggests that the paradigm that all territorial damselfish negatively impact roving herbivores through territorial behaviour is an over-simplification of a series of complex interactions.

Chapter 2

Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes

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2.1 Summary

A major goal of ecology is to explain the mechanisms that drive species distributions and ecological partitioning along gradients in the natural environment. The distributions of ecologically similar animals may depend on the degree of habitat specialization and behavioural interactions within and among species. The extent of ecological partitioning in guilds of coral reef fishes has been a matter of debate, but the roles of habitat selectivity and agonistic interactions have received little attention. Here these effects were examined by investigating fine-scale species distributions, microhabitat use, and aggression in a guild of 7 territorial damselfish species in Kimbe Bay, Papua New Guinea. We documented patterns of habitat partitioning across the 3 reef zones—reef flat, reef crest, and reef slope—with distinct patterns of distribution within these zones at extremely fine scales (1 − 2 m). Distinct differences between neighbouring species in the substrata selected were also observed. We hypothesized that fine-scale differences in distribution and microhabitat use could be maintained by aggressive interactions. To test this, we employed a 'bottle' experiment, where stimulus fish were introduced into a resident's territory, and aggression was recorded. Aggression elicited by neighbouring species was significantly higher for all species, compared with non-adjacent species. Levels of aggression differed among species, with the most aggressive species dominating the reef crest where the most distributional overlap occurred. This study revealed a fine level of spatial partitioning among reef zones and microhabitats in this guild of damselfish, which is likely to be maintained by agonistic interactions among neighbouring species. We demonstrate that when exploring coexistence in reef fish communities, the more traditional niche mechanisms operate alongside competitive dynamics, and within highly diverse systems these ecological processes are magnified.

2.2 Introduction

Partitioning of space and other critical resources theoretically facilitates the coexistence of ecologically similar species in natural communities (MacArthur 1958, Schoener 1974, Connell 1978). Interactions among ecologically similar species, often congenerics, can directly influence their local distribution and can result in ecological separation among habitats or along environment gradients (Connell 1983, Schoener 1983, Hixon and Johnson 2009). However, differences in species distributions along ecological gradients may also arise as each species independently becomes adapted to different local biotic and abiotic conditions, even without the influence of interspecific competition (Connell 1978, Ross 1986, Gaston 1996, Lomolino et al. 2010). Some of the most conspicuous patterns of apparent ecological partitioning occur along steep physical gradients such as altitude, latitude, and depth (Hawkins 1999, Jankowski et al. 2015). Similar species may use different resources along these gradients to minimize competition, and dominant species may exclude others from preferred zones (Connell 1983, Schoener 1983). However, differences in distributions may also reflect species-specific differences in habitat preferences and degrees of habitat specialization. Studies that combine patterns of habitat selectivity and interspecific interactions can together help define the mechanistic drivers underlying the (often distinct) boundaries between species along important ecological gradients.

Ecological partitioning is recognized to be a core mechanism structuring coral reef fish assemblages, but its role is controversial (Bonin et al. 2015). Early studies stressed intense interspecific competition for living space as the main driver behind niche partitioning (Smith and Tyler 1972, 1973, Smith 1978). However, the apparent instability of reef communities sparked an early and founding debate on species coexistence. Sale (1976, 1977, 1978) stressed that a high degree of overlap in ecological niches and stochastic recruitment events sustains species co-existence. This ‘lottery hypothesis’ argued that space is the limiting resource and that species with similar niche requirements and competitive abilities could coexist through chance colonization of vacant space after a random gain or loss occurs. Other studies suggested that predation maintains populations below carrying capacity and limits the need for immense competition (Talbot et al. 1978). The ‘neutral model’ furthered the debate by accepting that a lottery for space at recruitment exists but proposed that biodiversity is maintained by chance variations in demographic and evolutionary rates (Bell 2000, Hubbell 2001). This theory was subsequently classified into competition models based on stabilizing mechanisms (‘niche theory’) and fitness equivalence (‘neutral theory’) to explain the coexistence of competing species (Adler et al. 2007, Bode et al. 2012). Studies suggest that aspects of both niche and neutral processes can change through ontogeny within a species and may operate in many communities simultaneously (Schmitt and Holbrook 1999, Munday et al. 2001, Gravel et al. 2006, Pereira et al. 2015). However, the ongoing debate on the mechanisms of coexistence has been largely pursued in the absence of detailed information on the extent of habitat partitioning or knowledge of species-level interactions (Gravel et al. 2011, Connolly et al. 2014).

There is now a large body of empirical evidence that the distributions of coral reef fishes are constrained across broad habitat zones, with characteristic distributions along the reef flat and reef crest habitats and down the reef slopes. Distinctive patterns of zonal distribution are a feature of many reef fish families (Bouchon-Navaro 1980, 1981, Russ 1984, Fowler 1990, Williams 1991). Within these families of fishes, some members are widely distributed and act as generalists, whereas others have restricted distributions and are more specialized (Fishelson 1980, Williams 1991). This range of niches and specialization has resulted in increased habitat partitioning and the need for further ecological separation due to limited resource availability (Connell 1978, Ross 1986, Lomolino et al. 2010). Few coral reef studies provide evidence of habitat specialization as a means to facilitate distributional patterns among ecologically similar species (but see Meekan et al. 1995, Bay et al. 2001, Dirnwöber and Herler 2007). However, habitat partitioning has been widely described for a variety of reef fishes across multiple tropical regions (Doherty 1983, Robertson and Gaines 1986, Wainwright 1988, Shpigel and Fishelson 1989, reviewed by Williams 1991). Thus, ecologically similar species should facilitate coexistence through the partitioning of habitat and space when constrained by physical zones. When resources and space are limited, competitive interactions further influence spatial distributions (Robertson and Gaines 1986, Srinivasan et al. 1999, Pratchett et al. 2008, Kane et al. 2009, McCormick and Weaver 2012). However, the majority of evidence for mobile reef fish species has involved measuring pairwise interactions and not competitive networks within a community (reviewed by Bonin et al. 2015). Studies that document microhabitat use and partitioning among competing species have largely focused on coral gobies and blennies as study organisms (Munday et al. 2001, Hobbs and Munday 2004, Munday 2004, Dirnwöber and Herler 2007, Medeiros et al. 2014, Pereira et al. 2015). Few studies have documented the distribution within reef zones and fine-scale microhabitat use of competing territorial damselfish and the extent to which aggressive interactions play a role in influencing these abundance patterns.

Territorial damselfish provide an ideal model for such studies. For most damselfishes, ecological parameters can be effectively obtained due to their highly site-attached habits and territorial behaviour. Furthermore, patterns of distribution among reef zones (Williams 1991, Meekan et al. 1995, Robertson 1995, 1996, Ceccarelli et al. 2001, Bay et al. 2001, Ceccarelli 2007, Chaves et al. 2012) and microhabitat partitioning (Robertson and Lassig 1980, Waldner and Robertson 1980, Robertson 1984, 1996, Medeiros et al. 2010, 2016, Leal et al. 2015) have been well documented within the guild. Aggression and interspecific com- petition has also been found to structure these patterns and limit subordinate abundances (Robertson and Lassig 1980, Ebersole 1985, Robertson 1995, 1996). Very few studies couple experimental evidence of aggressive interactions and habitat partitioning within the guild of coral reef territorial damselfish (but see Bay et al. 2001, Medeiros et al. 2010).

In this article we document the extent to which habitats are partitioned in a guild of territorial damselfish. We then examine the importance of microhabitat selectivity and agonistic interactions as potential determinants of spatial segregation between neighbouring species. We focused on 7 species of territorial damselfish that are commonly found in Kimbe Bay, West New Britain, Papua New Guinea (PNG) along a gradient that extends from the reef flat to the reef crest and down the reef slope. We explored the following 3 predictions: (1) Species should partition space along this ecological gradient. (2) Species found in the same reef zones would show elevated levels of micro- habitat partitioning. (3) There would be elevated levels of aggression between adjacent species on a habitat gradient that may explain the high degree of space and microhabitat partitioning within the guild.

2.3 Methods

Study site and species

This study was conducted in Kimbe Bay on the northern coast of West New Britain in PNG (Fig. 2.1; 5° 30’ S, 150° 05’ E). Kimbe Bay lies within the Coral Triangle of the Indo-Pacific, the region recognized for the highest coral reef biodiversity (Roberts et al. 2002). Over 800 species of reef fishes and some 300 species of corals are recorded in this region (Spalding et al. 2001, Maniwavie et al. 2000). The study sites had a particularly high density and diversity of small, shallow-water territorial damselfish that form the focus of this study. All research was conducted on inshore platform reefs (<2 km from shore), which extend down to depths of >100 m, rendering them geographically isolated for adults but not necessarily larvae. The reefs can be clearly divided into typical coral reef zones, comprising reef flat (which breaks the surface at low tide), reef crest, and reef slope habitats (Table 2.1; Berkström et al. 2012). Community structure, species distribution, microhabitat preference, and data on aggressive interactions were collected from 3 reef sites (Garbuna, Hanging Gardens, and Luba Luba) from 2014 to 2015.

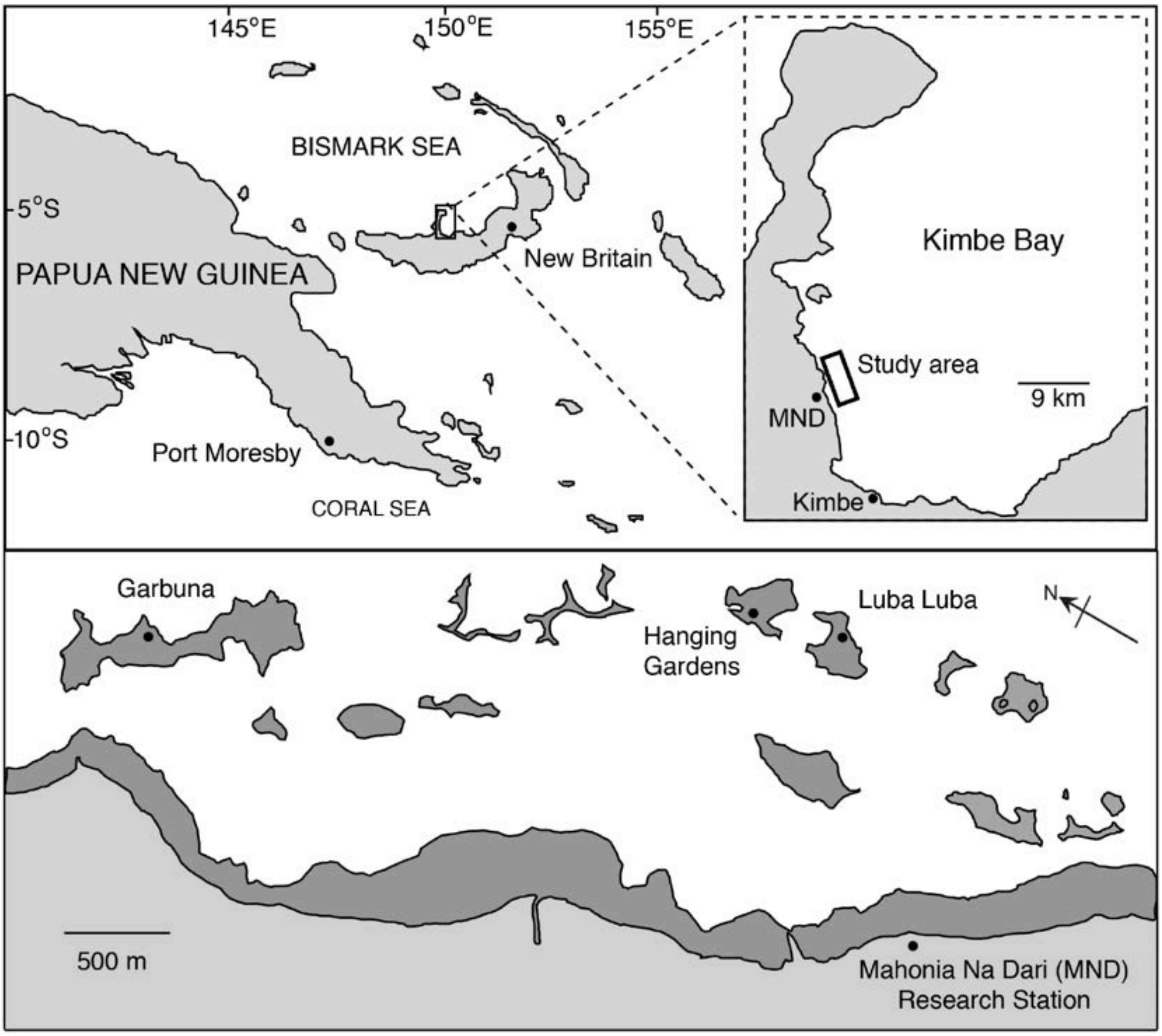

Figure 2.1 Location of Kimbe Bay, West New Britain, Papua New Guinea, and the 3 reef sites (Garbuna, Hanging Gardens and Luba Luba).

Table 2.1 Definitions of categorization of reef zones. Differences in depth represent tidal flux and changes in aspect.

Zone (depth)	Dominant substrate
Reef flat (0.5 – 1.5 m)	Macroalgae, some live, dead hard coral, and soft coral, some rubble, little sand
Reef crest (1 – 2 m)	Live, dead hard coral, and soft coral, little rubble
Reef slope (2 – 8 m)	Live, dead hard coral, and soft coral, rubble, some sand

Seven species of territorial damselfish are commonly found in Kimbe Bay along a gradient that extends from the reef flat to the reef crest and down the reef slope in the respective order (maximum size from Allen et al. 2003, Randall 2005); *Pomacentrus tripunctatus* (10 cm), *Chrysiptera unimaculata* (8 cm), *Pomacentrus bankanensis* (10 cm), *Pomacentrus adelus* (8.5 cm), *Plectroglyphidodon lacrymatus* (10 cm), *Neoglyphidodon nigroris* (11 cm), and *Pomacentrus burroughi* (8 cm). All 7 species are known to inhabit discrete territories (mean 1−1.5 m^2 territory sizes per individual), which they defend from conspecifics, congenerics, and other grazers, and which account for a substantial proportion of the substratum (Ceccarelli 2007). They are highly aggressive and are commonly seen defending, charging, and engaging in territorial displays with associated species. Other pomacentrid species (planktivorous damselfish) occurred within the study area but were not associated with the microhabitats used by the territorial species. Additionally, no direct interactions were observed in preliminary observations. Thus, other damselfish were omitted from analysis.

Damselfish distribution

The horizontal and vertical distribution of the 7 damselfish species across the reef flat, reef crest and reef slope were recorded from systematic searches in which the positions of all individuals were recorded. The observer slowly searched a 40 m wide strip of reef from 20 m down the reef slope (starting deep and moving to shallow) up the reef crest and back to the reef flat ending at the sand sloping back reef. Prior to the census, a diver laid out a 40 m transect tape parallel to the reef crest. From each end point, perpendicular transects were laid: (1) down the reef slope, and (2) from the reef crest back to the reef flat until the sand sloping back reef was reached. The perpendicular transect tapes were marked every 2 m using flagging tape for reference. This enabled vertical positions to be recorded down to a scale of 1 m. This search zone covered the entire reef profile and all zones (reef flat; reef crest; reef slope) occupied by territorial damselfish. The profile was further categorized into 3 subzones (back/upper; mid; front/ lower) within each of the 3 habitat zones based on the aspect, depth, and distance relative to the reef crest (Table 2.1). During the search, the observer (J. G. Eurich) swam at a constant depth parallel to the reef crest zig-zagging shallower in 2 m vertical increments within the survey area. Species identity, size, life stage, reef zone, subzone, and depth were recorded within each contiguous 2 m transect. Searches were repeated at 3 different locations per reef for each replicate reef (n = 9).

Microhabitat use, availability, and selectivity

Microhabitat use was recorded for each fish observed as the substrate directly beneath an individual when it was first noticed. For analysis, substratum was classified as one of 8 microhabitat categories: (1) hard corals; recorded by growth form but pooled as live coral for the purpose of this study, (2) non-biological substrate (e.g. sand, boulder), (3) sediment or detritus, (4) rubble (incl. fragments of dead coral), (5) turf algae, (6) *Turbinaria* sp., (7) *Padina* sp., or (8) other (e.g. dead standing coral, other macroalgae, crustose-coralline algae, *Fungia* spp., sponges, and bivalves). For the purpose of this study, we used the definition of turf algae from Hay (1981) as masses of tightly packed upright branches that were dominated by filamentous species. If any points had multiple categories within the area, the majority was chosen. All surveys were conducted on SCUBA at mid or high tide by one observer (J. G. Eurich).

The availability of the different microhabitats at each site (n = 9) was quantified by a series of 10 m transects parallel to the crest at 2 m vertical intervals within the damselfish survey area. A total of 12 transects per site were used with 4 on the slope, 4 on the crest, and 4 on the reef flat. Benthos was recorded for each reef subzone using the random intercept point method (n = 80 points zone^{-1} site^{-1}; Jones et al. 2004). Substratum was classified into the same 8 categories as used in the microhabitat use surveys.

Microhabitat selectivity was estimated by calculating Manly’s resource selection ratios (Manly et al. 2002) based on the estimates of habitat use and availability from independent animals with equal access to resource units. Manly’s resource selection ratio was chosen due to the ability to quantify microhabitat use at the population level from individual-specific data. The resource selection ratios ($\hat{w}_i = o_\mathrm{i} / \pi_i$) were used to determine whether a species used a microhabitat type more or less frequently than expected based on their availability, where o_i is the proportion of fishes on category *i*, and π_i is the proportion of microhabitat *i* available (for full equations and explanations see Manly et al. 2002). Microhabitat availability data were merged across replicate benthic transects to estimate overall percent cover by zone, and the mean of the 3 reefs was used in calculations, as there was no site difference (by ANOVA, χ^2 (df 2) = 2.427, p = 0.297; Appendix: Table S2.1). To quantify species-level microhabitat selectivity, only microhabitat types (grouped into the above categories) that were occupied by the fish species were used and unused categories were omitted from the analysis. To allow multiple comparisons between micro habitat types, a Bonferroni-corrected 95% confidence interval was calculated for each selection ratio (Manly et al. 2002). A confidence interval containing the value of 1 indicates that a microhabitat is used in proportion to its availability (i.e. 1:1 or non-significant). A confidence interval which spans greater or less than 1, but does not include 1, indicates that a microhabitat is selected or avoided, respectively, than expected by its availability in the study area (Manly et al. 2002).

Agonistic interactions

A field experiment was used to quantify levels of aggression within and among species as a potential determinant of spatial segregation between neighbouring species. The levels of aggression toward the intruding stimulus-individuals were assessed using a ‘bottle’ experiment (Myrberg and Thresher 1974), following Draud and Itzkowitz (1995), Sale et al. (1980), Harrington (1993), and Osório et al. (2006). However, similar to Bay et al. (2001), a plastic bag was used instead of a glass bottle to allow the intruding individual more volume, thereby decreasing stress, and to minimize visual distortion of the fish within the bag. In the present study, ‘stimulus’ fish were placed in bags inside the territories of a ‘response’ fish, and the intensity of response by the resident towards the stimulus was quantified (Fig. 2.2). Using this methodology, Osório et al. (2006) demonstrated similar results in the aquarium and field. In the present study, a field experiment was chosen over a laboratory study to limit the stress and manipulation of the fishes and to maintain natural variables that may influence fish behaviour. In the field a resident species can engage in shelter and habitat maintenance, defecation, foraging, and other activities in addition to territorial defense. While the relative response towards intruding species is unlikely to be influenced by the experimental design (Osório et al. 2006), the magnitude of response and rates of agonistic interactions are more representative of natural conditions when executed in the field.

Figure 2.2 *Neoglyphidodon nigroris* resident with a conspecific stimulus during a bottle experiment trial. The focal laterally displayed (left, category 2) and charged (right, category 3) as it swam around the stimulus.

The stimulus fishes were captured using hand nets and clove oil (50 ml in 100 ml 95% ethanol with 350 ml seawater) as an anaesthetic and kept in a holding tank for 15−30 min prior to use to regain normal behaviour and colour. If the fish did not return to a natural state post-anaesthesia it was released and not used. Fish were held for a maximum duration of 4 h. For each trial, a single adult of each stimulus species was then placed into a sealed 9 l seawater-filled transparent plastic bag. A pilot study indicated that the presence of a diver observing the trial affected interactions and thus all trials were recorded on video using tripods with the diver not present. Before initiating the experiments, each resident species was observed for 4−5 min to establish the boundaries of the territory, neighbouring species, and to allow the resident damselfish species to acclimate to the tripod prior to the experimental trial start time. The diver then introduced the stimulus individual into the centre of the territory, secured the bag to the substratum via rubber band, and immediately vacated the area. The resident responses were recorded for 5 min with a video camera (GoPro). The videos were analysed and the frequency and intensity of the territory holder’s behavioural interactions were quantified and categorized based on the severity of the response (Table 2.2). If at any point during a trial the stimulus individual exhibited irregular or stressed behaviour, colour changes, or exerted aggression back to resident, the trial was abandoned and omitted from the analysis. However, this rarely occurred, with most stimulus individuals swimming from side to side within the bag.

The sampling design included 56 different combinations of stimulus and response treatments. Eight different stimuli (conspecific, heterospecifics: 6 other species, and an empty bag control) were replicated 10 times each for the 7 species of interest (n = 560). Each trial was conducted using a different resident species. After each trial, the stimulus species (i.e. fish in the bag) was given fresh seawater and a 2 – 3 min break before being used in another trial. If the stimulus species did not resume normal behaviour within 5 min, the stimulus species was released and a new individual was used.

Table 2.2 Definitions of behavioural interactions used to quantify aggression between resident and stimulus species.

Category	Behaviour
1. Investigation	Non-aggressive change of behaviour, movement towards the bag with limited action and no further attention; inspection
2. Display	Fin flare, tail flick, body oscillation; directed colour change
3. Charge	Aggressive quick movement towards the bag to an abrupt stop before contact
4. Bite	Contact of mouth with the bag

Statistical analysis

To describe the distribution of the 7 damselfish species across reef zones and sites, abundance and location within the reef profile was compared among adult individuals only across the species range. Due to irregular recruitment pulses during the survey periods, a lack of territoriality or aggression towards recruits from adults in preliminary observations, and because recruits occupied the same distribution as their respective adults, recruits and sub-juveniles (<1.5 cm) were omitted from the analysis. Because we were unable to determine a transformation for the data that clearly met parametric assumptions, we used the nonparametric Kruskal-Wallis 1-way ANOVA (Zar 1999). A Bonferroni correction of alpha levels was made to adjust for the number of comparisons made. For substrate and microhabitat availability (used for microhabitat use), a binomial generalized linear mixed model was used to evaluate the effects of zone and site using the R package ‘car’ (Crawley 2007, Fox and Weisberg 2011, R Development Core Team 2013). ‘Replicates’ within reef site and transects was considered a random factor in the mixed model using the R package ‘lme4’ (Bates et al. 2011). For substrate and microhabitat availability, a full model was fitted with all explanatory variables (depth and transect) and interactions (reef zone and site). From this full model, we subsequently generated simpler models and used the Akaike information criterion (AIC) to choose the most parsimonious model with the lowest AIC (Appendix: Table S2.2). While all comparisons involved replicate fish and benthic microhabitat sampled from 3 different reefs, data were pooled and smoothed for graphical presentation and final analysis where there were no differences among reefs.

2.4 Results

Habitat partitioning

The distribution and relative abundance of adult damselfish differed markedly among the 3 reef zones and subzones, with minimal overlap among species (Fig. 2.3; Table 2.3). There were significant differences in abundance among zones for all species, with no significant differences among sites (Table 2.4). All 7 species occupied a distinct subzone within the reef flat, reef crest, and reef slope. The reef flat was dominated by *Pomacentrus tripunctatus* ($p = 0.022$) and *Chrysiptera unimaculata* ($p = 0.022$), with further partitioning into the subzones reef flat back and reef flat mid, respectively (Fig. 2.3). The population of *Pomacentrus bankanensis* also was mainly restricted to the reef flat front, directly in front of *C. unimaculata* with minimal overlap, and the reef crest back ($p = 0.053$). *Pomacentrus adelus* occupied the broadest range of any species and occurred in all 3 zones, with no significant differences among zones ($p = 0.269$). However, despite a non-significant pattern when comparing between zones, *P. adelus* did show a unique bimodal distribution at the subzone level. It occupied the reef flat front with *P. bankanensis* and the upper reef slope with *Neoglyphidodon nigroris*, with reduced densities around the main reef crest. *Plectroglyphidodon lacrymatus* was exclusively found on the reef crest and its abundance was inversely proportional to the abundance of *P. adelus* ($p = 0.055$). The reef slope (mid to lower) was almost entirely occupied by *N. nigroris* until ~5 m depth, where *Pomacentrus burroughi* became prevalent. The 2 reef slope species had minimal overlap and were exclusive to these zones on all sites ($p = 0.023$ and $p = 0.021$, respectively).

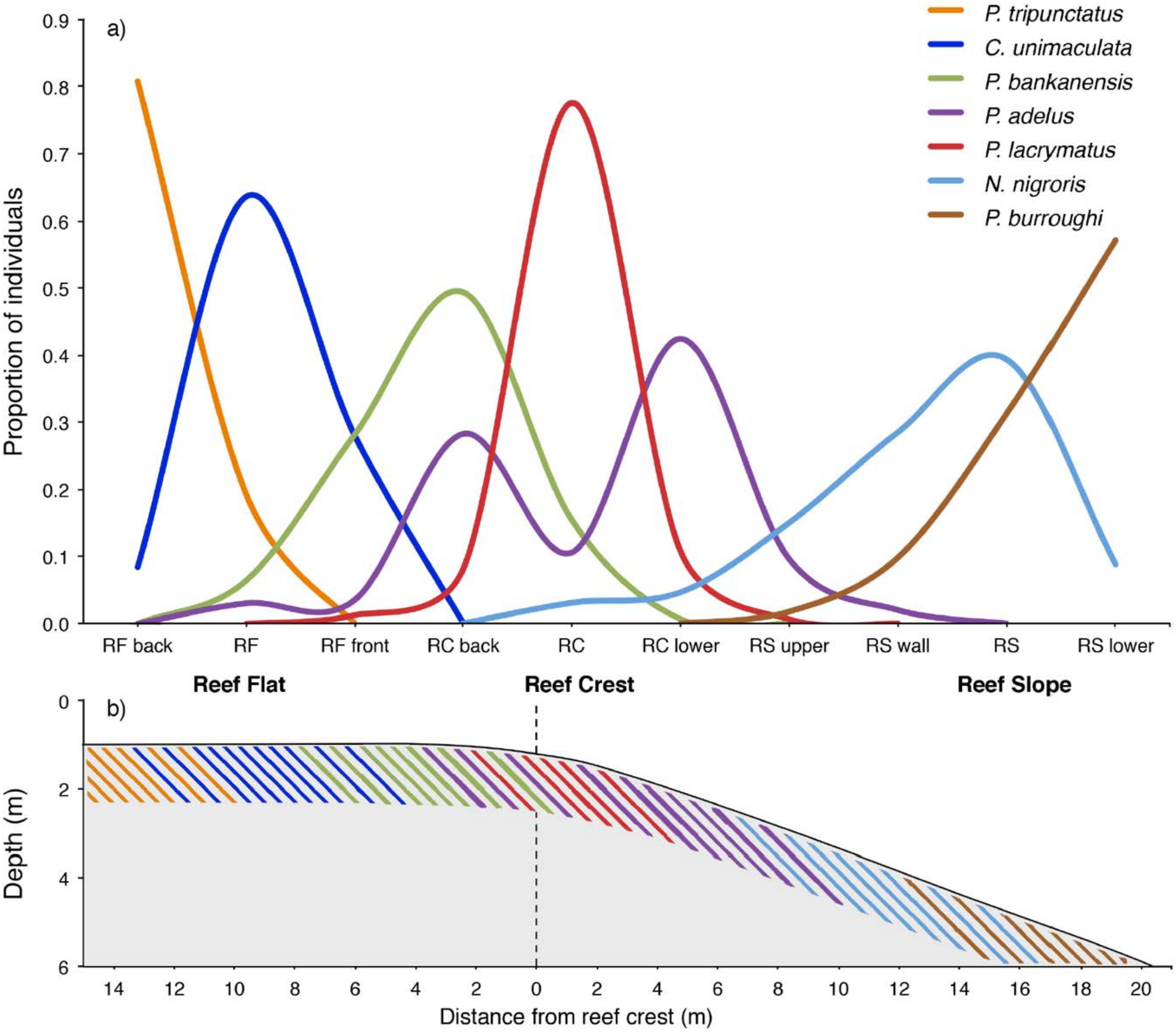

Figure 2.3 Distribution of adult territorial damselfish by (a) proportion of individuals across the reef zones (RF: reef flat; RC: reef crest; RS: reef slope) and related linear subzones (back/upper; mid, denoted in figure by bolded zone; front/lower) (b) reef profile cross-section. Proportion of individuals based on pooled populations from all sites (n = 3) for each subzone. Subzone spacing and distance from reef crest is averaged across sites. Reef slope wall is omitted from reef profile depiction. Species: *Pomacentrus tripunctatus*, *Chrysiptera unimaculata*, *Pomacentrus bankanensis*, *Pomacentrus adelus*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris*, *Pomacentrus burroughi*.

Table 2.3 Pairwise percent overlap in distribution of damselfish. Mean (± SE) percent overlap between sites (n = 3) of the total population (row) relative to other species (column). Count data was pooled by subzone. If 2 species occurred within the same subzone they were categorised as overlapping. Species are abbreviated to the first four letters of the species name.

	P. trip	*C. unim*	*P. bank*	*P. adel*	*Pl. lacr*	*N. nigr*	*P. burr*
P. trip		73.3 ± 27.7	8.7 ± 4.3	8.7 ± 4.3	0.0	0.0	0.0
C. unim	55.0 ± 21.7		39.0 ± 20.0	6.0 ± 3.0	0.0	0.0	0.0
P. bank	5.3 ± 2.7	25.7 ± 13.7		61.0 ± 20.6	40.0 ± 23.7	0.7 ± 0.3	0.0
P. adel	1.7 ± 0.8	3.3 ± 1.7	46.3 ± 23.4		74.0 ± 17.9	12.3 ± 9.4	1.7 ± 0.8
Pl. lacr	0.0	2.3 ± 1.2	55.0 ± 23.7	93.3 ± 1.9		10.0 ± 7.2	0.0
N. nigr	0.0	0.0	0.0	23.3 ± 16.9	7.7 ± 2.7		67.7 ± 13.6
P. burr	0.0	0.0	0.0	4.3 ± 2.3	1.7 ± 0.8	97.3 ± 2.7	

Table 2.4 Kruskal-Wallis testing for differences in distribution of the 7 species across reef zone and site.

Source	X^2	df	*P*-value
P. tripunctatus			
Zone	7.623	2	0.022
Site	0.125	2	0.939
C. unimaculata			
Zone	7.623	2	0.022
Site	0.125	2	0.939
P. bankanensis			
Zone	5.843	2	0.053
Site	1.382	2	0.501
P. adelus			
Zone	2.621	2	0.269
Site	1.681	2	0.432
Pl. lacrymatus			
Zone	5.793	2	0.055
Site	0.276	2	0.870
N. nigroris			
Zone	7.513	2	0.023
Site	0.301	2	0.860
P. burroughi			
Zone	7.623	2	0.021
Site	0.125	2	0.939

Microhabitat use and selectivity

The microhabitats used by 1269 damselfish were recorded and compared to availability to determine selectivity (Appendix: Text S2.1 and Fig. S2.2). All species positively selected rubble, although strength of selectivity varied (Fig. 2.4). Conversely, the pooled category ‘other’ of limited or rare substrate types (i.e. dead coral, CCA, *Fungia*, sponges, and macroalgae) was either unused or non-significant for all species. All other microhabitat categories differed among species, particularly between neighbouring species that occurred within the same zone.

Other than an avoidance for live coral, the reef flat species markedly differed in microhabitat selectivity. The population of *P. tripunctatus* was positively associated with multiple different substrate types (Fig. 2.4a). *P. tripunctatus* actively selected non-biological substrate (predominantly fine sand and bare rock), sediment, rubble, *Turbinaria*, and *Padina*, and avoided turf. There was no trend towards a specific microhabitat type as the population was distributed equivalently amongst 6 out of the 8 microhabitat types recorded. *C. unimaculata*, the other main occupier on the reef flat, differed significantly from *P. tripunctatus* in its microhabitat preference (Fig. 2.4a). Unlike *P. tripunctatus*, the majority of the population was exclusively on one microhabitat type, with 66.1% of the individuals observed on rubble. The only other positive association was with sediment, which was not observed frequently on benthic transects and was found in close proximity to rubble. All other microhabitat types were either unused or used in proportion to availability.

Of the 3 reef crest-associated species, *P. bankanensis* and *P. adelus* overlapped in microhabitat preferences and use (Fig. 2.4b). Both species heavily selected rubble, with 58.0 and 68.3% of the total population (respectively) using rubble and showed a preference for non-biological substrata, which mainly comprised of sand and bare rock in gutters or channels through the crest (J. G. Eurich pers. obs.). Both species actively avoided live coral and turf, despite these being abundant substrate categories with 29.6 and 22.9% of total cover, respectively. Additionally, *P. adelus*, the only species to occur in more than one zone, occupied the same microhabitats in equal proportion with or without the presence of *P. bankanensis* (Fig. 2.5). *Plectroglyphidodon lacrymatus* differed substantially in microhabitat use and selectivity compared to *Pomacentrus bankanensis* and *P. adelus* (Fig. 2.4b). The majority of individuals were found associated with turf (80.7% of the population), with only a small number on rubble (13.7%).

On the reef slope, *N. nigroris* displayed similar preferences to *Plectroglyphidodon lacrymatus*, with a strong preference for rubble (39.5% of the population) and turf (44.3%; Fig. 2.4c). Live coral was avoided despite covering 32.5% of the area. *Pomacentrus burroughi*, the deepest-occurring species at the base of the reef slope, shared a microhabitat preference for rubble (38% of the population) with *N. nigroris*, but also actively chose sediment (26.8%; Fig. 2.4c). Turf was actively avoided, with only 7.8% of the population observed on this category despite 13.8% benthic cover on the reef slope.

Agonistic interactions

The levels of aggression displayed against a neighbouring species were significantly higher than non-neighbouring species for all 7 species (Table 2.5; Fig. 2.6a; Appendix: Table S2.3). Reef flat species, *P. tripunctatus* ($p < 0.0001$) and *C. unimaculata* ($p < 0.0001$), and the deeper reef slope species, *P. burroughi* ($p < 0.0001$) displayed significantly more aggression towards neighbouring species, but exhibited lower aggressive interactions than the reef crest species at ≤8.3 mean interactions per trial. The species situated near the reef crest also showed significantly higher mean aggression towards neighbouring species when compared to non-neighbouring species but at a higher intensity of ≥8.6 mean interactions per trial when compared to the reef flat and reef slope species. However, *P. bankanensis* ($p = 0.011$) and *N. nigroris* ($p < 0.0001$) were more aggressive towards neighbouring species on average (27.4 and 21.3 mean interactions per trial, respectively) than *Plectroglyphidodon lacrymatus* ($p = 0.029$) or *Pomacentrus adelus* ($p < 0.0001$; 14.8 and 8.6 mean interactions per trial, respectively).

For all species, a conspecific stimulus species elicited a significantly greater amount of aggression than heterospecific stimulus species (Table 2.5; Fig. 2.6b; Appendix: Table S2.3 MEPS Supplement). Furthermore, heterospecific stimulus species rarely lead to a charge or bite by the focal residents. Relative to other species, the reef flat species *P. tripunctatus* and *C. unimaculata* exhibited the lowest aggression. Despite still showing significantly higher aggression towards conspecifics ($p = 0.002$ and $p < 0.0001$, respectively), their mean numbers of aggressive behaviours were 1 to 2 orders of magnitude less than the reef crest and reef slope species. Conversely, the highest levels of aggression towards conspecifics were observed on the reef crest. *P. bankanensis* showed the highest rate and variability of aggressive behaviours, ranging from 25 − 65 interactions per trial towards conspecifics and 5−20 interactions per trial towards heterospecifics ($p < 0.0001$). For all species, negligible interactions were made towards the control other than rare single investigations (Category 1) immediately following bag placement (Appendix: Table S2.4).

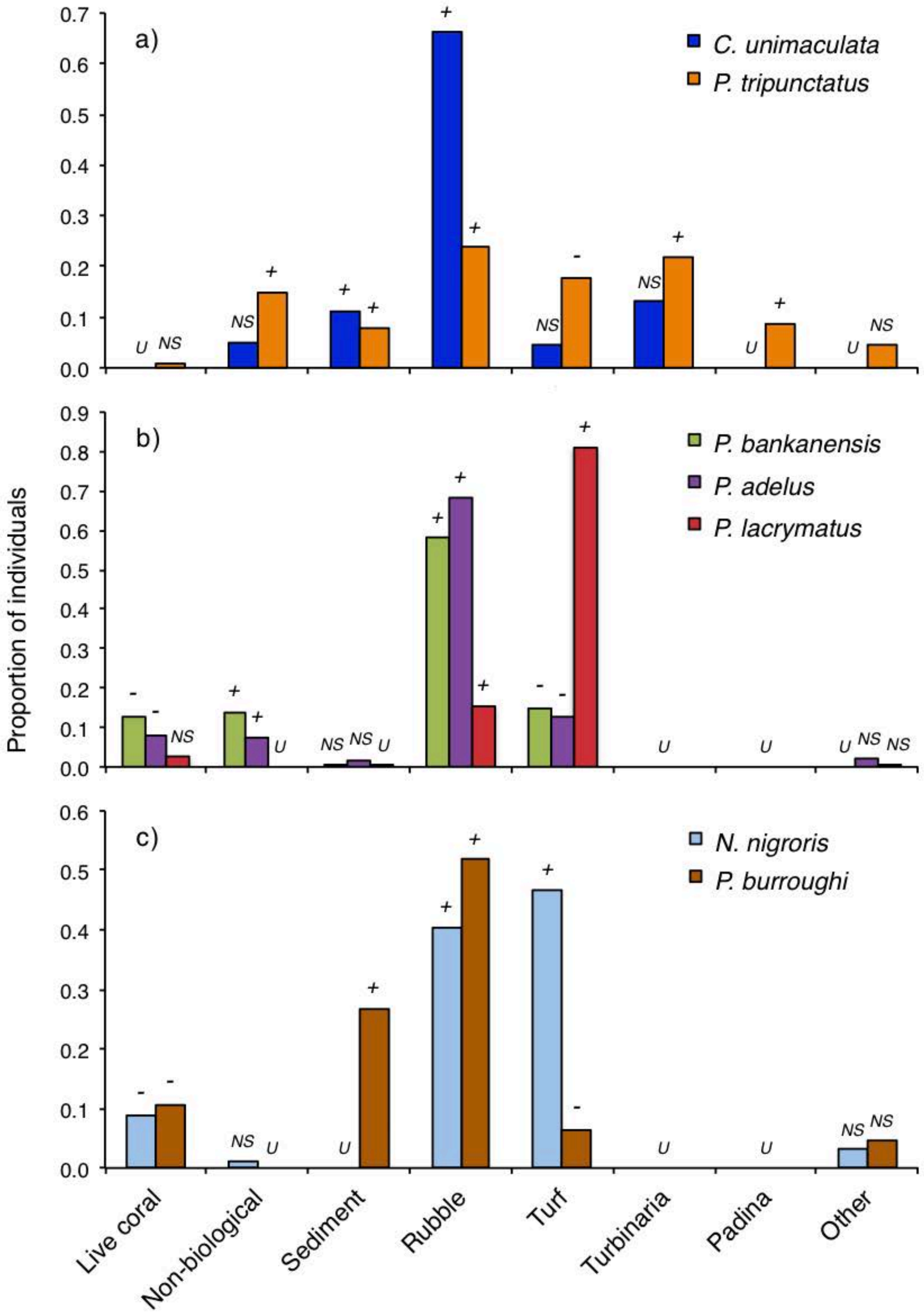

Figure 2.4 Microhabitat use of (a) reef flat species, (b) reef crest species, and (c) reef slope species. Resource selection: + microhabitat used more than available, - microhabitat used less than available, *NS* microhabitat was used in proportion to availability, and *U* microhabitat was never used. Bonferroni-corrected 95% confidence intervals was calculated with standard error for each selection ratio.

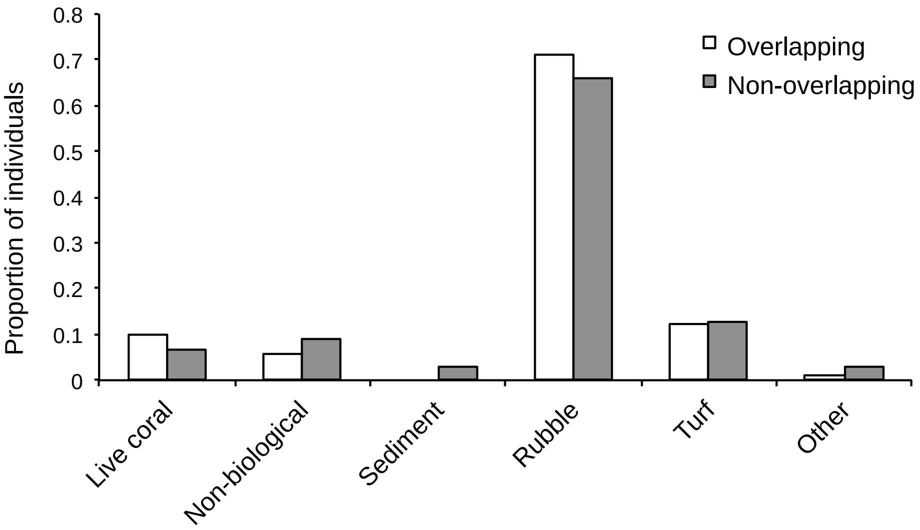

Figure 2.5 Microhabitat use of *Pomacentrus adelus* when spatial distributions overlap (white bars, n = 99) and do not overlap (black bars, n = 109) with *Pomacentrus bankanensis* (black bars, n = 109). *Turbinaria* and *Padina* were omitted from presentation as the microhabitats were never used.

Table 2.5 Results of ANOVAs on differences between the level of aggression towards; 1) conspecifics and heterospecifics stimulus species, and 2) neighbouring and non-neighbouring stimulus species.

Source	X^2	df	*P*-value
P. tripunctatus			
Conspecific	9.909	1	0.002
Neighbours	20.630	1	< 0.0001
C. unimaculata			
Conspecific	20.842	1	< 0.0001
Neighbours	23.532	1	< 0.0001
P. bankanensis			
Conspecific	18.907	1	< 0.0001
Neighbours	6.461	1	0.011
P. adelus			
Conspecific	7.986	1	0.004
Neighbours	15.459	1	< 0.0001
Pl. lacrymatus			
Conspecific	5.589	1	0.018
Neighbours	4.754	1	0.029
N. nigroris			
Conspecific	22.475	1	< 0.0001
Neighbours	21.762	1	< 0.0001
P. burroughi			
Conspecific	43.852	1	< 0.0001
Neighbours	34.464	1	< 0.0001

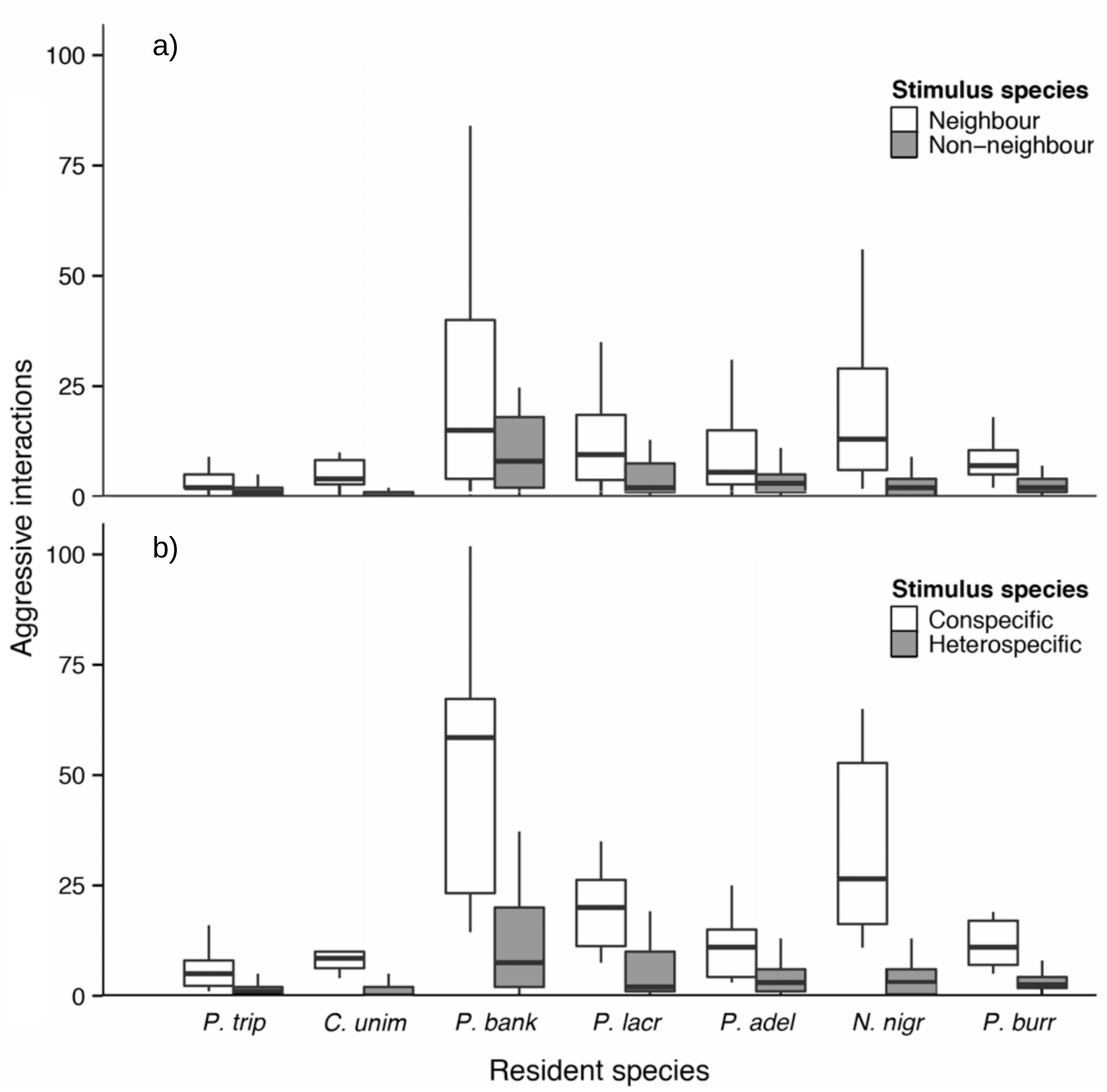

Figure 2.6 Resident species mean aggressive interactions towards (a) neighbouring/non-neighbouring and (b) conspecific/heterospecific stimulus species per 4 min trial (abbreviated to the first four letters of the species name). Box and whisker plot displays lowest and highest values omitting outliers, with box showing interquartile range and the median represented by the bold line.

2.5 Discussion

This study provides evidence for fine-scale partitioning of coral reef zones in a guild of territorial damselfish on a high-diversity coral reef. Distribution patterns were characterized by a distinct zonation parallel to the reef crest that saw all 7 resident species restricted to subzones of just a few meters wide along the reef flat, reef crest, and upper reef slope. Each species had a unique distribution with a relatively small overlap between neighbouring species. These distributions were clearly linked to levels of microhabitat selectivity and aggression between species. When the distribution of species overlapped, these species exhibited a marked difference in microhabitat use and selectivity. Adjacent species exhibited intense aggression towards one another compared with species separated from one another. We argue aggression plays an important role in reinforcing the patterns of habitat partitioning. Our research demonstrates that when exploring coexistence in adult reef fish communities, the traditional niche mechanisms operate alongside competitive dynamics, and within highly diverse systems these ecological processes are magnified.

Ecological partitioning along natural resource gradients has been found in plants (Grace and Wetzel 1981), reptiles (Schoener 1974), birds (Burger et al. 1977), rodents (Ziv et al. 1993), and many other taxa. Our research confirms the widely documented patterns of distinct non-overlapping spatial distributions of damselfish along reef gradients (Robertson 1996, Bay et al. 2001, Emslie et al. 2012). Previous work has clearly shown that fishes may partition space along depth gradients down reef slope habitats (McGehee 1994, Nanami et al. 2005, Jankowski et al. 2015, MacDonald et al. 2016). For territorial damselfish and other families, these distributional patterns can also be seen across the reef crest and reef flat (Russ 1984, Bay et al. 2001, Ceccarelli 2007). However, previous studies that quantify spatial gradients among reef fishes have been applied at relatively coarse spatial scales and do not quantify distributions on a scale of meters. In the present study, damselfish within each reef zone revealed partitioning of space with distinct distributions over a distance of 1−2 m. This represents the finest scale of habitat partitioning yet documented for this guild. This level of partitioning may reflect the high species diversity of territorial damselfish within the Coral Triangle. Where species richness is high, ecologically similar species partition resources to a greater extent and are more specialized (Schoener 1974, Ross 1986, Bellwood et al. 2006). In other regions with a lower abundance of territorial damselfishes, space occupancy, and diversity (e.g. Great Barrier Reef), the fine-scale spatial partitioning observed in this study may not be as prevalent or ecologically necessary (Ceccarelli 2007).

Resource partitioning is most likely refined by interactions among neighbouring species that regularly come into contact with one another (MacArthur 1958). Ecologically similar animals may be able to coexist by acting as generalists or specialists when resource availability is limited (MacNally 1995). On coral reefs where habitat is limited, neighbouring fishes with overlapping distributions may co-exist if they have contrasting patterns of habitat selectivity and versatility. In the present study, species within the same reef zone exhibited differences in microhabitat selectivity. While there was some overlap in microhabitat use among the 7 species, with all commonly associated with rubble substrata, there were distinct differences in the substrata used. Moreover, we observed the pairing of a species with generalist microhabitat use to a species with specialist microhabitat use within each zone, despite all habitats being relatively abundant across reef zones. Together, this suggests that neighbouring damselfish are constraining their microhabitat use to facilitate the co-habitation of reef zones and that microhabitat selectivity alone is insufficient in explaining the distinct zonation and limited distributional overlap.

It is notable that of the 3 species that cohabited the reef crest−*Pomacentrus bankanensis, Pomacentrus adelus*, and *Plectroglyphidodon lacrymatus*−2 species had similar microhabitat use and selectivity. *Pomacentrus bankanensis* and *P. adelus* displayed generalist qualities by occupying 4 microhabitats in contrast to *Plectroglyphidodon lacrymatus*, which displayed specialist habitat use for turf substrata—a well documented trait for this species (Jones et al. 2006, Hata and Kato 2006, Ceccarelli 2007, Hoey and Bellwood 2010). While the generalist-specialist pairing is still seen for this zone relative to *P. lacrymatus*, the 2 species did not constrain or partition habitat use. *Pomacentrus bankanensis* and *P. adelus* occupied identical microhabitats in equal proportion. Furthermore, *P. adelus* is the only species found to occupy multiple reef zones. This raises the question of whether the presence of *P. bankanensis* alters the habitat associations of *P. adelus* in areas where both species occur. Interestingly, *P. adelus* occupied the same microhabitats in equal proportion between zones with or without the presence of *P. bankanensis*. This suggests interspecific competition may also play a role in the spatial segregation of these species.

Early coral reef studies stressed intense interspecific competition for living space as the main driver behind niche partitioning (Smith and Tyler 1972, 1973, Smith 1978, Jones 1991). A large body of literature has since confirmed that interspecific aggression results in the spatial segregation of many fishes (Ebersole 1977, 1985, Robertson and Gaines 1986, Robertson 1996, Bay et al. 2001, Jones and McCormick 2002, Boström-Einarsson et al. 2014). The present study provides additional evidence that agonistic interactions among species within the guild can explain the high degree of resource partitioning and limited distributional overlap. For all 7 species, significantly higher levels of aggression were reserved for conspecifics and neighbouring territorial damselfish. Species that did not commonly come into contact with one another received little or no aggression despite occupying relatively similar niche breadths. These findings support the logic of animal conflict and competition theory (Maynard Smith and Price 1973, Connell 1983, Schoener 1983, Maynard Smith and Harper 1988). Aggression is expensive because it imposes energy and time costs and increases the risk of injury (Clutton-Brock and Parker 1995, Tibbetts and Dale 2004). Individuals do not need to be aggressive to all species, just the ones that pose a direct threat. Within a reef zone, damselfish showed higher aggression towards a neighbouring species due to the increased competition for space and habitat. Thus, interspecific aggression helps maintain the distributional boundaries between neighbouring populations.

Aggression towards neighbouring species was not ubiquitous among reef zones. Species on the perimeter of the physical gradient exhibited less aggression relative to species occupying the middle zone (i.e. the reef crest). A similar study showed that the most densely occupied zone in Kimbe Bay is the reef crest, where damselfish territories encompass almost 100% of the substratum (Ceccarelli 2007). When habitat is limited, animals are compelled to display more aggression in an effort to maintain access to the resource (Maynard Smith and Price 1973, Connell 1978). In the present study, *P. bankanensis*, which occupies the front reef flat to the back reef crest, was the most aggressive species, with more bites than any other species. Conversely, the species further away from the reef crest (*Pomacentrus tripunctatus* and *Chrysiptera unimaculata* on the reef flat and *P. burroughi* on the reef slope) displayed lower levels of aggression regardless of the stimuli. Our results suggest that competition for space among the guild is likely higher on the reef crest due to limited space.

The possibility of a dominance hierarchy as a result of interference competition among overlapping species cannot be discounted. *P. bankanensis* and *P. adelus*, the only co-inhabiting species with similar microhabitat use, differed in levels of aggression. An explanation is that *P. adelus*, the less aggressive species, is subordinate and consequently may be driven off the reef crest and down the reef slope where space is less limited. This may explain the bimodal distribution of *P. adelus* around the central reef crest and the reason for occupancy within 2 zones. Munday et al. (2001) previously documented that coexistence and a dominance hierarchy among 6 closely related goby (genus *Gobiodon*) species is maintained by a variety of mechanisms. Experimental removals of the competitively dominant or most abundant species (such as Robertson 1996) are required to determine if zone reversals or distributional shifts may occur.

While this study focuses on adult interactions, it is clear that spatial patterns of distribution may be explained by multiple factors (Ebeling and Hixon 1991, Hixon 1991, Jones 1991). Early theory suggested chance colonization of vacant space via recruitment exclusively determines patterns of abundance (Sale 1976, 1977, 1978). While such a mechanism may not be universal, larval supply and recruitment is known to shape the distribution of adult populations at a large scale with habitat selection influencing settlement (Williams and Sale 1981, Sale et al. 1984, Levin 1991). Pereira et al. (2015) demonstrated that the competitive mechanism between 2 goby species shifted from a lottery for space at settlement to niche partitioning among larger individuals. Research on territorial damselfish shows that juveniles often occur in the same zones as adults, and that aggressive interactions do not play a large role in the distribution of juveniles (Bay et al. 2001). In Kimbe Bay territorial damselfish juveniles and adults occupied similar distributions within the reef profile but refined recruitment surveys are needed to empirically corroborate the findings of Bay et al. (2001) and assess if an ontogenetic change in the mechanisms of coexistence exists (Munday et al. 2001, Pereira et al. 2015). While spatial distributions may be generated initially by recruitment patterns in other coral reef fishes or at a broader scale, post-recruitment events likely modify territorial damselfish distributions (Jones 1997).

Here we used a ‘bottle’ experiment to obtain a standardized quantification of the aggression between 2 individuals. Similar protocols have commonly been used to quantify fish aggression (Myrberg and Thresher 1974, Draud and Itzkowitz 1995, Sale et al. 1980, Harrington 1993, Bay et al. 2001, Osório et al. 2006). While the interaction is somewhat artificial, we argue that the differential aggression found among species using this technique is a useful relative measure of aggression. This methodology had the advantage over unmanipulated field observations because it enabled the quantification of aggression between species that may not normally interact due to their spatial separation. Because competitive interactions are energetically expensive (Maynard Smith and Price 1973, Connell 1978), a measure of relative aggression is an ecologically relevant proxy for the competition that may underlie the spatial partitioning among multiple species.

Conclusions

We demonstrate that when exploring coexistence in reef fish communities, the more traditional niche mechanisms operate alongside competitive dynamics. Evidence presented here suggests that the distribution of territorial damselfish along a physical gradient in Kimbe Bay, PNG is the result of microhabitat partitioning and interspecific competition. These 2 potentially independent processes likely contribute to a fine-scale partitioning of space within reef zones and the limited distributional overlap of species within the guild. Elevated levels of microhabitat partitioning and ecological versatility among neighbouring species also appeared to facilitate coexistence. The levels of aggression elicited by neighbouring species were significantly higher for all species compared with non-adjacent species, suggesting that interference competition contributes to a sharp transition from one species to another along the reef profile. This study expands on competitive interaction networks by providing insight into the mechanisms of aggression in a multi-species comparison. Evidence suggests that variation in the strength of interspecific competition among ecologically similar species influences habitat partitioning in a highly complex and diverse region.

Chapter 3

Stable isotope analysis reveals trophic diversity and partitioning in territorial damselfishes on a low latitude coral reef

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This chapter is in revision for *Marine Biology*

3.1 Summary

Investigating the niche overlap of ecologically similar species can reveal the mechanisms that drive spatial partitioning in high-diversity systems. Understanding how food resources are used and whether neighbouring species' diets are different are particularly important when considering the coexistence and functional role of species. Territorial damselfish on coral reefs are usually considered to be herbivores that often defend conspicuous algal mats from other food competitors. However, this guild contains numerous small species whose functional role and dietary diversification is poorly understood. Here, we investigate the relationships between diet and spatial distribution of seven small territorial damselfishes at Kimbe Bay, Papua New Guinea. These species partition habitat across three reef zones - the flat, crest, and slope, with distinct patterns of distribution within these zones. We predicted that neighbouring species with similar distributions would partition food with minimal dietary overlap. Examination of isotope ratios of carbon and nitrogen delineated three distinct feeding strategies, analagous to previous literature, within this group: 1) Pelagic feeders consuming zooplankton and particulate organic matter; 2) Reef-based feeders likely consuming algae, vagile invertebrates and detritus; 3) An intermediate group opportunistically feeding on both pelagic and benthic prey. None of the species appear to be strict herbivores. Adjacent species on the flat, crest, and slope exhibited high to intermediate trophic niche partitioning when examining pelagic versus reef-based dietary sources, with two species previously described as benthic herbivores actually exhibiting pelagic feeding. We argue that diet choice reinforces the patterns of spatial partitioning and coexistence among ecologically similar species. These findings add to a growing view that interspecific differences among similar species are lost when categorizing species into broad functional classifications, and that previous studies suggesting that territorial damselfish are strictly reef-based feeders may not be applicable in all systems or for all species.

3.2 Introduction

Coral reefs harbour exceptional diversity and two primary goals of reef fish ecology are to understand the mechanisms that allow similar species to coexist and the functional importance of each species. Niche partitioning has been viewed as one of the key factors in promoting the diversification of fishes (Cavender-Bares et al. 2009, Ndiribe et al. 2013, Gajdzik et al. 2016). Thus, investigating resource use of coral reef fishes (e.g., food and habitat) and describing species in the context of broad functional roles has received considerable attention (Pratchett et al. 2011, Hughes et al. 2017, Richardson et al. 2018). The identification of a species' trophic niche, defined as the place of an organism in the environment in relation to its food (Silvertown 2004), is one of the main ecological parameters that provide the basis of these functional groups (Mouillot et al. 2013). However, interspecific differences among similar species are lost when categorizing species into broad functional classifications (Brandl and Bellwood 2014, Tebbett et al. 2017a). The species-specific differences are particularly important when considering the functional role and coexistence of a taxon that is abundant and important to the overall community.

Damselfishes (Pomacentridae) are a major component of coral reef fish assemblages (Choat 1991). Their diversity and abundance has resulted in more attention from researchers than any other family of coral reef fishes, and they were the focus of early theoretical advancements in reef-fish ecology (Smith and Tyler 1972, 1973, Sale 1976, 1977, Doherty 1983). The highly site-attached habits, relatively small bodies, and territorial behaviour allow ecological parameters, niche properties, behavioural interactions and patterns of co-existence to be readily quantified (Robertson and Lassig 1980, Waldner and Robertson 1980). Within species, competitive effects on survival (Jones 1987a, b) and the drivers of abundance and distribution across coral reef habitats are well known (Meekan et al. 1995, Robertson 1996). Among species, habitat partitioning along the natural reef profile gradient - the reef flat, reef crest, and reef slope (Bay et al. 2001, Ceccarelli 2007, Chaves et al. 2012, Eurich et al. 2018a), and microhabitat partitioning (Medeiros et al. 2010, 2016) have been well documented. Recently, damselfish have again been used as a model species to test the mechanisms of coexistence due to the family's interspecific differences in habitat use and competitive interactions (Bonin et al. 2015, Eurich et al. 2018b). Ecological theory has since progressed from a focus on pairwise interactions among species to a multifactorial perspective of the process and mechanisms that govern competition within a community (Jones 1991, Hixon et al. 2002, Wiens et al. 2010, Pereira et al. 2015). Thus, when examining niche partitioning and coexistence within reef fish communities it is important to document similarities and differences among species on all important resource axes. While studies of habitat partitioning have generated a substantial amount of evidence, the diet or trophic niche of pomacentrids have received much less attention at this scale (but see, Ceccarelli 2007, Frédérich et al. 2009, Gajdzik et al. 2016).

Territorial damselfish, commonly referred to as “farmers” play an integral role in the benthic structure of coral reefs through their role as small-bodied consumers and aggressive holders of benthic space (Hixon and Brostoff 1983, 1996, Hata and Kato 2004, Ceccarelli et al. 2005b). Early dietary research defined the guild as herbivorous, but studies were biased towards a few larger, more aggressive species that maintain conspicuous algal mats, such as extensive farming species from the genera *Stegastes*, *Dischistodus*, and *Hemiglypltidodon* (Meekan et al. 1995, Wilson and Bellwood 1997, Ceccarelli et al. 2001, Jones et al. 2006). In addition, early studies that examined the trophic niche of territorial damselfish used gut content (stomach) analysis, which favors the observer to categorize matter as algae or detritus instead of pelagic materials (Polunin and Klumpp 1989, Ceccarelli 2007, Feitosa et al. 2012). However, it is important to note there are ambiguities associated with the functional term “herbivorous” within the context of territorial damselfish (reviewed by Horn 1989). Commonly, herbivores are described as species that remove algal matter from the substratum for consumption, but species that incidentally or deliberately remove algae for other means, such as farming, were included in early studies (Lassuy 1980, Steneck 1988). For the purposes of this study, any species that removes algae from the substratum for direct consumption is described as herbivorous to differentiate between diet contributions and farming behaviour. Successive studies have now provided contrary evidence indicating that not all farming damselfish are strictly herbivorous (reviewed by Hata and Ceccarelli 2016). Instead, territorial damselfishes appear to act as benthic-associated omnivorous generalists, with highly opportunistic diets and feeding plasticity (Frédérich et al. 2016). Nonetheless, our empirical understanding of territorial damselfishes trophic niche has been limited by the absence of detailed information on the extent of diet and resource partitioning for the majority of smaller territorial species from the genera *Pomacentrus, Chrysiptera*, *Plectroglyphidodon*, and *Neoglyphidodon* (but see Ceccarelli 2007).

Stable isotopes are increasingly used in ecology to study diet and trophic niche analysis as they reflect tissue assimilation from prey and are not hindered by stomach content analysis biases (pomacentrids reviewed by Frédérich et al. 2016). While stomach content data are a snapshot that reflects the most recent meals and may not represent the overall diet, stable isotopes of a consumer are concurrently integrated from various prey tissues at a rate slower than digestion (Matley et al. 2016). Thus, stable isotope analysis provides a measure of the diet contributions over longer periods of time (Post 2002). Although stable isotope analysis does not provide high-resolution dietary information, it can be used to estimate contribution of dietary sources (Jackson et al. 2011, Parnell et al. 2012). The ratio of carbon ($\delta^{13}C$) is commonly used because it indicates food sources or habitat (i.e., limited enrichment between predator and prey; Michener and Schell 1994), while the ratio of nitrogen ($\delta\ ^{15}N$) indicates trophic level (i.e., consistent enrichment between predator and prey; Minigawa and Wada 1984). Moreover, stable isotope analysis can be used to assess the trophic niche width and overlap among populations or species at similar spatial and temporal scales (Bearhop et al. 2004, Frédérich et al. 2009, Gajdzik et al. 2016). Few studies have segregated pelagic and reef-based diet contributions for a multi-species community of competing fishes to directly explore trophic niche partitioning within a guild.

Here, we explore the trophic niche diversification and partitioning in a guild of seven territorial damselfish. At our study location, Kimbe Bay, Papua New Guinea (PNG), these species partition the reef flat, reef crest, and upper reef slope habits on a fine scale (1 – 2 m) (Eurich et al. 2018a). The distinctive pattern of zonal distribution along this steep physical gradient provides an experimentally tractable system for isolating niche partitioning. Eurich et al. (2018a) found that neighbouring damselfish constrain their microhabitat use to facilitate the co-habitation of reef zones, but that microhabitat selectivity alone was insufficient in explaining the distinct zonation and limited distributional overlap. We hypothesise that in this highly partitioned ecological community, where there appears to be intense competition for resources (Eurich et al. 2018b), neighbouring territorial damselfish may partition food resources. Studies have previously quantified diet contributions, but no isotopic analysis has been conducted for territorial damselfish to date to specifically target pelagic-based food sources. In the present study we quantify trophic niches of the seven damselfish through the use of stable isotopes ($\delta^{13}C$ and $\delta\ ^{15}N$). Specifically, we asked: 1) To what degree does the generalization that territorial damselfish are herbivores apply to the seven PNG species?; 2) What is the variation in trophic position among species and to what extent does body size influence trophic diversification; and 3) Are neighbouring species more likely to partition food resources than non-neighbouring species?

3.3 Methods

Study site and species

Samples were collected from platform reefs in Kimbe Bay, PNG (5°30’S, 150° 05’E) from December 2014 to January 2015, and prepared at Mahonia Na Dari Research and Conservation Centre. Kimbe Bay lies within the Coral Triangle of the Indo-Pacific, the region recognized for the greatest richness of marine species world-wide (Roberts et al. 2002). The two inshore reefs, Garbuna and Luba Luba, were selected as sample locations due to similarities in species composition and reef aspect. Both reefs are nearshore (<1 km from land), and have a similar reef profile that can be clearly divided into typical coral reef zones, comprising a reef flat (exposed during low tides), reef crest, and reef slope.

At Kimbe Bay seven species of territorial damselfish partition space along a gradient that extends from the reef flat to the reef crest and down the reef slope in the respective order; *Pomacentrus tripunctatus*, *Chrysiptera unimaculata*, *Pomacentrus bankanensis, Pomacentrus adelus*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris,* and *Pomacentrus burroughi*. Distribution patterns are characterized by a distinct zonation parallel to the reef crest with each species restricted to subzones of just a few meters wide along the reef profile gradient (described in Eurich et al. 2018a). Further, the seven species are known to inhabit fixed territories (mean $1 - 1.5$ m^2 territory sizes per individual) and are highly site attached (Ceccarelli et al. 2001). In Kimbe Bay, all species occupy rubble (dead coral fragments) and filamentous algae microhabitats and defend their territories against conspecifics, interspecific competitors, and other benthic feeding fishes (Eurich et al. 2018a, c). All species have recently been categorised as predominantly (though not necessarily exclusive) benthic-feeding ‘intermediate farmers’, with the exception of *Pl. lacrymatus*, which was classified as an ‘extensive farmer’ (reviewed by Pratchett et al. 2016). Where, intermediate farmers maintain discrete, but significantly different to the surrounding environment, areas of algal turf (Emslie et al. 2012), and extensive farmers maintain small amounts of filamentous rhodophytes and a diverse assemblage of indigestible macroalgae (Hata and Ceccarelli 2016 and its citations). Despite intermediate farmers influencing the environment to a lesser degree, the territories support greater quantities of palatable filamentous algae (Ceccarelli 2007) and reduce coral larvae settlement (Casey et al. 2014).

All seven occurring species of territorial damselfish in Kimbe Bay influence the algal assemblage within the territorial boundary by weeding or farming (Hata and Kato 2004, Ceccarelli 2007). The act of farming makes it difficult for an observer to visually census the bite composition and targeted food resource of territorial damselfishes successfully. Thus, most recent studies have examined gut content to assess diet contribution, with only two employing isotopic analysis (Table 3.1). Prior isotopic research has included only two of the territorial damselfish species fused in the present study (Frédérich et al. 2009, Gajdzik et al. 2016). There has been no common methodology to describe diet and information for most species is conflicting, limited, or non-existing.

Table 3.1 Summary of previous studies on territorial damselfish diet contributions using different methods. Methods: *SI* stable isotopes, *GC* gut content analysis (stomach content), and *VIS* visual observation (direct feeding). Location: *PNG* Papua New Guinea, *GBR* Great Barrier Reef, *M* Madagascar, Indian Ocean, and *FP* French Polynesia, Pacific Ocean. Species: *Pomacentrus tripunctatus*, *Chrysiptera unimaculata*, *Pomacentrus bankanensis*, *Pomacentrus adelus*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris, Pomacentrus burroughi*.

Species	Method	Pelagic	Detritus	Algae	Inverts	Location	Reference
P. tripunctatus	GC		~70%	~30%		PNG	Ceccarelli 2007
	GC		~55%	~45%		GBR	Ceccarelli 2007
C. unimaculata	SI			Herbivore		M	Frédérich et al. 2009
	GC		~65%	~35%		PNG	Ceccarelli 2007
	GC	~3%	~7%	~90%		M	Frédérich et al. 2009
P. bankanensis	GC		~45%	~55%		PNG	Ceccarelli 2007
	VIS			Herbivore		GBR	Meekan et al. 1995
P. adelus	GC		~25%	~75%		PNG	Ceccarelli 2007
	GC		~5%	~85%	~10% [a]	GBR	Kramer et al. 2013
Pl. lacrymatus	SI			Herbivore		FP	Gajdzik et al. 2016
	SI		Omnivore [b]			M	Frédérich et al. 2009
	GC		~25%	~75%		FP	Gajdzik et al. 2016
	GC	~15%	~1%	~60% [c]		M	Frédérich et al. 2009
	GC		~10%	~90%	~25%	PNG	Ceccarelli 2007
	GC/VIS		NA	~95% [d]		PNG	Jones et al. 2006
	VIS		NA	99.9%		GBR	Polunin & Klumpp 1989
	VIS			Herbivore			Meekan et al. 1995
N. nigroris	VIS		Omnivore			GBR	Allen 1975
P. burroughi	GC		~40%	~60%		PNG	Ceccarelli 2007

[a] Kramer et al. (2013) recorded vagile invertebrates in the stomach of some individuals.
[b] Frédérich et al. (2009) stated that *Pl. lacrymatus* is an omnivore that feeds mainly on benthic algae.
[c] Frédérich et al. (2009) recorded ~25% vagile/sessile invertabrates in the stomach.
[d] Jones et al. (2006) recorded ~40% epiphytic diatoms in the stomach, and ~5% bites on live coral substrate.

Table 3.2 Putative functional groups and sample metrics for focal territorial damselfish, representative obligates, diet sources, and primary producers that were collected at Kimbe Bay, Papua New Guinea.

Taxa	Putative group	Abbreviation	Sampling method	No. of samples	Mean body size ±SE (mm L_t)	Range of body sizes (mm L_t)
Pomacentrus tripunctatus	Focal	*P. trip*	Spearfishing	12	56 ± 1.5	46 − 64
Chrysiptera unimaculata	Focal	*C. unim*	Spearfishing	12	61 ± 0.8	56 − 66
Pomacentrus bankanensis	Focal	*P. bank*	Spearfishing	12	59 ± 1.5	51 − 67
Pomacentrus adelus	Focal	*P. adel*	Spearfishing	12	65 ± 0.9	58 − 69
Plectroglyphidodon lacrymatus	Focal	*Pl. lacr*	Spearfishing	12	83 ± 1.5	75 − 91
Neoglyphidodon nigroris	Focal	*N. nigr*	Spearfishing	12	85 ± 3.4	63 − 100
Pomacentrus burroughi	Focal	*P. burr*	Spearfishing	12	69 ± 1.8	55 − 77
Chromis xanthura	Pelagic planktivore	*Ch. xant*	Spearfishing	6	102 ± 5.7	88 − 122
Pomacentrus nigromanus	Demersal planktivore	*P. nigr*	Spearfishing	6	72 ± 2.5	62 − 80
Siganus vulpinus	Herbivore	*S. vulp*	Spearfishing	6	167 ± 5.5	146 − 185
Ctenochaetus striatus	Detritivore	*Ct. stri*	Spearfishing	6	141 ± 9.3	95 − 156
Mussel	Consumer	−	By hand	12	−	−
Barnacle	Consumer	−	By hand	4[a]	−	−
Red algae (*Hypnea*)	Producer	−	By hand	12	−	−
Green algae	Producer	−	By hand	12	−	−
Brown algae (*Turbinaria*)	Producer	−	By hand	12	−	−
Mixed turf (incl. *Amphiroa, Gelidiopsis*)[b]	Producer	−	By hand	12	−	−
Vagile invertebrates (Crustacea)	Omnivore consumer	−	By hand	12	−	15 − 50
Zooplankton	Pelagic consumer	−	Tow net	4[a]	−	0.25 − 0.50[c]
Organic matter (detritus)	Producer	POM	By hand	4[a]	−	−

[a] Each sample consisted of many pooled individuals from one site and temporal period.

[b] For the purpose of this study, we used the definition of turf algae from Hay (1981) as masses of tightly packed upright branches that were dominated by filamentous species.

[c] Presumed range of body sizes based on mesh size of plankton net.

Sample collection

All samples were collected in the morning (between 8 am and 12 pm) within a 20 m wide section of reef extending from the back of the reef flat to 25 m down the reef slope. To compare the seven territorial damselfish trophic niches, we aimed to capture dominant producers and consumers to represent the key functional groups common to all sites, rather than trying to sample all possible producers and consumers (Table 3.2). Four representative obligate fishes with known diets were selected as comparative species: herbivore *Siganus vulpinus* (Brandl and Bellwood 2014), detritivore *Ctenochaetus striatus* (Tebbett et al. 2017a), pelagic planktivore *Chromis xanthura* (Greenwood et al. 2010), and demersal planktivore *Pomacentrus nigromanus* (Pratchett et al. 2016). The focal territorial damselfish and obligate fishes were captured with clove oil or speared and brought to the surface immediately, euthanized in a 50% seawater-ice bath, and placed on ice for transport to the lab. The total length and details of capture of each fish were recorded. To represent planktonic production, we targeted filter feeding invertebrates: mussels *Septifer bilocularis* and barnacles Cirripedi (Post 2002, Baker et al. 2013). Tissue samples of epaxial and adductor muscles were dissected from the fishes and bivalves, respectively, and immediately frozen (–20°C) for isotopic analysis.

Different primary food sources (zooplankton, organic matter, algae, and benthic invertebrates) were taken from the same locations where the fishes were collected (Table 3.2). Zooplankton was sampled using a 250 μm plankton tow net. The net was towed in a zig-zag pattern from the reef slope to the reef crest and reef flat at 1 – 2 m off the substrate avoiding prior sampled areas (Gajdzik et al. 2016). The tow was replicated three times within the fish-sampling period for two days (total 6 tows per site). Zooplankton samples were then pooled by day and site for analysis. Concurrently, particulate organic matter (POM) was obtained by collecting large quantities of settled particulates from thick algal turf mats (Frédérich et al. 2009). For the purposes of this study POM is used in a broad sense, i.e., to describe amorphous material with no visible structure (Wilson and Bellwood 1997). The particulates were transferred from the substrate to seawater filled plastic bags by pipette dropper. Visible algal pieces, crustaceans, and sand particles were later removed by sieve and microscope. Consequently, POM may include feces, live material such as microscopic algae (<1 mm), fungi, and/or bacteria. While POM samples were collected from the substrate, this material may also be suspended in the water column or represent settled material that would have been available to pelagic feeders when suspended. Similar to the zooplankton, the POM samples were then pooled by day and site for analysis. Four different types of alga were collected for dietary comparisons (following Ceccarelli 2007): red algae *Hypnea*, green algae, brown algae *Turbinaria*, and mixed turf (incl. *Amphiroa* and *Gelidiopsis*; defined by Hay 1981). All algae samples were rinsed and cleaned of epiphytes, other algal species, crustaceans, and POM. Crustaceans (vagile invertebrates; Portunid and Xanthid crabs) were collected from the mixed turf samples under a microscope and pooled.

Stable isotope analysis

Samples were rinsed and soaked in distilled water for >30 min to remove salts, and dried for 48 h at 70°C. After no residual water weight was found, samples were ground into homogeneous fine powder using a glass ball mill grinder (Biospec Mini Bead Beater Model 3110BX milling unit). Carbonate contamination of algae, zooplankton, barnacle, and POM samples were tested using three drops of 1N HCl on a small subsample. If effervescence was visible, the presence of carbonates was removed from the subsample by overnight acidification, rinsing, and re-drying (Baker et al. 2013). The process was repeated until no inorganic carbon was found to ensure the carbon stable isotope ratios were unbiased (Frisch et al. 2014). For acid-treated samples (i.e. turf algae, zooplankton, and POM), $\delta^{13}C$ was measured in the acid-treated subsample and $\delta^{15}N$ was measured in the untreated subsample (Pinnegar and Polunin 1999).

Samples were encapsulated in tin cups and weighed five times to the nearest 0.0001 g and averaged. Stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were measured using an isotope ratio mass spectrometer (PDZ Europa 20-20, Sercon Ltd., Cheshire, UK) coupled in continuous-flow to an elemental analyser (PDZ Europa ANCA-GSL, Sercon Ltd., Cheshire, UK) at the UC Davis Stable Isotope Facility, Davis, California, USA. Stable isotope ratio values are expressed in parts per thousand (‰) using the standard δ notation:

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

where X is ^{15}N or ^{13}C, R_{sample} is the ratio ($^{15}N/^{14}N$ or $^{13}C/^{12}C$) in the sample, and $R_{standard}$ is the ratio in the standard (Coplen 2011). The standard reference material was Pee Dee Belemnite (vPDB) carbonate and atmospheric N_2 for carbon and nitrogen samples, respectively. Experimental precision (standard deviation of replicates of internal laboratory standard) was 0.1 ‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$.

Data analyses

Isotopic biplots ($\delta^{13}C$ or $\delta^{15}N$) were created to visualize niche space by two main approaches. First, the mean ±SE of all species sampled were plotted. The second approach utilized the SIBER package (Jackson et al. 2011) in R (R Core Team 2017), in which standard ellipses were fitted (40% confidence level) for each fish species. The size of ellipses were compared among damselfish after fitting Bayesian models (10^4 iterations) adjusted for small sample size (SEA_C) to the data as described by Jackson et al. (2011). Differences in SEA_C size were considered significant when ≥95% of posterior draws for one species were smaller than the other. The area overlap between species/ellipses was also quantified as a percentage of shared isotopic space, to determine if neighbouring species were more likely to partition food resources than non-neighbouring species. Species with shared overlap >60% were considered to have significant shared-niche space based on a criterion used by Schoener (1968). Standard ellipses were also plotted for the obligate consumers (*S. vulpinus*, *Ct. striatus*, *P. nigromanus*, and *Ch. xanthura*) as a reference considering their known feeding patterns. Data from Garbuna and Luba Luba were pooled for graphical presentation and final analysis where there were no differences among reefs.

The trophic positions (TP) of damselfish were calculated to reduce any inter-reef differences associated with baseline $\delta^{15}N$ values. Scaled TP were calculated following Hussey et al. (2014):

$$(2) \quad TP_{scaled} = \frac{\log(\delta^{15}N_{lim} - \delta^{15}N_{baseline}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{consumer})}{k} + TP_{baseline}$$

where $\delta^{15}N_{lim}$ represents the saturating isotope limit as TP increases, and occurs when rates of ^{15}N and ^{14}N uptake equal those of ^{15}N and ^{14}N elimination, as determined through meta-analysis for fish (21.93 ‰); and k is the rate at which $\delta^{15}N_{consumer}$ approaches $\delta^{15}N_{lim}$ per trophic transfer (0.14; Hussey et al. 2014). *Siganus vulpinus* ($TP_{baseline} = 2$) was selected as the baseline organism because it is an obligate herbivore demonstrating consistent within-reef $\delta^{15}N$ values. Analysis of variance (ANOVA – type III error) tested if TP was influenced by damselfish species, reef, or habitat zone. The same ANOVA model was run with $\delta^{13}C$ as a response variable instead of TP to explore whether feeding habitat was affected by the same explanatory variables. Tukey's HSD was applied as a *posthoc* test to determine within-factor differences if any of the above variables were significant ($p < 0.05$). Linear regressions were applied to each damselfish species to test for variation in TP or $\delta^{13}C$ and assess how body size influences trophic diversification.

To estimate the contributions of pelagic versus reef-based sources of primary production, we used Bayesian mixing models from the *simmr* package (Parnell 2016) in R (R Core Team 2017). A two-source model was used with all algal species combined to represent reef-based contribution, whereas zooplankton and POM were pooled for pelagic sources. POM was used as a pelagic source rather than a reef-based source due to the sampling method and the observed $\delta^{13}C$ and $\delta^{15}N$ values (similar $\delta^{13}C$ and $\delta^{15}N$ to planktivorous obligates and zooplankton). For comparative purposes, a separate model was produced using the following food items as independent source materials: zooplankton, POM, red algae, green algae, brown algae, mixed turf, and vagile invertebrates. Correction means (or diet-tissue discrimination factors) were set to 1.62 ‰ for $\delta^{13}C$ and 3.69 ‰ for $\delta^{15}N$. These values were chosen using stable isotope output from obligate consumers relative to food sources. Specifically, correction mean for $\delta^{13}C$ was calculated by subtracting the mean $\delta^{13}C$ values of zooplankton from mean $\delta^{13}C$ values of obligate planktivores (*P. nigromanus* and *Ch. xanthura*). Alternatively, $\delta^{15}N$ correction mean was derived by subtracting the mean $\delta^{15}N$ values of algae (pooled) from mean $\delta^{15}N$ values of the obligate herbivore (*S. vulpinus*). This approach was deemed adequate because obligate consumers demonstrated consistent isotope values relative to the isotope axis ($\delta^{13}C$ or $\delta^{15}N$) pertaining to the animal's known diet regime (i.e., the herbivore had little variation in $\delta^{15}N$ values; the planktivores had little variation in $\delta^{13}C$ values). Correction error was set at a conservative 0.5 ‰ for all diet items based on values calculated by Matley et al. (2016). Matrix plot correlations were used to evaluate if the model had difficulty separating prey sources due to proximity in isospace. Dietary contributions are presented as the range between 25% and 75% credibility quantiles with error bars extending to the maximum and minimal values (97.5% and 2.5%, respectively).

3.4 Results

Trophic diversification among species

The stable isotope biplot of $\delta^{15}N$ and $\delta^{13}C$ values for all organisms showed evident segregation between and within main trophic groups (e.g., algae, zooplankton/invertebrates, and fish; Fig. 3.1). Along the $\delta^{15}N$ axis (equivalent to TP), as expected, fish (damselfish and obligates) had the highest values, followed by primary consumers/producers and algae, respectively. Within each trophic group, $\delta^{15}N$ values had limited variation (i.e., between 1 and 3‰). Greater variation existed along the δ^{13}C axis (i.e., 4 – 7‰) demonstrating a gradient between pelagic-based (e.g., POM and zooplankton; more negative δ^{13}C values) and reef-based (e.g., vagile invertebrates and *Ct. striatus*; less negative δ^{13}C values) input. Specifically for the fishes, the obligate consumers bounded the isotopic extent of the damselfish, again, with greater variation in δ^{13}C values compared to δ^{15}N values.

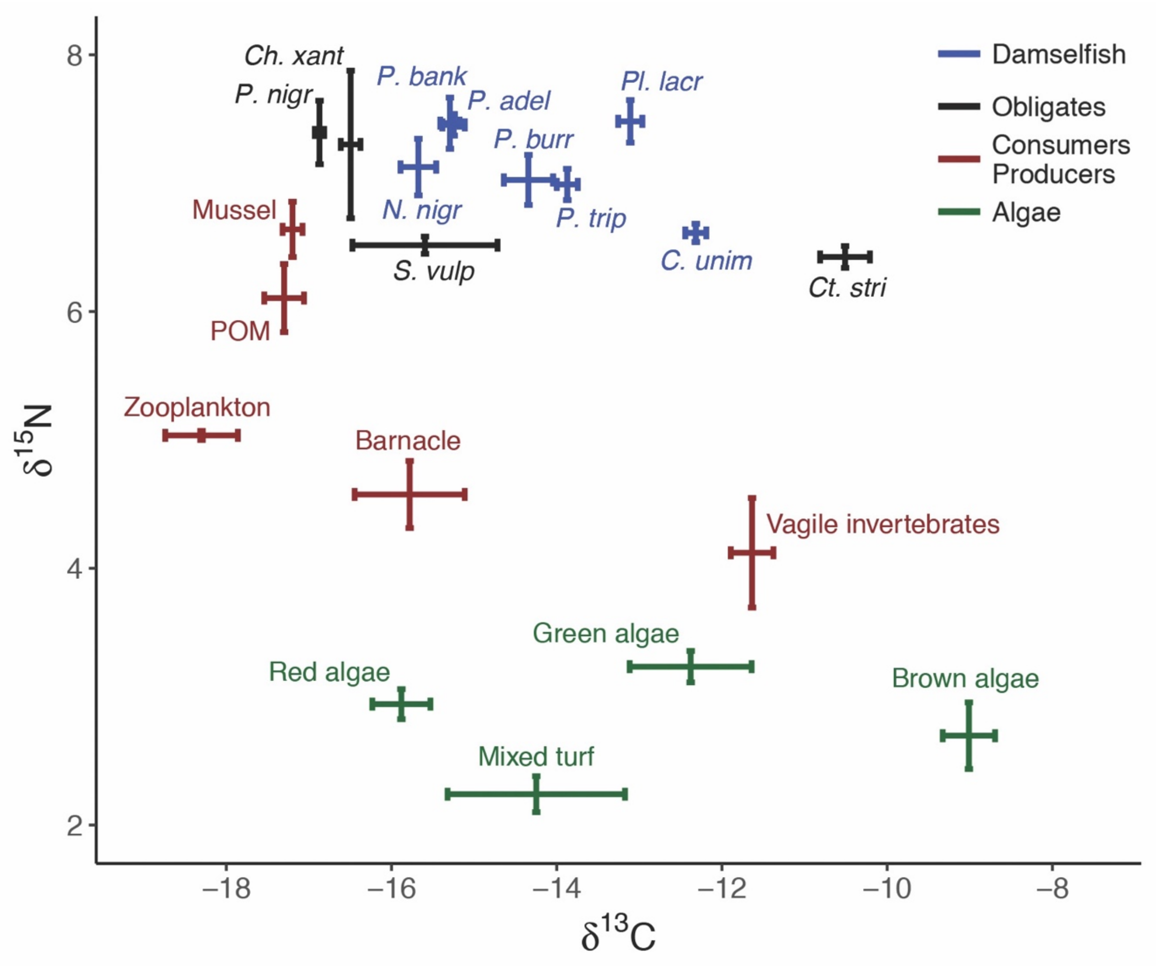

Figure 3.1 δ^{15}N and δ^{13}C (expressed in ‰) signatures of producers and consumers at Kimbe Bay. Data points are group means with error bars representing ± SE. Species abbreviations and sample sizes and are defined in Table 3.2.

To assess the generalization that territorial damselfish are herbivores, a two-source mixing model was used to provide further insight into the proportion of pelagic dietary input compared to that of reef-based contribution. Pelagic sources contributed at least 75% (based on 25 – 75% quantiles and max-min values) of prey for *P. bankanensis* and *N. nigroris*, whereas reef-based sources contributed to the majority of prey for *C. unimaculata* (Fig. 3.2a). Other species were more difficult to resolve within the two-source context because they likely feed on a variety of pelagic and reef-based sources, nevertheless, the mixing model showed *P. adelus* consumed a greater proportion of pelagic prey, while *P. tripunctatus*, *Pl. lacrymatus*, and *P. burroughi* consumed more reef-based prey (Fig. 3.2a). Similar results were found when all prey were analyzed as independent sources; specifically, zooplankton was an important prey source for *P. bankanensis* and *N. nigroris*, and red algae contributed >50% of prey (based on 25 – 75% quantiles and max-min values) to *P. tripunctatus, P. burroughi,* and *C. unimaculata* (Appendix: Fig. S3.1). The mixing model for the obligate consumers verified the results of the present study with prior knowledge. The mixing model indicated high pelagic contribution in the muscle tissue of *Ch. xanthura* and *P. nigromanus*, and high reef-based contribution in *S. vulpinus* and *Ct. striatus* (Fig. 3.2b).

The ANOVA testing whether species, reef, or habitat zone influenced TP or δ^{13}C showed that species (ANOVA, F (6,82) = 3.89, *P* = 0.002) and reef (ANOVA, *F* (1,82) = 12.12, *P* < 0.001) influenced TP values, while only species (ANOVA, *F* (6,82) = 36.41, *P* < 0.001) influenced δ^{13}C values. Trophic position of territorial damselfish at Garbuna was typically higher than at Luba Luba, and TP values of *C. unimaculata* were lower than *Pl. lacrymatus*, *P. adelus*, and *P. bankanensis* (Fig. 3.3a). For δ^{13}C, Tukey’s test showed that *C. unimaculata* and *Pl. lacrymatus* had higher (less negative) values than all other species. Also, *P. tripunctatus* had higher δ^{13}C values than *P. adelus, N. nigroris, and P. bankanensis*. Finally, δ^{13}C values of *P. burroughi* were higher than *N. nigroris* (Fig. 3.3b).

The range in body size and stable isotope values for each damselfish species sampled were small (Table 3.2). Additionally, the influence of body size on both TP and δ^{13}C values were not uniform among species (Appendix: Fig. S3.2). Consequently, linear regressions were calculated separately to determine whether body size affected isotope values at a species level. There was a significant positive relationship between body size and TP values for *P. tripunctatus, P. bankanensis,* and *N. nigroris*. Carbon isotope values did not show any significant relationship with body size for any species (Appendix: Fig. S3.2).

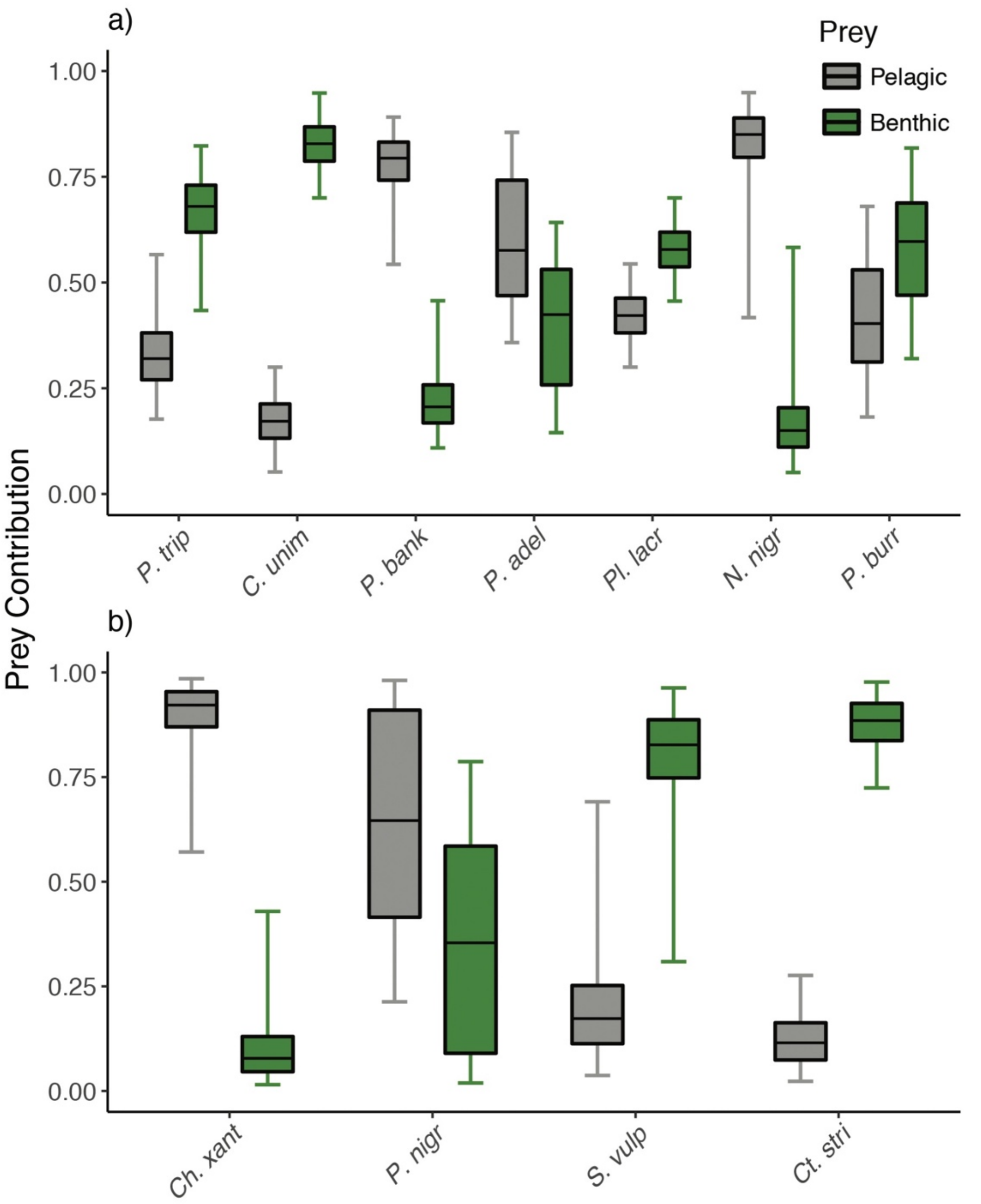

Figure 3.2 Prey contribution of (a) territorial damselfish and (b) obligate consumers from the two-source pelagic (gray) vs. reef-based (benthic; green) mixing model. Box and whisker plot displays the range between 25% and 75% credibility quantiles, with error bars extending to the maximum and minimal values (97.5% and 2.5%, respectively), and the median represented by the bold line. Species abbreviations and sample sizes are defined in Table 3.2.

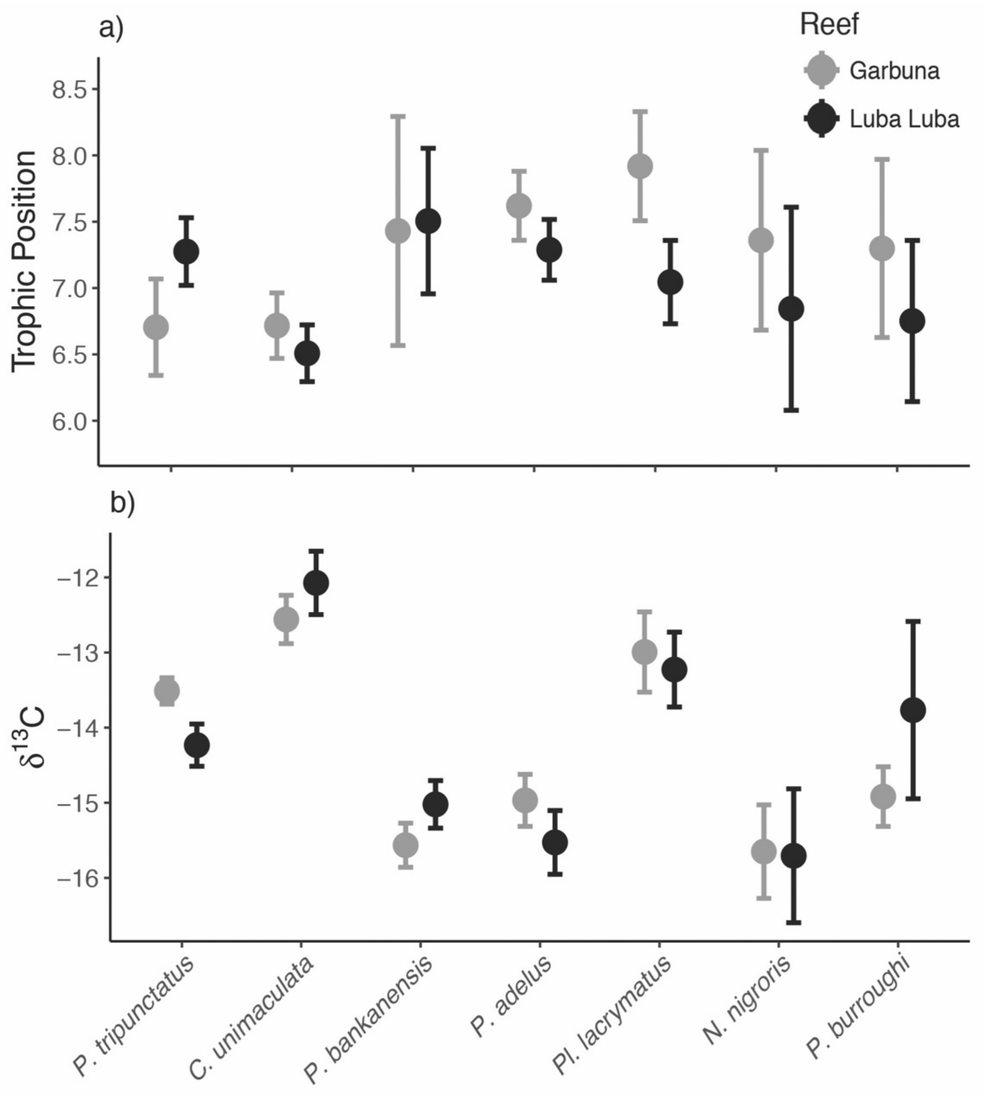

Figure 3.3 Territorial damselfish (a) trophic position and (b) $\delta^{13}C$ (expressed in ‰) signatures between Garbuna (gray) and Luba Luba (black). Data points are group means with error bars representing ± SE. Species abbreviations and sample sizes are defined in Table 3.2. Vertical axes are not comparable.

Trophic partitioning between neighbours

The isotopic biplots of territorial damselfish differed markedly within each of the 3 reef zones (Fig. 3.4a). There were significant differences in isotopic space, with minimal to no overlap among neighbouring species for all but one co-occurring pair (Table 3.3). There was no significant shared isotopic overlap among *Pomacentrus tripunctatus* and *Chrysiptera unimaculata* (0%), the species co-occurring on the back and middle reef flat, respectively. Additionally, on the other distribution boundary of *C. unimaculata* there was no observed isotopic overlap between the 3 neighbouring reef crest species: *C. unimaculata* –

Pomacentrus adelus (0%), *C. unimaculata – P. bankanensis* (0%), and *C. unimaculata – Plectroglyphidodon lacrymatus* (0%). On the reef crest, no significant isotopic overlap was observed between *P. adelus – Pl. lacrymatus* (0%) and *P. bankanensis – Pl. lacrymatus* (0%), although *P. adelus – P. bankanensis* (62%) demonstrated significant isotopic overlap. The ellipses of both *Neoglyphidodon nigroris* and *Pomacentrus burroughi*, the co-occurring reef slope species, were larger than all other damselfish (i.e., ≥95% posterior draws of these species were larger than others), but had limited overlap in isotopic space (13%).

The obligate consumers showed clear trends in isospace reflecting their feeding modes (Fig. 3.4b). Specifically, the planktivorous damselfish, *Pomacentrus nigromanus* and *Chromis xanthura*, showed little variation in δ^{13}C values but a large range along the δ^{15}N-axis with values typically larger than the herbivorous *Siganus vulpinus*. In contrast, *S. vulpinus* exhibited a large range along the δ^{13}C-axis, while δ^{15}N values remained stable across individuals. *Ctenochaetus striatus* was centered at low δ^{15}N and high δ^{13}C within the biplot, distinct from the other obligates.

Table 3.3 Results of pairwise percent niche overlap (gray, top right) and isotopic area overlap (blue, bottom left) of territorial damselfish. Data are the mean of a species (row) relative to another species (column). One cell represents the overlap between the two species. Species are in order of distribution from the back of the reef flat to the reef crest and down the reef slope from left to right and top to bottom. Neighbouring species are shaded darker (dark gray and dark blue) to highlight ecologically important pairs. Species abbreviations and sample sizes and are defined in Table 3.2.

Percent niche overlap

Overlap area (‰^{2})

	P. trip	*C. unim*	*P. bank*	*P. adel*	*Pl. lacr*	*N. nigr*	*P. burr*
P. trip		0%	0%	0%	4%	0%	61%
C. unim	0		0%	0%	0%	0%	0%
P. bank	0	0		62%	0%	59%	15%
P. adel	0	0	28		0%	50%	7%
Pl. lacr	3	0	0	0		0%	14%
N. nigr	0	0	68	26	0		13%
P. burr	57	0	19	4	19	25	

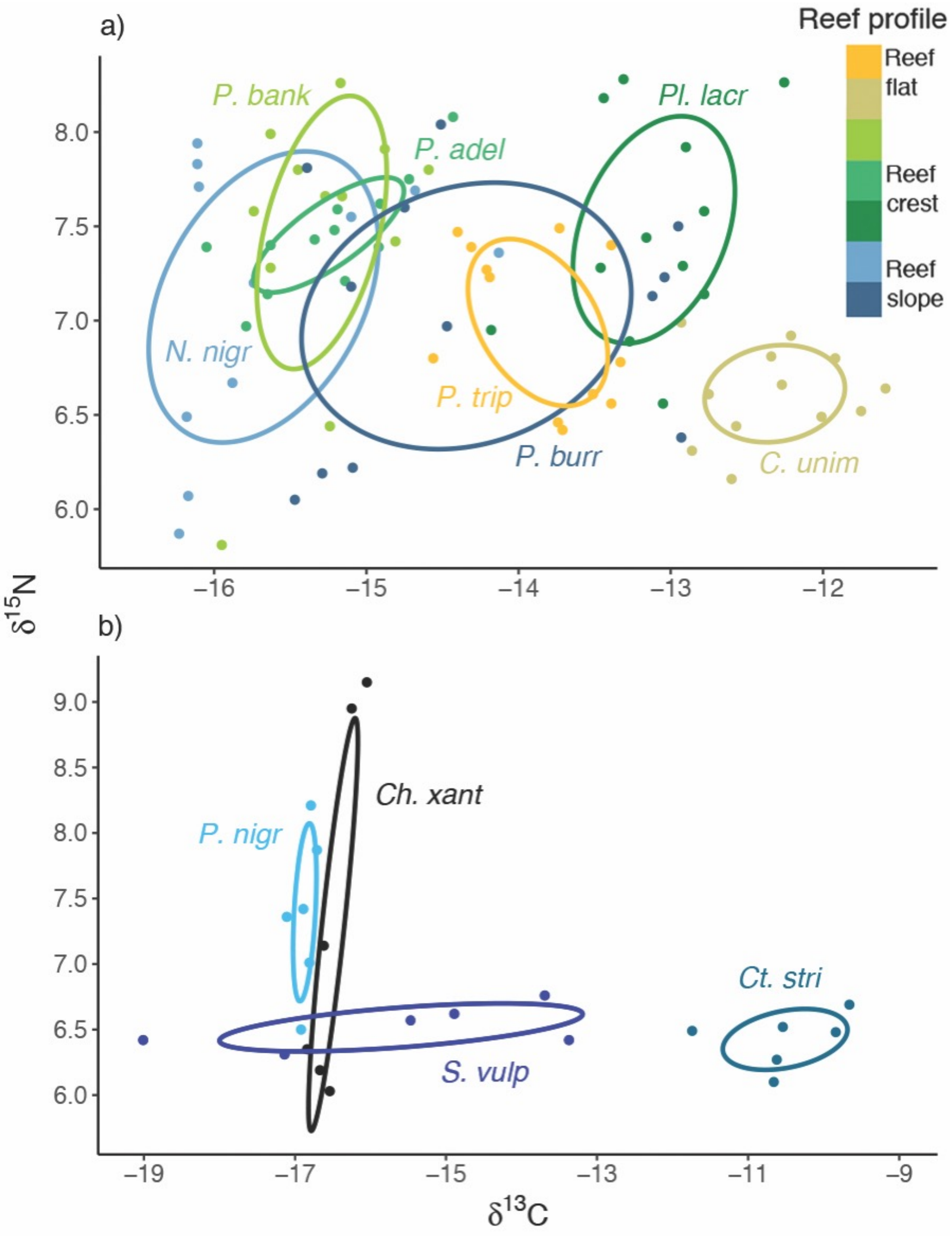

Figure 3.4 Isotopic niche overlap for (a) territorial damselfish and (b) obligate consumers as a reference considering their known feeding patterns. Standard ellipse area (SEA_C) is depicted by a solid line with $\delta^{15}N$ and $\delta^{13}C$ values expressed in ‰. Territorial damselfish (a) are coloured to match the distribution patterns along the reef profile gradient – reef flat (orange/yellow), reef crest (green), and reef slope (blue). Obligate consumers (b) are not coloured to the reef profile gradient. Species abbreviations and sample sizes are defined in Table 3.2. Horizontal and vertical axes are not comparable.

3.5 Discussion

This study provides evidence for high levels of trophic diversification and niche partitioning in a guild of territorial damselfish on a high-diversity coral reef. The isotopic biplots of all 7 territorial damselfish differed in $\delta^{15}N$ and $\delta^{13}C$ values. The isotopic distributions were linked to distribution patterns along the reef profile gradient – reef flat, reef crest, and reef slope. Where the distribution of species overlapped, these species were characterised by differences in source contributions. Adjacent species exhibited high to intermediate trophic niche partitioning when examining pelagic versus reef-based (benthic) dietary sources. We argue diet plays a supplementary role to habitat partitioning and competition in reinforcing the patterns of spatial partitioning and coexistence among ecologically similar species. In addition, our research also demonstrates the importance of considering interspecific differences when categorizing a guild of species to a single functional classification. We support prior evidence that territorial damselfish act as omnivorous generalists, with potentially opportunistic diets and feeding plasticity.

Damselfishes, including known planktivores, corallivores, and territorial herbivorous species, have been previously assigned to three trophic groups based on feeding strategies: *pelagic feeders* zooplanktivores, *reef-based feeders* corallivores, algivores or herbivores, and an *intermediate group* omnivores (Frédérich et al. 2009, 2016, Gajdzik et al. 2016). While comparative studies have not focused solely on territorial damselfish, a similar trophic diversity was observed within the guild of territorial damselfish in the present study. The trophic diversity within this group was much higher than expected based on the literature. Territorial damselfish are commonly classified as herbivorous or omnivorous (Ceccarelli et al. 2001, Frédérich et al. 2016). However, we found evidence of planktivory within the guild. While this is not unique for pomacentrids, as damselfish (e.g., Chrominae) have served as a model for this trophic strategy (Frédérich et al. 2013), territorial damselfish have not previously been described as pelagic feeders. Through the integrated perspective of trophic role provided by stable isotopes, the present study documents *Pomacentrus bankanensis* and *Neoglyphidodon nigroris* as pelagic feeders (supporting prior J. G. Eurich pers. obs.) under the suggested criterion of a species to consume ≥70% zooplanktonic prey or filamentous algae to not be considered an intermediate omnivore (Frédérich et al. 2016). This designation is supported based on similar trends in isospace as the obligate planktivores *Pomacentrus nigromanus* and *Chromis xanthura*. Both *P. bankanensis* and *N. nigroris* were previously described as herbivores and benthic feeders under the intermediate trophic grouping (see

Table 3.1; Hata and Ceccarelli 2016). The present study represents the first isotopic values for these species and highlights the need for species-specific evidence when assigning a species to broad taxa-related functional classifications.

Based on the isotope values and source-based mixing models, only one of the seven territorial damselfish species, *Chrysiptera unimaculata*, can be defined strictly as a reef-based (benthic) feeder and none were specialized herbivores. Our evidence supports a comparable isotopic study from Madagascar (Frédérich et al. 2009) and gut content analysis from the same region as the present study, Kimbe Bay (Ceccarelli 2007). However, while we define the species as a reef-based feeder, we explicitly do not provide evidence for this species to be classified functionally as an algivore (as in Frédérich et al. 2009). Instead, based on prior literature and the isotopic values (prey source not directly sampled), we argue the species primary source of nutrients is detritus. In addition to detritus comprising ~65% of the stomach content for *C. unimaculata* in a prior study (Ceccarelli 2007), the isotopic values in the present study are consistent with *Ctenochaetus striatus*, a known detritivore (Tebbett et al. 2017a). Consequently, the broad trophic groups traditionally used to classify reef fishes need to be refined and subdivided to reflect differences in ecosystem function as new methodology is established (e.g., Brandl and Bellwood 2014, Pratchett et al. 2016, Tebbett et al. 2018).

The intermediate group, also considered generalists or omnivorous, are comprised of species that consume planktonic and benthic copepods, detritus, small vagile invertebrates, and filamentous algae (Kramer et al. 2013, Frédérich et al. 2016, Hata and Ceccarelli 2016). Our research confirms the paradigm from recent literature (see Table 3.1) that the majority of territorial damselfish conform to this grouping. In the present study, four species belong to the intermediate feeding strategy: *Pomacentrus tripunctatus, Pomacentrus adelus, Pomacentrus burroughi*, and *Plectroglyphidodon lacrymatus.* While the resolution of stable isotopes does not provide dietary information at the prey species-level (i.e., to corroborate vagile invertebrates; Ceccarelli 2007, Kramer et al. 2013), the four species exhibited distinct isotope ratios for C and N. We argue the four species are omnivorous with a diet comprising zooplankton, detritus and local, benthic prey. Cecarelli (2007) found *P. tripunctatus, P. adelus,* and *P. burroughi* were generalists feeding on detritus, corticulated algae, and filamentous algae in (almost) equal proportions, with *Pl. lacrymatus* acting as a specialist consuming microalgae. While Ceccarelli (2007) found no evidence for pelagic derived materials, this was likely a limitation of gut content analysis. Furthermore, only the diet of *Pl. lacrymatus* has been previously examined through stable isotope analysis (Frédérich et al.

2009, Gajdzik et al. 2016). The discrepancies in diet at the species-level between studies within the intermediate group can also be linked to opportunistic feeding. Frédérich et al. (2009) documented planktivorous species shifting to demersal fish eggs to opportunistically exploit nutrient-rich food. Similarly, species with reef-based diets, including *Pl. lacrymatus* (Kuo and Shao 1991), occasionally switch exclusively to coral propagules in the water column during mass coral spawning events (Pratchett et al. 2001, McCormick 2003). While damselfish are known to feed opportunistically, the explicit partitioning of resources is a key factor in promoting the coexistence of closely related and otherwise ecologically equivalent species (Robertson and Lassig 1980, Waldner and Robertson 1980).

Ecological partitioning of distinct non-overlapping spatial distributions of damselfish along the reef gradient has been well documented globally (Bay et al. 2001, Ceccarelli 2007, Medeiros et al. 2010, Chaves 2012). At Kimbe Bay the seven species of territorial damselfish partition space along the reef profile gradient with each species restricted to subzones of just a few meters wide. Eurich et al. (2018a) found that the species distributions were linked to levels of microhabitat selectivity and aggression between species. Further, through the use of a large-scale removal experiment, it was demonstrated that both direct and indirect competition among neighbouring species helps to maintain the population boundaries (Eurich et al. 2018b). The present study provides additional evidence of trophic niche partitioning between adjacent species reinforcing the patterns of coexistence. The diets of co-occurring territorial damselfish within each of the 3 reef zones differed markedly with the (1) reef flat comprising a reef-based omnivore *P. tripunctatus* and detritivore *C. unimaculata*, (2) reef crest comprising a planktivore *P. bankanensis*, pelagic-based omnivore *P. adelus*, and a reef-based omnivore *Pl. lacrymatus*, and (3) reef slope comprising a planktivore *N. nigroris*, and a reef-based omnivore *P. burroughi*. This level of partitioning may reflect the high species diversity of territorial damselfish within the region. Previous work has clearly shown that pomacentrids can partition food types along various functional axes of their niches that relate to biological, ecological, and environmental factors (Frédérich et al. 2009, 2014, Gajdzik et al. 2016), but did not demonstrate differences in the trophic ecology among territorial damselfish. Kimbe Bay's high richness likely drives the need for ecological diversification within the guild of territorial damselfish (Gajdzik et al. 2018).

The dietary diversification observed is likely refined by differences in ecological versatility between adjacent species. While opportunistic feeding has been previously documented (as discussed above), neighbouring territorial damselfish individuals exploited different feeding strategies over long-term diet trends during mutually inclusive time periods. Bearhop et al. (2004) discriminated between different types of generalists within a population, with species either all taking a wide range of food types (type A) or specializing in a different but narrow range of food types (type B). The large variation of $\delta^{13}C$ values with little difference in trophic position in the present study could be related to perpetual intra-population variability in prey choice (i.e., type B), thus facilitating coexistence (Frédérich et al. 2016). For example, the pelagic feeding species, *P. bankanensis* and *N. nigroris,* are within each respective neighbouring species habitat space (i.e. reef zone and microhabitat use; Eurich et al. 2018a), but by foraging in the water column on pelagic resources competition is reduced. The generalist and flexible feeding strategies observed in this guild likely support the coexistence of multiple territorial damselfish species within a coral reef zone.

While this study focuses on adults due to the strong territorial interactions and spatial partitioning of adult territorial damselfish species (Bay et al. 2001, Ceccarelli 2007, Eurich et al. 2018a), it is notable that ontogenetic shifts in diet have been observed for pomacentrids and other fishes. Damselfishes mainly consume pelagic copepods during the larval phase and switch to benthic invertebrates and algae upon settlement (see Sampey et al. 2007). Further, some species shift between pelagic and reef-based foraging strategies from the juvenile to adult stage. Thus, for the purposes of determining dietary overlap and niche widths among species with known small-scale distribution differences, only adult individuals were used in the present study. While we observed a significant positive relationship between body size and TP values for *P. tripunctatus*, *P. bankanensis*, and *N. nigroris*, no significant relationship was found between carbon isotope values and body size for any species. Ontogenetic niche shifts can also lead to intraspecies variation between co-occurring individuals when sampling at different life history stages (Araújo et al. 2011). In Kimbe Bay territorial damselfish juveniles and adults occupied similar distributions within the reef profile but more sampling is required to empirically corroborate the findings of Araújo et al. (2011) and assess if ontogenetic size-related shifts or intraspecies variation is occurring (Frédérich et al. 2016). Explicit spatial and temporal sampling (e.g. multiple tissues and sampling periods) is required to further explore how feeding regimens and diet assimilation change within a species.

Conclusions

We demonstrate that trophic niche partitioning contributes to fine-scale partitioning of space within reef zones and the limited distributional overlap of species on a high-diversity coral reef. Evidence presented here suggests neighbouring species utilise different feeding strategies that may facilitate coexistence. Dietary diversification, with microhabitat selectivity, likely minimises direct and indirect competition for space, potentially a limiting factor on coral reefs. Despite territorial damselfish typically being described functionally as intermediate omnivores or herbivores, we found novel evidence of pelagic-based feeding within the guild through stable isotope analysis. These findings add to a growing view that interspecific differences among similar species are lost when categorizing species into broad functional classifications, and that previous studies suggesting that territorial damselfish are strictly reef-based feeders may not be applicable in all systems or for all species.

Chapter 4

Direct and indirect effects of interspecific competition in a highly partitioned guild of reef fishes

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4.1 Summary

Competitive interactions and resource partitioning facilitate species coexistence in complex ecosystems. However, while pairwise interactions between ecologically similar species have been well-studied, multi-species competitive networks have received less attention. When interference competition between two species results in partitioning of resources, this may have indirect consequences for other species distributed along the same resource gradient. Here we tested whether interference competition between two territorial damselfish influenced the fine-scale species distributions of five other territorial damselfish in Kimbe Bay, Papua New Guinea. These species partition habitat across three reef zones - the flat, crest, and slope, with distinct patterns of distribution within these zones. We predicted the two species with similar distributions and microhabitat use, *Pomacentrus adelus* and *P. bankanensis,* would display the greatest level of aggression towards one another. This was tested through an intruder-experiment where stimulus fish were introduced into a resident's territory, which confirmed disproportionately high levels of interspecific aggression between these two species. We also predicted that the fine-scale differences in the distribution of each species were maintained through multi-species interference competition among neighbouring species, with further indirect effects on species that did not directly interact. To test this, we conducted a large-scale (22 m x 10 m) experimental removal of the most abundant species, *P. adelus*, and quantified the abundance and distribution of all territorial damselfish species for 6 months to a 25 cm resolution. The main direct competitor, *P. bankanensis*, exhibited a marked increase in abundance and expanded its distribution (+1.33 m) to acquire the space previously occupied by *P. adelus*. This competitive release triggered indirect effects on the distribution of other neighbouring species further back on the reef flat, with *Chrysiptera unimaculata* moving into the zone formerly occupied by *P. bankanensis*. This study indicates

that the distinct distribution patterns among the reef crest species are linked to levels of interspecific agonistic behaviour. We argue that the competitive release following the removal of a superior competitor resulted in both direct and indirect effects, with the immediate neighbour shifting into the newly available space, followed by successive shifts in species responding to the change in the distributions of their immediate neighbours.

4.2 Introduction

Competitive interactions among ecologically similar species are fundamental in shaping many ecological communities (Connell 1978, Schoener 1983). In structurally complex ecosystems (e.g., tropical forests and coral reefs), each species occupies an ecological niche in which it is the most effective competitor (Whittaker et al. 1973). Traditionally, interspecific competition for finite resources was viewed in terms of a winner and a loser with the dominating species either partitioning or eliminating the subordinate from the habitat (Case and Gilpin 1974, Colwell and Fuentes 1975, Diamond 1978). Ecological theory has progressed from a focus on pairwise interactions to a multifactorial perspective of the processes and mechanisms that govern competition within a community (Jones 1991, Hixon et al. 2002, Wiens et al. 2010, Pereira et al. 2015). However, experimental studies on interspecific competition are still dominated by studies testing the effects that pairs of species have on one another (Bonin et al. 2015). Hence, our empirical understanding of competitive networks has been limited by the absence of detailed information on the extent of resource partitioning and competition at a community scale, and the effects of interactions among species that do not come into direct contact (Amarasekare 2003, Salomon et al. 2010, Siepielski and McPeek 2010, Hixon 2011).

When resources are limited, theory holds that species may coexist by partitioning resources via e*xploitative competition* (depletion of a common resource) or *interference competition* (aggressive interactions that prevent access to a resource) (Case and Gilpin 1974, Schoener 1983). While competition theory is largely based on exploitative competition among sympatric species (Amarasekare 2002), interference competition is the main mechanism leading to interspecific differences in patterns of distribution or use of resources. There is ample empirical evidence that interference competition influences the abundance or distribution of subordinate species for insects (Kunte 2008), birds (Pimm et al. 1985), mammals (Brown 1971), and fishes (Robertson and Gaines 1986, Munday et al. 2001, McCormick and Weaver 2012). In nature, interference competition is linked to interspecific territoriality and aggressive interactions among species that regularly come into contact, with the most aggressive species gaining priority access to resources (Grether et al. 2013). Experimental removals of dominant species invariably result in niche expansion of inferior competitors (Paine 1966, 1974, Robertson 1996, Kunte 2008). Species in the community that do not openly share a resource or compete may be indirectly linked by species that lie between them on a resource axis. Hence, when interference competition between two species results in a partitioning of resources, this may have indirect consequences for other species distributed along the same resource gradient.

In community ecology, indirect or knock-on effects are most often observed as cascading effects between trophic levels, as a result of predator-prey, plant-herbivore interactions. Indirect effects, generally defined as how ‘one species alters the effect that another species has on a third’, can include a multitude of phenomena where the presence or density of a species influences the community (reviewed by Strauss 1991). The most well-known aquatic examples include the removal or extinction of keystone predators, triggering subsequent competitive exclusion (Paine 1966, 1974) or an ecosystem shift (Hughes 1994, Dayton et al. 1998). Changes to important trophic links between two species can indirectly alter the distribution and abundance of species between trophic levels. However, they can also have indirect effects on interactions among species within the same trophic levels (Pace et al. 1999, Shurin et al. 2002). Similar knock-on effects of subordinate competitors within trophic levels may be present after the collapse of a primary competitor and have received much less attention (Navarrete et al. 2000, Gosnell and Gaines 2012).

Coral reefs are composed of a complex network of hard corals that support rich communities of fish. Historically, the role of interspecific competition and niche partitioning in explaining the coexistence of many ecologically similar coral reef fishes was controversial. While early ecologists emphasised niche partitioning (e.g. Smith and Tyler 1972, Robertson and Lassig 1980), Sale (1977, 1978, 1980) provided evidence that competition for space was more of a lottery, with stochastic recruitment preventing any one species from excluding others. The underlying assumption of intense competition for space was later challenged, and for many years the idea that reef fish communities were limited by recruitment prevailed in the literature (Doherty 1983, Doherty and Fowler 1994). Nevertheless, researchers have continued to address basic ecological interactions such as competition and predation (see reviews by Hixon 1991, Jones 1991, Hixon and Webster 2002, Jones and McCormick 2002, Forrester 2015, Hixon 2015). Several decades of research have generated a substantial amount of evidence that limited available habitat can result in competitive interactions, which in turn influences the structure of reef fish communities (e.g., Robertson 1996, Holbrook and Schmitt 2002, Forrester et al. 2006, Boström-Einarsson et al. 2014). Further, interactions among interspecific competitors plays an important role in reef fish spatial distributions (Robertson and Gaines 1986, McCormick and Weaver 2012). However, the majority of evidence for mobile reef fish species has involved measuring pairwise interactions experimentally and not expanded competitive networks within a community (see reviews by Forrester 2015, Bonin et al. 2015). Few studies have documented competitive interaction networks between species with similar resource requirements.

In reef fish ecology removal experiments can be used to measure the effect of a species on its environment at a community scale. Studies have demonstrated that the selective removal of fishes from a habitat is followed by a redistribution of conspecific (Williams 1978, Webster and Hixon 2000, Meadows 2001) and heterospecific (Belk 1975, Sale 1978, 1979, Robertson and Gaines 1986, Robertson 1996) neighbouring species. Of the studies that demonstrated heterospecific acquisition of space following the removal of a dominant competitor, few studies examined more than one competitor within the community (but see, Sale 1978, 1979, Robertson and Gaines 1986, Robertson 1996). Additionally, most studies have used field experiments to measure variation in the strength of competition spatially, but few expand on this to look at how species respond over time (Schmitt and Holbrook 2007, Forrester and Steele 2008, Hixon et al. 2012). By examining how species recover after a selective removal we can address how and if competitive interactions and recruitment interacts.

Guilds of territorial damselfish (Pomacentridae) provide ideal model systems for understanding the outcomes of competition. Territorial damselfish play an integral role in the structure of coral reefs through their abundance and role as small-bodied consumers (Hata and Kato 2004, Ceccarelli et al. 2005b, Jones et al. 2006). For most species, ecological parameters, or the measurable niche properties whose value is a determinant of the ecosystem characteristics, can be effectively obtained due to their highly site attached habits, territorial behaviours, and lack of concern for observer presence (Ceccarelli et al. 2005a, Ceccarelli 2007). Furthermore, patterns of distribution and partitioning of space along the natural reef profile gradient - the reef flat, reef crest, and reef slope, have been well documented (Robertson and Lassig 1980, Waldner and Robertson 1980, Meekan et al. 1995). A distinctive pattern of zonal distribution along this steep physical gradient provides an experimentally tractable system for isolating the direct and indirect effects of any one species on all others occupying the same resource gradient.

In the present study, we explore the direct and indirect effects of agonistic interactions and interference competition on distribution and abundance in a guild of seven territorial damselfish. At our study location (Kimbe Bay, Papua New Guinea) these species partition the reef flat, reef crest and upper reef slope habitats on a fine scale (1 – 2 m) (Ceccarelli 2007, Eurich et al. 2018a). All species are aggressive and defend discrete territories (mean 1 – 1.5 m^2 territory sizes per individual) against conspecifics, interspecific competitors, and other benthic feeding fishes (Ceccarelli 2007, Eurich et al. 2018c). Eurich et al. (2018a) found that neighbouring damselfish constrain their microhabitat use to facilitate the co-habitation of reef zones, but that microhabitat selectivity alone was insufficient in explaining the distinct zonation and limited distributional overlap. Additionally, it was suggested that interspecific aggression helps maintain the distributional boundaries between neighbouring species. Two abundant species, *Pomacentrus adelus* and *Pomacentrus bankanensis*, have overlapping distributions with similar microhabitat use and selectivity. The partitioning raises the question of whether the presence of *P. adelus* alters the abundance and distribution of *P. bankanensis* and other species within the community. However, an experimental removal of a dominant competitor is necessary to see if interference competition is present and if subordinate distributional shifts would occur.

Here, we employ an observational experiment and a manipulative field experiment to examine the intensity of agonistic interactions among species and the extent to which *P. adelus* influences the distribution and abundance of neighboring and non-neighboring species in the guild. To test which species *P. adelus* is most likely to competitively influence, we conducted an intruder-experiment to measure aggression. We hypothesised: 1) *P. adelus* and *P. bankanensis,* the co-inhabiting species with similar microhabitat use, would display the greatest levels of aggression to each another compared to other neighbouring species. We then evaluated the direct and indirect effects of a competitive release from *P. adelus* on the distribution and abundance of other species in the guild using a long-term experimental removal of *P adelus.* Spatial patterns of all territorial damselfish were described down to a resolution of 25 cm prior to the experimental field manipulation and continuously thereafter for 6 months. Post-removal we predicted: 2) *P. bankanensis* would increase in abundance and expand its distribution to acquire the previously occupied space; 3) Adjacent reef flat species would also increase in abundance and spatially shift towards the preferred habitat due to *P.*

bankanensis having the ability to occupy the reef crest; and 4) The larger reef crest occupying species, *Plectroglyphidodon lacrymatus*, and the two species associated with the reef slope, *Neoglyphidodon nigroris* and *Pomacentrus burroughi*, would be unaffected due to lack of resource overlap.

4.3 Methods

Study location and species

The study was conducted on inshore platform reefs in Kimbe Bay, West New Britain, Papua New Guinea (Fig. 4.1; 5˚30' S, 150˚05' E) between July 2015 and March 2016. Kimbe Bay lies within the Indo-Australian Archipelago (IAA; Coral Triangle), a region recognised for exceptionally high diversity of fish and corals (Roberts et al. 2002). Extensive preliminary surveys were conducted in the Tamare-Kilu reef sector to find reefs with similar aspect and topography. All work, including quantifying the intensity of agonistic interactions and a removal experiment, was conducted on two reef locations (Garbuna and Luba Luba; Fig. 4.1). The observational experiment and the manipulative field experiment were executed on different areas of the reefs to assure individuals were not manipulated twice. Study sites were located on sections of reef with non-exposed reef flats, an unbroken and continuous reef crest, and steady non-vertical reef slopes to >10 m. Although sections of the reef flat break the surface, the tidal range here is relatively small (1 m) and the study locations were not exposed at low tide.

The seven species of benthic associated territorial damselfish found in Kimbe Bay are found along a gradient that extends from the reef flat to the reef crest and down the reef slope in the respective order (maximum size from Kimbe Bay, J. G. Eurich, unpubl. data); *Pomacentrus tripunctatus* (9 cm), *Chrysiptera unimaculata* (7 cm), *Pomacentrus bankanensis* (7 cm), *Pomacentrus adelus* (7.5 cm), *Plectroglyphidodon lacrymatus* (10 cm), *Neoglyphidodon nigroris* (10 cm), and *Pomacentrus burroughi* (8 cm). The study species occupy a similar ecological niche and rely on microhabitats that mainly consist of dead coral fragments (rubble), sediment or detritus, and filamentous algae (Ceccarelli 2007, Eurich et al. 2018a).

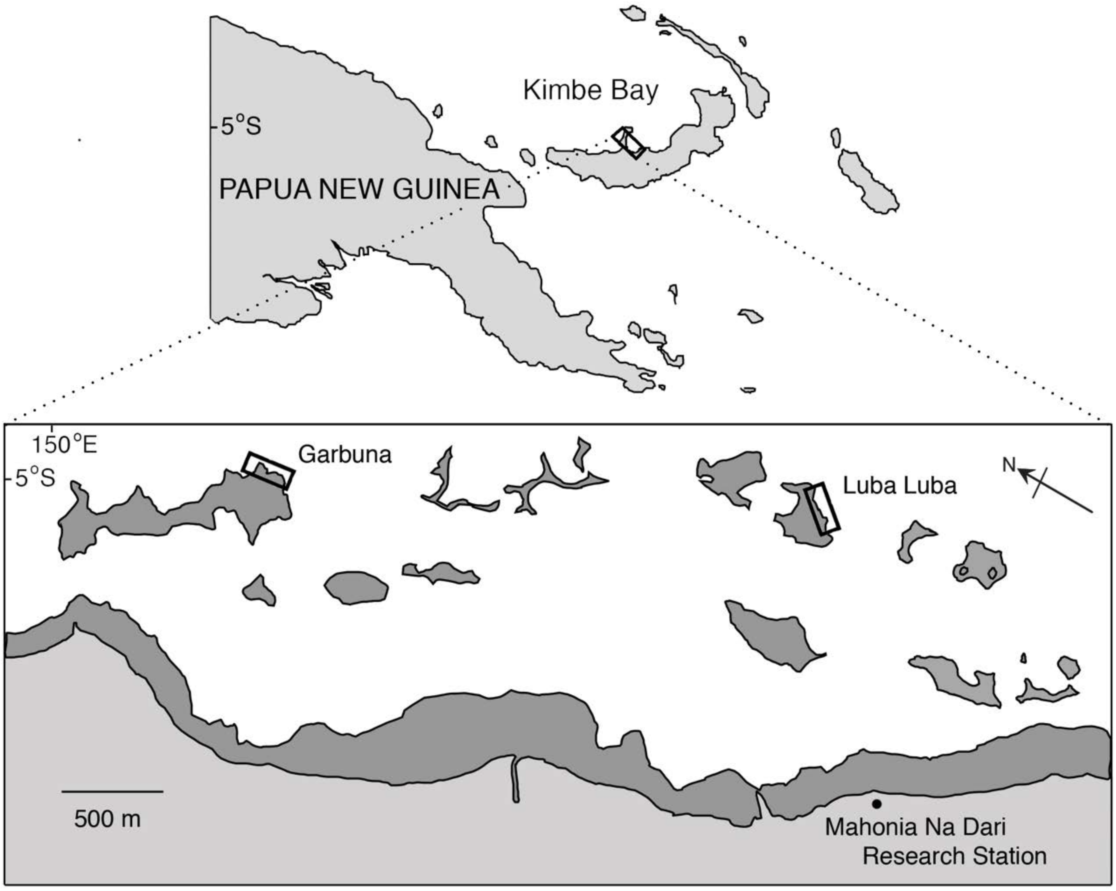

Figure 4.1 Map showing the location of Kimbe Bay, West New Britain, Papua New Guinea and study locations (Garbuna and Luba Luba) within the Tamare-Kilu reef sector.

Levels of interspecific aggression

Levels of aggression can be an indicator of the intensity of interference competition, with species competing for similar resources likely to be more aggressive towards one another. Eurich et al. (2018a) reported that conspecifics and neighbouring species at the study site elicited significantly higher aggression, compared with heterospecific and non-adjacent species, and that levels of aggression were higher on the reef crest. Here we employed a "bottle" experiment, where a stimulus individual is experimentally introduced into a residents territory (Myrberg and Thresher 1974, Bay et al. 2001, Osório et al. 2006), to quantify levels of aggression among species to predict the competitive influence of *P. adelus,* the most abundant species on the reef crest (Eurich et al. 2018a). The aim was to quantify levels of *P. adelus* aggression towards potential competitors, the six damselfish, and the reciprocal levels of aggression of potential competitors towards *P. adelus*. Stimulus fishes were captured using an anaesthetic and hand nets and kept in a holding tank for 15 – 30 min prior to use to regain normal behaviour. First, to elicit aggression, a stimulus individual was placed in a 9 L seawater-filled weighted transparent bag inside a *P. adelus* territory (following Bay et al. 2001) and the intensity of responses by *P. adelus* towards the stimulus were quantified. Second, bagged *P. adelus* were introduced into the territories of the six potential competitors and the intensity of responses towards *P. adelus* were quantified. A control treatment, in which each response fish was presented with an empty bag, was also applied. After observing the resident species for 4 – 5 min to establish the territorial boundaries, the stimulus bags were introduced into the centre of the territory and secured to the substratum. The frequency and intensity of responses were recorded for 5 min (following the aggressive categories used in Eurich et al. 2018a; displays, charges, and bites). Each replicate was conducted using a different resident fish. To obtain aggression estimates for the different combinations of stimulus (six competing damselfish, *P. adelus*, and an empty bag control) and resident treatments, each resident was exposed to each type of stimulus 10 times. Negligible interactions were made towards the control stimulus, so it was omitted from analyses (0.02 mean interactions per trial).

Aggression trials were analysed separately by resident species using a generalised linear mixed effects model. The distribution of the response variable (count of aggressive interactions: representing the summation of displays, charges, and bite attempts) was significantly different from normality (Kolmogorov–Smirnov test, $p < 0.05$) due to frequent low intensity aggression and minimal high intensity aggression for some species. Therefore, the parameter estimates, coefficients, and 95% likelihood profile confidence intervals for the model were fitted using a negative binomial family for overdispersion (using Pearson goodness-of-fit as the dispersion statistic). Location (reefs: Garbuna and Luba Luba) was considered a random factor in the mixed model. Differences in levels of aggression towards stimulus species were tested using Tukey’s HSD.

Removal experiment

To examine whether the removal of a dominant species affected the spatial distributions of neighbouring species, we conducted a controlled large-scale experimental removal of *Pomacentrus adelus*. Two plots, a removal (treatment) and control, measuring 22 m in length from the reef flat to the upper reef slope and 10 m wide (220 m^2 total monitoring area per plot), were established on each of the two reef locations (Garbuna and Luba Luba). The paired removal and control plots were set approximately 75 m apart, with the plot treatment type assigned randomly. The plots (removal: $n = 2$; control: $n = 2$) were spaced to ensure they were independent and sized so as to include the total habitat distribution limits of *P. adelus*. Territorial damselfish are highly site attached with home ranges ~1 to 2 m^2 (reviewed by Ceccarelli et al. 2001), so all fish observed on the grid were residents. To facilitate the census of fishes, individual plots were divided with permanent nylon strings and metal rods into eleven 2 m x 10 m contiguous transects forming rectangles that stretched parallel to the reef crest. Additionally, each nylon string was visibly marked at 2 m intervals creating a 2 m x 2 m grid throughout. All plots were established around the existing *P. adelus* distribution with roughly 12 m of reef flat and 10 m of reef slope on either side of the central reef crest. In the present study we refer to this lower area as the reef slope, but acknowledge it is the upper section of this habitat.

All individuals of *P. adelus* were speared from the two removal plots and along a 5 m buffer around the plot to limit immigration into the census plots. A total of 321 and 275 individuals were removed over a 1 day period from the two removal plots. There was no immigration into the experimental plots from *P. adelus,* but other adult species moved freely into the plot from bordering territories. Following the removal, no further *P. adelus* were disturbed or removed and natural recruitment was permitted. Control plots were artificially disturbed with divers emulating removal techniques and swimming patterns.

The abundance and distribution of damselfish were quantified, both before and after the removal, down to a resolution of 25 cm with the use of the spatial grids. Fish were censused over the gridded area at high tide and each fish was identified to species, placed into a developmental category (recruit, juvenile, medium adult, and large adult), and its position was plotted on a scaled map. Individual fish positions were then entered as coordinates for analysis. Territorial damselfish were censused three times pre-removal and five times post-removal. ‘Pre’ observations were made on alternating days prior to the removal (pre 1: 5 days prior; pre 2: 3 days prior; and pre 3: the day of removal or time 0), with the final pre-removal survey occurring directly before the removal. ‘Post’ observations were conducted the following morning (post 1 day), and consecutively thereafter: post 3 days, post 1 week, post 3 months, and post 6 months.

To examine differences in abundance after the removal, species were separately tested for unequal distribution between time period (fixed continuous factor), after accounting for differences between location (random factor: Garbuna, Luba Luba) using a repeated measures analysis of variance (ANOVA) and a generalised linear mixed effects model with Poisson distribution. A conservative test for compound asymmetry was used for ‘‘time’’ to address the auto-correlated nature of time series data. The three pre-removal surveys were treated as nested replicates (n = 3) within the pre-removal time category. The pre-removal abundances were then compared to the post-removal abundances for each time period using Tukey's post-hoc pairwise comparisons of levels within significant factors to assess changes in abundance over time. Recruits (<1 cm) of all species (other than *P. adelus*, which was analysed separately) were omitted from the final analysis due to irregular recruitment pulses and high mortality.

Coordinate data within the spatial grids were used to determine if other species would shift their distributions to acquire the space previously occupied by *P. adelus*. For each survey period (pre-removal and 6 months post-removal) species' abundances were binned into 1 m increments from the reef flat to the reef slope (1 m x 10 m contiguous rectangles, n = 22) parallel with the reef crest for presentation. A two-sample Kolmogorov-Smirnov test (K-S) was used to determine if the two distributions significantly differed. The mean centre of each population pre-removal was calculated and compared graphically to 6 months post-removal to quantify movement over time. Replicate pre-removal surveys were used to estimate natural spatial variability.

4.4 Results

Levels of interspecific aggression

The intruder-experiment confirmed the presence and asymmetry of aggression between *P. adelus* and the other six territorial damselfishes. The levels of aggression *P. adelus* displayed against *P. bankanensis* were significantly higher than any other stimulus species (8.5 mean interactions per trial; Tukey's HSD, p = 0.001) (Fig. 4.2a). Reef flat species, *P. tripunctatus* (2.3 mean interactions per trial) and *C. unimaculata* (4.2 mean interactions per trial) received lower levels of aggression when compared to *P. bankanensis* (Tukey's HSD, p = 0.008, and p = 0.026 respectively). While *P. adelus* displayed some aggression towards all stimulus species, less aggression was observed in trials with *Pl. lacrymatus* (1.9 mean interactions per trial; Tukey's HSD, p = 0.004) and the reef slope associated species, *N. nigroris* (2.3 mean interactions per trial; p = 0.009) and *P. burroughi* (1.8 mean interactions per trial; p < 0.0001).

When *P. adelus* was the intruder within the plastic bag, they elicited the greatest amount of aggression from *P. bankanensis* compared to other resident species (Tukey's HSD, p < 0.0001) (Fig. 4.2b). *P. bankanensis* displayed the highest amount of aggression toward *P.*

adelus at 11.7 mean interactions per trial followed by *Pl. lacrymatus*, which displayed 4.8 mean interactions per trial towards *P. adelus*. Additionally, *P. bankanensis* showed the highest rate and variability of aggressive behaviours, ranging from 3 to 49 agonistic interactions per trial. All other resident species exhibited lower aggressive interactions at ≤2.4 mean interactions per trial.

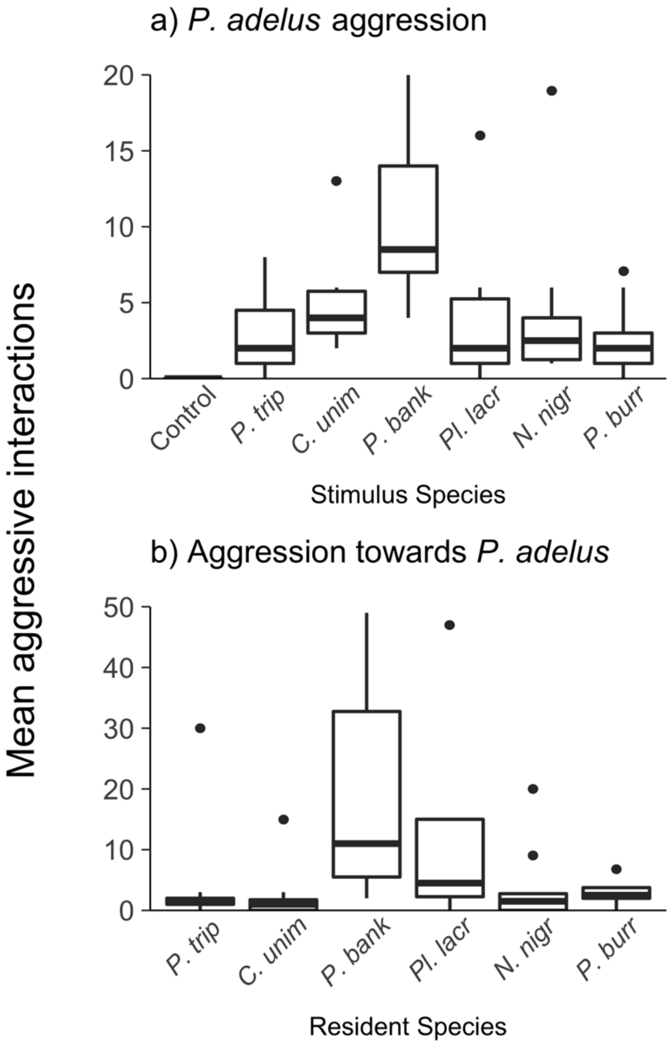

Figure 4.2 Mean aggressive interactions of (a) *P. adelus* towards conspecific stimulus species and (b) conspecific resident species towards *P. adelus* per 4 min trial. Box and whisker plot displays lowest and highest values, with the box showing interquartile range, the median represented by the bold line, and outliers represented as black dots. Vertical axes are not comparable. Species: *Pomacentrus tripunctatus*, *Chrysiptera unimaculata*, *Pomacentrus bankanensis*, *Pomacentrus adelus*, *Plectroglyphidodon lacrymatus*, *Neoglyphidodon nigroris*, *Pomacentrus burroughi*.

Removal experiment

Abundance: The abundance of the removed species, *P. adelus*, was successfully reduced to 0 immediately following the removal (post 1 day) (Fig. 4.3a). Additionally, there was no immigration from neighbouring adults, as no adult *P. adelus* were observed in the subsequent post 3 days and post 1 week census periods. Recruitment of *P. adelus* did occur 3 days post-removal (3 ± 1, mean individuals per 220 m^2 ± SE within replicates) and increased to pre-removal amounts 1 week post-removal (11 ± 1; Tukey's HSD, $p = 0.984$) (Fig. 4.3b). Despite regular recruitment, *P. adelus* abundance remained significantly low 3 months (14 ± 5; Tukey's HSD, $p < 0.0001$) and 6 months post-removal (39 ± 7) when compared to the pre-removal census (153 ± 8; $p < 0.0001$). However, a significant increase in abundance was observed when comparing post 3 months to post 6 months (Tukey's HSD, $p < 0.0001$).

The experimental removal of *P. adelus* significantly altered the abundance of all reef flat associated species. *P. bankanensis*, the main co-inhabiting species of *P. adelus* with similar microhabitat use, immediately increased in abundance from pre-removal levels of 24 ± 4 individuals to 32 ± 5 individuals 3 days post-removal as adults immigrated into the plot (Fig. 4.4a; Appendix: Table S4.1). Moreover, *P. bankanensis* abundance continued to significantly increase compared to pre-removal levels 1 week (38 ± 5; Tukey's HSD, $p = 0.032$), 3 months (52 ± 4; $p < 0.0001$) and 6 months post-removal (56 ± 3; $p < 0.0001$).

This pattern was also observed with *C. unimaculata*, which was distributed further onto the reef flat than *P. bankanensis* (Fig. 4.4b; Appendix: Table S4.1). *C. unimaculata* immediately increased in abundance 1 day (29 ± 8; Tukey's HSD, $p < 0.0001$), 3 days (36 ± 10, $p < 0.0001$), and 1 week post-removal (42 ± 11, $p < 0.0001$) from pre-removal levels (14 ± 1) and remained stable 3 months (35 ± 6, $p < 0.0001$) and 6 months thereafter (37 ± 4, $p < 0.0001$).

P. tripunctatus increased in abundance following the removal of *P. adelus* despite not having any distributional overlap with *P. adelus* (Fig. 4.4c; Appendix: S4.1). Abundance increased compared to pre-removal censuses from 2 ± 0 individuals pre-removal to 5 ± 1 (Tukey's HSD, $p = 0.135$) individuals 1 day post-removal and 5 ± 0 ($p = 0.136$) individuals 3 days post-removal. *P. tripunctatus* continued to increase significantly 1 week post-removal (7 ± 1; Tukey's HSD, $p = 0.015$) and remained significantly higher than pre-removal levels 6 months thereafter (10 ± 2, $p < 0.0001$).

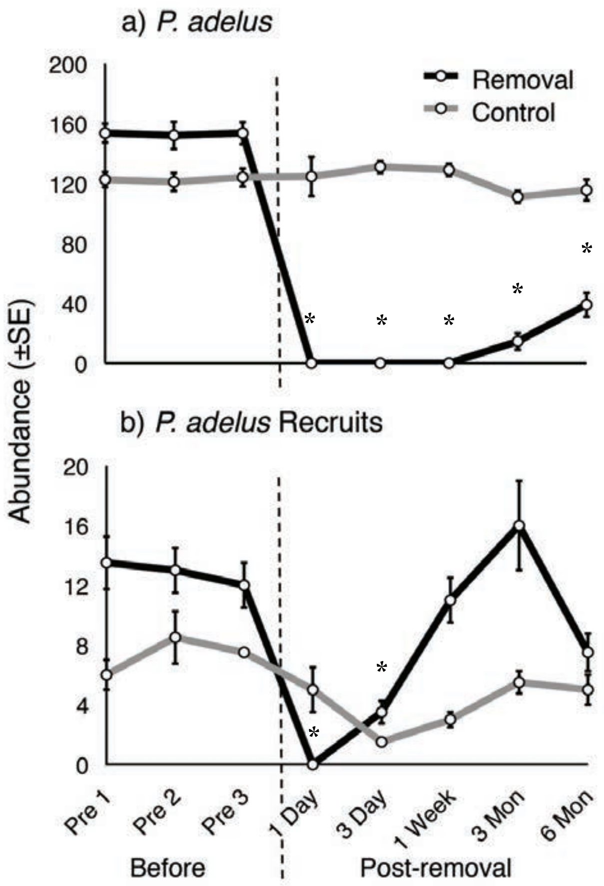

Figure 4.3 Species abundances (± standard error) on removal (black, n = 2) and control plots (gray, n = 2) of (a) *Pomacentrus adelus* and (b) *P. adelus* recruits before and consecutively after the experimental removal of *P. adelus* denoted by the dashed line. Asterisks represent significantly different values ($p \leq 0.05$) from the pre-removal abundance levels using Tukey's post-hoc pairwise comparisons (Appendix: Table S4.1 for values). Vertical axes are not comparable.

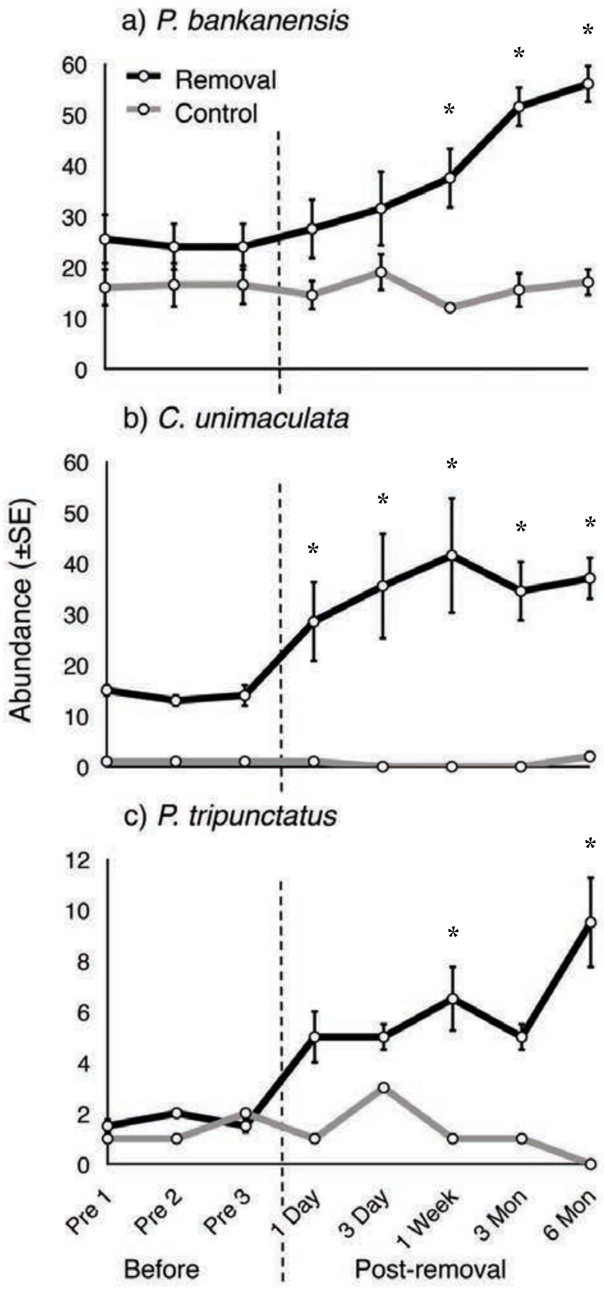

Figure 4.4 Species abundances (± standard error when available) on removal (black, n = 2) and control plots (gray, n = 2) of (a) *Pomacentrus bankanensis*, (b) *Chrysiptera unimaculata*, and (c) *P. tripunctatus* before and consecutively after the experimental removal of *P. adelus* denoted by the dashed line. Asterisks represent significantly different values ($p \leq 0.05$) from the pre-removal abundance levels using Tukey's post-hoc pairwise comparisons (Appendix: Table S4.1 for values). Vertical axes are not comparable.

As predicted, all other reef crest and reef slope associated species were unaffected by the removal of *P. adelus*. Despite occupying similar distributions on the reef crest, *Pl. lacrymatus* abundance remained constant throughout the experimental period (Tukey’s HSD, p = 0.970). Additionally, the abundance of *N. nigroris* and *P. burroughi* on the reef slope were unaffected (Tukey’s HSD, p = 0.990 and p = 0.937, respectively). On all control plots there were no significant changes in abundance observed for any species over the monitoring period (Appendix: Table S4.2).

Distribution: The interspecific competitors that increased in abundance following the removal of *P. adelus* also exhibited significant distributional shifts 6 months thereafter within the removal plots (Fig. 4.5a, b; Appendix: Table S4.3). The three populations of reef flat species began the distributional shift 1 day after the removal and retained the space 6 months later. The mean distribution of *P. bankanensis* significantly shifted 1.33 ± 0.28 m (change in mean distribution towards reef crest ± variance among replicate pre-removal surveys; K-S test: p = 0.033) toward the reef crest to acquire the space previously occupied by *P. adelus* (Fig. 4.5a, b). Moreover, the distributional spread, or tail of the populations, verifies population movement into the reef zone where *P. adelus* was removed. 37 individuals relocated to the front of the reef flat/back of the reef crest where *P. bankanensis* previously did not occupy.

The distributions of *C. unimaculata* and *P. tripunctatus* subsequently expanded out of pre-removal distributions with 30 and 5 individuals relocating to space on the reef occupied by *P. bankanensis*, respectively (Fig. 4.5a, b). A 0.75 ± 0.13 m shift in the *C. unimaculata* population was also observed but no differences in distribution were detected at the population level because the entire distribution was not within the experimental plot (K-S test: p = 0.329). Likewise, a significant population shift in *P. tripunctatus* was not observed due to only the tail of the population being within the experimental plot (0.38 ± 0.15 m, K-S test: p = 0.518). The removed species, *P. adelus*, recovered to its previous distribution on both removal plots 6 months after removal. The distributions of all other species within the removal plots and all seven damselfish species within the control plots did not display any significant spatial movement over time during the experimental period (Appendix: Table S4.3).

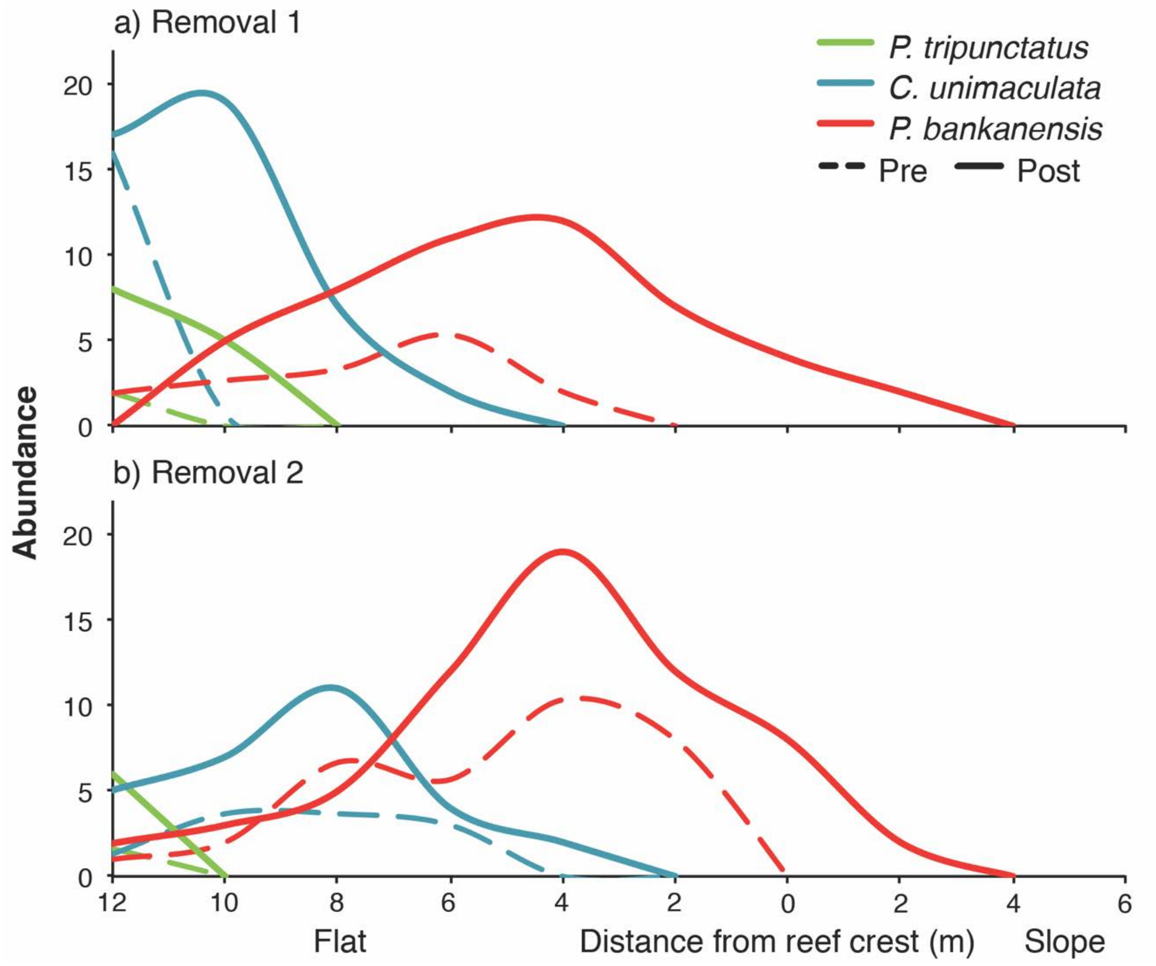

Figure 4.5 Distribution frequency histogram showing the changes in reef flat species (green: *Pomacentrus tripunctatus*, blue: *Chrysiptera unimaculata*, red: *Pomacentrus bankanensis*) distributions before the removal (dotted line; averaged between pre-removal replicates: n = 3) and 6 months after the removal of *P. adelus* (solid line) on (a) Luba Luba and (b) Garbuna. The 0 mark on the x-axis represents the middle of the reef crest, with the distance from the crest to the flat (left) and slope (right) in meters, respectively. Note that only the upper reef slope is presented, as no fish were observed deeper.

4.5 Discussion

Our results support the conclusion that interference competition contributes to explaining the spatial structure and abundance in a multi-species guild of territorial damselfish. The distinct distribution patterns characterised by a high degree of spatial partitioning among the main reef crest species were linked to levels of agonistic behaviour. Two neighbouring species in particular, *Pomacentrus adelus* and *P. bankanensis*, were highly aggressive toward one another. When *P. adelus* was removed, *P. bankanensis* exhibited a marked increase in abundance and expanded its distribution to acquire the previously occupied space on the reef flat and reef crest. The competitive release triggered indirect effects, likely mediated by *P. bankanensis,* between two other neighbouring species that did not directly share resources with *P. adelus*. Our study uniquely demonstrates that competitive networks within a community can operate directly and indirectly among ecologically similar species. Over time, a competitive release can lead to the expansion of a species realized niche as they readjust to the new competitive hierarchy.

The concept that interference competition for a limiting resource influences the abundance and distribution of animals is well established (Case and Gilpin 1974, Schoener 1983). In a community, many species interact with one another directly by aggressively impeding access to a resource. Our research confirms the widely documented theory that interference competition plays a role in ecological segregation (Colwell and Fuentes 1975, Diamond 1978). Previous work has clearly shown that coral reef fishes compete for space and deny access to subordinate competitors when the profit of a resource is high (Robertson and Gaines 1986, McCormick and Weaver 2012, Pereira et al. 2015). In our study system, *P. bankanensis* distribution was regulated by the presence of *P. adelus*. Both species exhibited intense aggression towards one another, compared to other adjacent species. The aggression is likely due to similar microhabitat use and semi-overlapping distributions (Eurich et al. 2018a). After the competitive release from *P. adelus*, *P. bankanensis* population increased immediately and shifted to occupy the reef area where *P. adelus* previously was. The quick appropriation of space (1 – 3 days), likely from bordering adult immigration, reflects the intensity of interference competition between the two species.

Similar to the classical Connell (1961) intertidal experiments on *Balanus* and *Chthamalus*, this field experiment demonstrated *P. bankanensis* has a fundamental niche that extends to the reef crest, but naturally occupies a smaller realised niche when in competition with *P. adelus* (Whittaker et al. 1973). The majority of previous studies that quantify similar interactions among coral reef fishes have used laboratory experiments (Munday et al. 2001, Pereira et al. 2015), artificial patch reefs (Sale 1978, Williams 1978, Robertson 1996, Forrester et al. 2006, McCormick and Weaver 2012, Boström-Einarsson et al. 2014), or experimental manipulations at an individual level (Belk 1975, Robertson and Gaines 1986). In the present study, interference competition was observed experimentally in the field at the population level and over a natural, larger-scale reef profile. We provide additional strong evidence that species with similar resource requirements coexist through direct competitive mechanisms.

The study of competition among coral reef fishes has typically been tested experimentally through pairwise interactions among two species, as demonstrated above with *P. bankanensis* and *P. adelus*. However, an ecological community, by definition, is a naturally occurring assemblage of species that potentially interact within a habitat. The ecological processes and mechanisms that maintain coexistence among similar species within highly complex systems may not always be direct (Amarasekare 2003, Siepielski and McPeek 2010, Strauss 1991). The fine-scale spatial partitioning of seven territorial damselfish presented a unique system to test the maintenance of coexistence in a multi-species competitive network (Eurich et al. 2018a). In the present study, ecological indirect effects were observed on the reef flat and reef crest following the removal of *P. adelus*. As expected through direct interference competition, *P. bankanensis* distribution shifted towards the reef crest following the experimental removal taking advantage of open space. Moreover, although *P. tripunctatus* and *C. unimaculata* did not directly interact with *P. adelus*, both populations also shifted towards the reef crest. The shift was likely mediated by the change in abundance and distribution of *P. bankanensis*. It is notable that a time lag, or subsequent effects, among the three species was not observed. All three species shifted and increased in abundance within a day of the *P. adelus* removal. Thus, it is difficult to determine which species indirectly influenced *P. tripunctatus* and *C. unimaculata*. However, the three species increasing in abundance and shifting in order without altering composition suggests the guild is intrinsically linked through associated competitive networks. Without the removal of *P. adelus* the spatial partitioning remained unchanged and stable likely due to interspecific competition. The observed shift highlights the importance of indirect interactions among species in this highly diverse and partitioned ecological guild.

It is notable that increases in abundance and distributional shifts were not ubiquitous among all territorial damselfish. The contrasting results are likely due to two major differences. First, while the species on the central reef crest, *Pl. lacrymatus*, spatially overlaps with *P. adelus,* the majority of the population utilised a different microhabitat, which reduced any direct competition. Eurich et al. (2018a) showed that territorial damselfish situated on the reef flat, including *P. adelus*, exhibited a positive association with rubble and negative avoidance of algal turf, whereas *Pl. lacrymatus* was selective for algal turf. Despite this, in the present study aggressive interactions were still observed, which implies territorial interactions play a role in maintaining resources (Robertson 1996, Munday et al. 2001, Forrester et al. 2006). Second, the two species on the reef slope, *N. nigroris* and *P. burroughi,* do not often encounter *P. adelus* as their distributions do not directly overlap (Eurich et al.

2018a). Additionally, a similar study showed that the most densely occupied zone in Kimbe Bay is the reef crest, where territorial damselfish encompass almost 100% of the substratum, compared to 40% of the substratum on the reef slope (Ceccarelli 2007). A lack of association and increased available habitat likely explains why no changes were observed on the upper reef slope. These two examples show that within complex ecosystems, the intensity and importance of competition may vary due to resource availability and dissimilarities among sympatric species.

Given the success of *P. bankanensis* following the intense interspecific competitive release and the indirect effects observed among reef flat species, the question arises - How will the *P. adelus* population, the previously most abundant species, recover? As predicted, *P. bankanensis* retained its abundance and the habitat 6 months after the removal of *P. adelus*. Furthermore, the species on the reef flat, *P. tripunctatus* and *C. unimaculata,* continued to persist adjacent to *P. bankanensis*. However, 3 months post removal only *P. adelus* subadults were observed within this species' pre-removal distribution. Srinivasan and Jones (2006) showed damselfish recruit at a low level all year round in Kimbe Bay. These individuals therefore likely recruited in during the experimental monitoring period.

The pattern could indicate several mechanisms for coexistence among territorial damselfish. Firstly, it could indicate a competitive lottery for space at settlement, and an ontogenetic shift to niche partitioning among neighbouring adults (Sale 1977, 1978). Pereira et al. (2015) demonstrated the competitive mechanism between two *Gobiodon* species shifts from a lottery for space at settlement to niche partitioning among larger individuals. In our study, recruitment of *P. adelus* was observed throughout the experimental period and only subadults were observed in the experimental plots 3 months after the removal. 6 months after the removal these individuals were classified as adults. More detailed experiments at the recruitment and settlement level are needed for a definitive conclusion on the lottery for space or immigration from nearby habitat (as per Sale 1979). Alternatively, with the quick appropriation of space by competing adult species, a dominance hierarchy is a possible explanation for the delayed *P. adelus* recovery. Initially, adults of the subordinate species may out compete *P. adelus* recruits and juveniles for available habitat, but this may reverse when *P. adelus* individuals increase in size. In any case, the lack of pre-removal abundances of *P. adelus* adults within the experimental plots 6 months later demonstrates competitive displacement and niche partitioning. It is also possible that the *P. adelus* population was tracking towards a recovery, but if so, we would have expected *P. bankanensis* abundances to trend downwards. For a full assessment of a compensatory response by a population following its release from competition an experiment spanning multiple generations with the tracking of individuals would be needed (Schmitt and Holbrook 1990, Robertson 1996).

Conclusions

Revealing indirect relationships among ecologically similar species within a complex community remains a formidable challenge, yet it is necessary to gain generality and predictive power. We demonstrate that competitive networks within a community can operate directly, by interference competition, and indirectly through a competitive release among ecologically similar species. Evidence presented here suggests that, the loss of a species through local extinction may result in ecological indirect effects that will influence other species in the assemblage. In addition, it is known that reduced habitat quality through disturbances, such as ocean acidification and coral bleaching, can alter and even reverse pairwise competitive interactions between species (McCormick 2012, McCormick et al. 2013, Boström-Einarsson et al. 2014). With growing pressures, including climate change, globalization, and migration, on the world ecosystems, we hope these effects do not extend to the progressive loss of species that cannot compete for the dwindling resources.

Chapter 5

Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs

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5.1 Summary

Roving herbivorous fishes play an important role in coral reef communities by removing turf-algae, which can facilitate the settlement of coral larvae. Territorial damselfishes can influence the foraging patterns of roving herbivores by excluding them from their territories, altering the benthic assemblage. However, the impacts depend on the intensity of aggression and which taxonomic groups of roving herbivores are being excluded. Here we document the foraging activity of roving herbivores (Acanthuridae, Scaridae, Siganidae) and the extent to which they are subject to aggression by *Pomacentrus adelus,* the most abundant territorial damselfish in Kimbe Bay, Papua New Guinea. We then conducted experimental removals (220 m^2 plots on the reef flat) of *P. adelus* to examine its impact on roving herbivores and the benthic community structure. We hypothesized that the removal of *P. adelus* would lead to an increase in roving herbivore abundance and foraging activity and a decline in algal cover. The relative abundance (MaxN) and foraging activity (bite rate) of each taxon were examined pre and post-removal using video quadrats. The overall relative abundance of roving herbivores was not influenced by the removal of *P. adelus*. No changes in foraging patterns were observed for parrotfish, the family that received the highest rate of agonistic interactions, and rabbitfish. The removal of *P. adelus* resulted in a significant decrease in surgeonfish feeding, suggesting *P. adelus* alters foraging patterns indirectly through territorial maintenance and not aggression. The only measurable benthic impact of the *P. adelus* removal was an increase in sediment, while all other substratum types remained constant. These results indicate that *P. adelus* does not have a negative impact on all roving herbivores and instead may contribute to surgeonfish foraging indirectly through the removal of sediment. The generalisation that territorial damselfish reduce foraging rates of roving herbivores may not be applicable in all systems or for all species.

5.2 Introduction

Roving herbivorous fishes play an important role on coral reefs in reducing algal biomass and preventing alternative algal dominated stable states (Mumby et al. 2006, Hughes et al. 2007, Francini-Filho et al. 2010). Hence, they are considered important in maintaining healthy coral cover and promoting ecosystem resilience (Burkepile and Hay 2008, Hamilton et al. 2014, O'Leary and Mcclanahan 2016). The most important roving herbivores, in a broad use of the term, appear to be surgeonfish (Acanthuridae), parrotfish (Labridae: Scarini), and rabbitfish (Siganidae) in terms of algal biomass consumption or removal (Lewis and Wainwright 1985, Francini-Filho et al. 2010). However, these taxa do not have exclusive access to algal covered reef habitat. Territorial farming damselfish often influence the structure of algal communities though the deterrence of larger roving herbivores (reviewed by Hata and Ceccarelli 2016). The aggressive territorial defence may lead to an increase in turf algae, a desired food source of roving herbivores (Hixon and Brostoff 1983, Russ 1987, Hixon 1996, Ceccarelli et al. 2005a). Studies that combine the foraging patterns of roving herbivores and agonistic interactions within a healthy community can together help define the mechanistic drivers that underlie reef habitat structure and resilience.

Surgeonfish, parrotfish, and rabbitfishes cohabit the most productive coral reef zones where they may forage in mixed species groups and partition resources (Williams 1991). The difference in resource utilization among families is strongly related to morphology, with the recognition of three main functional groups: browsers, scrapers, and excavators (Ross 1986, Bellwood and Choat 1990, Streelman et al. 2002, Francini-Filho et al. 2008). Surgeonfish, typically categorized as browsers, largely feed on the epilithic algal matrix (Goatley and Bellwood 2010) with some species targeting detritus aggregates within algal turfs (Marshell and Mumby 2012, Tebbett et al. 2017a, b). Unlike surgeonfish, parrotfish alter the substratum by scraping or excavating the surface leaving distinct scars on the benthos (Bellwood and Choat 1990, Bellwood 1995, 1996). Despite recent work suggesting that parrotfish may be targeting endolithic microbes and detritus (Clements et al. 2017), the removal of microalgae in the process of foraging remains functionally important when considering the biotic composition of reef benthos (Morgan and Kench 2016). In contrast, rabbitfish feed significantly more in reef crevices than the other two families due to differences in morphology and dentition (Fox and Bellwood 2013, Brandl and Bellwood 2014). While the majority of rabbitfish species target macroalgae by browsing or cropping, the family also contains a distinct group of mixed feeders, which target microalgal material, cyanobacteria, and sediment (Hoey et al. 2013). The diversity of foraging methods, and their implications for impacts on benthic habitat structure, indicates that our understanding of how species interact with the surrounding community must be species and family specific (Choat and Clements 1993, Polunin et al. 1995, Fox and Bellwood 2007, Ong and Holland 2010). Therefore, it is important to assess the grazing ability of species individually as grazing rates can vary due to differences in community structure and species encountered.

Territorial damselfish (Pomacentridae) are highly abundant small-bodied consumers that often occupy the reef crest and reef flat habitats (Ceccarelli et al. 2001, Ceccarelli 2007, Eurich et al. 2018a). The modification of algae through farming behaviour and territorial defence is thought to play an important role on the benthic community structure (Wellington 1982, Hixon and Brostoff 1983, Ceccarelli et al. 2005a, Ceccarelli 2007, Barneche et al. 2009). Thus, territorial damselfishes influence on coral recruitment (Sammarco and Carleton 1981, Wellington 1982, Ceccarelli et al. 2005a), and the abundance and composition of algae within the territorial boundaries (Hixon 1996, Ceccarelli et al. 2005b), have been well documented. Territorial damselfish have been predominantly categorized into three guilds based off the species' effect on benthic assemblage structure and aggression: intensive farmers, extensive farmers, and an intermediate group (Hata and Kato 2004, Ceccarelli 2007, Hata and Ceccarelli 2016). Where, intensive farmers weed low diversity algal turfs intensively with aggressive defence, extensive farmers weed and defend larger territories to a lesser degree, and an intermediate group that maintains discrete, but significantly different to the surrounding environment, territories of algal turf (Emslie et al. 2012, Pratchett et al. 2016). Several experimental studies have shown that the aggressive exclusion of roving herbivores by extensive or intensive farming species affects the benthic assemblage structure (Hixon and Brostoff 1983, Russ 1987, Hixon 1996, Ceccarelli et al. 2005a). However, there is conflicting evidence that all territorial damselfish, especially intermediate farming species - the most abundant guild (Pratchett et al. 2016), hinder the foraging patterns of roving herbivores through agonistic interactions. Some studies have shown that roving herbivores will actively avoid the territories of territorial damselfish to feed on desirable algae without harassment (Robertson et al. 1976, Hamilton and Dill 2003). Additionally, surgeonfish and parrotfish periodically may use schooling behaviours to overwhelm territorial damselfish and gain access (Robertson et al. 1976, Foster 1985a). However, Ceccarelli et al. (2005b) found that extensive and intermediate territorial damselfish were fairly inefficient at excluding roving herbivores from their territories and roving herbivores had a significant impact on benthic habitat, both with and without the presence of territorial damselfish.

While both roving herbivores and territorial damselfish can exert a strong influence on the structure of the benthic community, the extent to which the general paradigm holds true for intermediate territorial damselfish remains unclear. In this study we document the natural foraging activity of roving herbivores and the extent to which this was affected by an intermediate farming territorial damselfish in Kimbe Bay, West New Britain, Papua New Guinea. We then undertook a large-scale removal of the most abundant territorial damselfish, *Pomacentrus adelus*, to evaluate how the abundances and foraging activity of roving herbivores would change following an agonistic release. Lastly, we determined whether the benthic community structure was altered in the absence of *P. adelus*. Specifically, we tested the following three predictions: (1) the local abundance of roving herbivores should increase in abundance following the removal of *P. adelus*; (2) the feeding activity of roving herbivores should increase after the removal of *P. adelus* as benthic resources are undefended; (3) the benthic habitat may be altered due to changes in herbivore foraging and the elimination of *P. adelus* farming and territorial behaviour.

5.3 Methods

Study location and species

This study was conducted in Kimbe Bay, West New Britain, Papua New Guinea (Fig. 5.1; 5°30’ S, 150°05’ E). Kimbe Bay lies within Oceania and is a region of West New Britain recognized for high coral reef biodiversity and large platform reefs (Roberts et al., 2002). Two inshore reefs, Garbuna and Luba Luba, were selected as the study locations due to similarities in species composition and reef aspect. Both reefs are nearshore (< 1 km from land), and have a similar reef structure: a shallow reef flat (exposed during extreme low tides), a reef crest, and a gentle reef slope ending in a sandy bottom at 30 – 50 m. Coral reefs in Kimbe Bay have a high diversity of both coral and fishes despite several regional coral mortality events (Jones et al. 2004, Boström-Einarsson et al. 2014). At least 20 families of reef fishes are found in Kimbe Bay (Jones et al., 2004), including many species belonging to families loosely described as herbivores, namely Acanthuridae, Labridae (Scarini tribe), and Siganidae. For the purposes of this study, only roving herbivores that occupied the zones where *P. adelus* occurred were analysed.

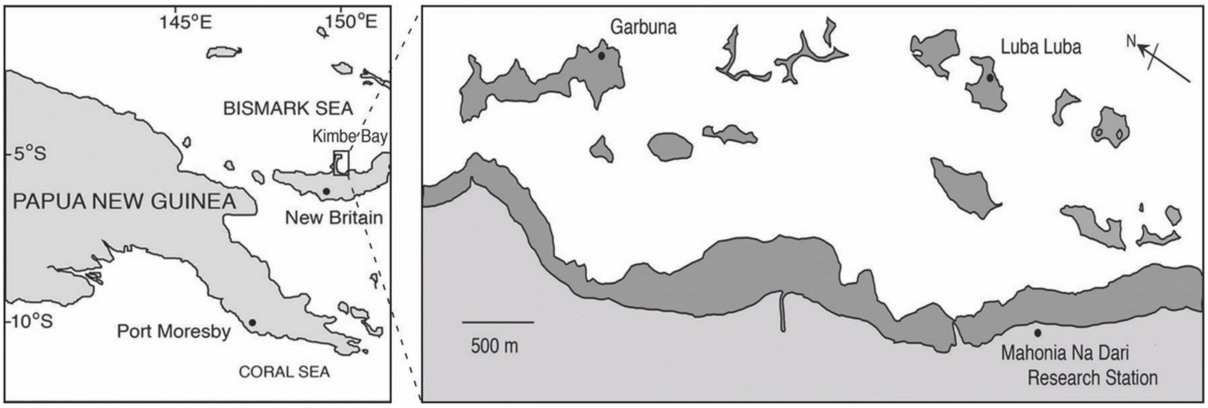

Figure 5.1 Location of Kimbe Bay, West New Britain, Papua New Guinea, and the 2 reef sites (Garbuna and Luba Luba).

The most abundant damselfish, *Pomacentrus adelus* (Pomacentridae), occupies the reef crest and adjacent zones (Ceccarelli 2007, Eurich et al. 2018a). *P. adelus* is a highly abundant, small bodied intermediate territorial damselfish that maintains territories on rubble and filamentous algae, and exerts aggressive defence on intruders (Ceccarelli et al. 2001, Pratchett et al. 2016, Eurich et al. 2018a). *P. adelus* influences the composition of algal assemblages by weeding or farming within the territorial boundary, though the benthic assemblage remains visually similar to the surrounding areas (Hata and Kato 2004, Ceccarelli 2007).

Removal experiment

A paired removal plot and control plot were established 75 m apart on each of the two study locations (4 plots total). The plots were spaced to ensure they were independent and sized so as to include the depth distribution of *P. adelus*. Each individual rectangular plot was 22 m onto the reef flat from the lower reef crest and 10 m wide parallel to the reef crest (220 m^2 total area), and was delimited by nylon strings and metal rods to create a 2 m by 2 m grid to facilitate census.

After the community was censused for preliminary comparisons, a removal experiment of the most abundant territorial damselfish, *P. adelus*, was conducted on the experimental plots. Fish were removed by hand spear or a dilute anesthetic clove oil solution, including recruits and all surrounding individuals within a 5 m wide buffer. Approximately 300 individuals were removed from each experimental plot. After establishment, the control plots were left experimentally undisturbed, but were visited as frequently as the removal plots to control for the potential effects of diver disturbance. Here divers conducted mock swimming activities emulating removal techniques. Following the removal of *P. adelus*, no further intervention took place on the experimental plots as no immigration was observed.

Abundance and foraging patterns: video analysis

Stationary cameras were used to obtain unbiased estimates of abundance and foraging patterns (e.g., Assis et al. 2013). At high tide cameras (GoPro) were placed within the experimental plot, above any structurally complex corals, and pointed towards the benthos. Cameras were placed so that they recorded a marked 2 m by 2 m area within the zone and territories used by *P. adelus*, thereby standardizing the ‘viewable’ and recordable area. 15 video censuses were collected during each treatment period, pre- and post-removal, on the four plots (total n = 120). Cameras were placed in the experimental areas 1 – 3 days prior to fish removal and then 1 – 3 days after removal.

For analysis, 5 min trials were subset from longer videos (20 to 30 min long). Each video was started 5 min in, then watched for 5 min prior to the trial to ensure there was no camera movement or diver influence that may have affected fish behaviour after tripod placement. If no disturbance was observed during the 5 min observation period the trial was initiated and data was collected for the subsequent 5 min. All videos were analysed by a single observer (S. M. Shomaker).

Pre-removal videos of control and removal plots were used to assess the undisturbed foraging patterns of fish species and interactions with *P. adelus* prior to experimental removal. The foraging patterns of all 17 species of surgeonfish, parrotfish, and rabbitfish present were observed and bites were recorded. Bite rate for the purpose of this study was determined as the mean total number of bites directed to the benthos by all fish species other than *P. adelus* per 5 min trial within the marked 2 m by 2 m area. Few species were abundant enough to get species-specific foraging estimates. The 13 species observed include the surgeonfish: *Ctenochaetus striatus, Ct. binotatus, Ct. strigosus*, *Acanthurus pyroferus, A. lineatus*, *Zebrasoma scopas*, and *Naso lituratus*; parrotfish: *Chlorurus bleekeri*, *Scarus rivulatus, Sc. dimidiatus, Sc. niger*; and rabbitfish: *Siganus vulpinus* and *Si. doliatus*. Bites were pooled by family groups to estimate the foraging effort for each family.

Pre-removal videos from the four plots (n = 60) were analysed once more to quantify aggressive interactions by *P. adelus* towards roving herbivores. The observer (S. M. Shomaker) first established a *P. adelus* territory within the marked 2 m by 2 m area and then recorded the interactions of a single individual for 5 min. Any aggressive charges from *P. adelus* resulting in a change or pause of behaviour and/or displaced movement to the herbivore were recorded as a ‘chase’.

Relative fish abundance was recorded using the maximum number of individuals (MaxN) for each species that occurred over the 5 min observation period. MaxN is the most commonly used method of estimating fish abundance from video recordings and is described as the maximum number of individuals of each species that are in the video frame at any one given time throughout the trial (Cappo et al. 2007). MaxN is a conservative metric for estimating minimum abundance of a species (Willis et al. 2000), and was designed to avoid the recurring counting of individuals that enter the camera field of view within a trial (Cappo et al. 2007). It should be noted that a potential limitation of MaxN is that the resulting value can be nonlinearly related to true site abundance when dealing with a large abundance of fish, therefore it can underestimate the population size (Schobernd et al. 2014). However, due to the restricted field of view of cameras, and the relatively low abundance of roving herbivores observed in the present study, MaxN was the best metric for analysis. Thus, within this study when we discuss abundance we are referring to a maximum relative abundance (not true abundance) within a 2 m by 2 m space at any one given time compared to other species.

Benthic habitat

It was predicted that if *P. adelus* were having an important influence on the overall benthic assemblage by farming algae or engaging in agonistic interactions with other fishes, there would be a significant difference in the algae and coral assemblages in the removal plots where *P. adelus* previously occurred. To estimate the benthic community structure plots were surveyed before the removal and 3 months thereafter by a single observer (J. G. Eurich). Benthic cover was estimated using three 10 m transects laid within each of the eleven 2 m by 10 m contiguous rectangles (i.e., permanent grid), parallel to the reef crest (n = 33 per survey period per plot). The substratum present beneath 20 uniform points along each transect was recorded (n = 660 per survey period per plot). Substratum was classified as one of nine microhabitat categories: (1) live coral; recorded by growth form but pooled as live coral for the purpose of this study, (2) dead coral, (3) macroalgae, (4) turf algae, (5) crustose-coralline algae, (6) rubble, (7) sand (incl. non-biological substrate), (8) sediment, or (9) other (e.g. *Fungia* spp., sponges, and bivalves). For the purpose of this study, we used the definition of turf algae from Hay (1981) as masses of tightly packed upright branches that were dominated by filamentous species. Previous studies demonstrate that *P. adelus* influences the composition of microalgal communities through intermediate farming (Ceccarelli et al. 2005b, Ceccarelli 2007). However, as the focus of the present study was to assess foraging microhabitats utilized by roving herbivores, a fine-scale taxonomic resolution to detect subtle changes in microalgal community differences was not used.

Statistical analysis

Relative herbivore abundance (MaxN) and changes in foraging activity (bite rate) were transformed using an aligned rank transformation and compared using a two-factor nonparametric ANOVA (i.e., treatment period and location) (Crawley 2007, Zurr et al. 2009). All data were analysed using R v. 3.0.2 with the 'ARTool' (Kay and Wobbrock 2016) and 'car' packages (Fox and Weisberg 2011) in R (R Development Core Team 2013). Species were analysed collectively to represent the total impact of roving herbivores, and then individually, in family groups (surgeonfish, parrotfish, and rabbitfish). The nature of the significant interaction was further explored with Tukey's HSD post-hoc tests using the 'lsmeans' package (Lenth 2016). All data in the text and figures are presented as the arithmetic mean ± one standard error (SE), unless otherwise stated. Recruits and reef slope species were omitted from presentation and final analysis due to irregular and low recruitment pulses and the deeper species having no contact with *P. adelus*, respectively.

Random intercepts mixed-effects logistic regressions were used to assess the difference in benthic community structure before and after the removal of *P. adelus* for each treatment type (experimental and control). Fixed effects were treatment period (pre- and post-removal), location (Garbuna and Luba Luba), and the interaction between them. Replicates and transects within a plot were both treated as random effects: the random intercepts model assumes that any effects of treatment period and location are similar between transects and replicates. The proportion of the total cover by each substratum type (response variable) was used to measure the benthic community structure. The model was fitted using the R package 'lme4' (Bates et al. 2011), and probability values for each successive term in the model were assessed using the ANOVA function provided by the R package 'car'. While all comparisons involved replicate reef locations (n = 2 for removal, n = 2 for control), data were pooled for presentation.

5.4 Results

Natural foraging patterns

A total of 17 species of roving herbivores, including 10 acanthurids, 5 labrids (Scarini) and 2 siganids, were present within the study area before the removal. Of the species observed, only 13 species foraged consistently enough to obtain reliable estimates of bite rate (Fig. 5.2; total bites per 5 min trial ± SE, n = 60). For mean total bites when an individual was actively foraging (trials where a bite was observed), surgeonfish accounted for the majority of total bites observed (69.6%) with *Ctenochaetus striatus* (36.2 ± 8.1) and *Ct. binotatus* (36.8 ± 7.2) foraging most frequently. *Chlorurus bleekeri* was the most active parrotfish (28.5 ± 8.7) accounting for 13.8% of total bites observed. For rabbitfish, *Siganus vulpinus* and *Si. doliatus* occurred in low abundances, and when observed tended to have low bite rates.

Aggressive interactions

In the 60 5 min observations prior to the removal, 21 total chases from *P. adelus* out of 779 encounters were observed: 6 chases directed at *Ct. striatus*, 14 chases at parrotfish, and 1 chase at *Si. vulpinus* (Fig. 5.3). *P. adelus* appeared to concentrate its territorial defence towards parrotfish with *Sc. dimidiatus*, the most targeted, accounting for 38% of chases observed. Relative to encounters, aggressive interactions were low with a 0.027% chance of being chased when encountered.

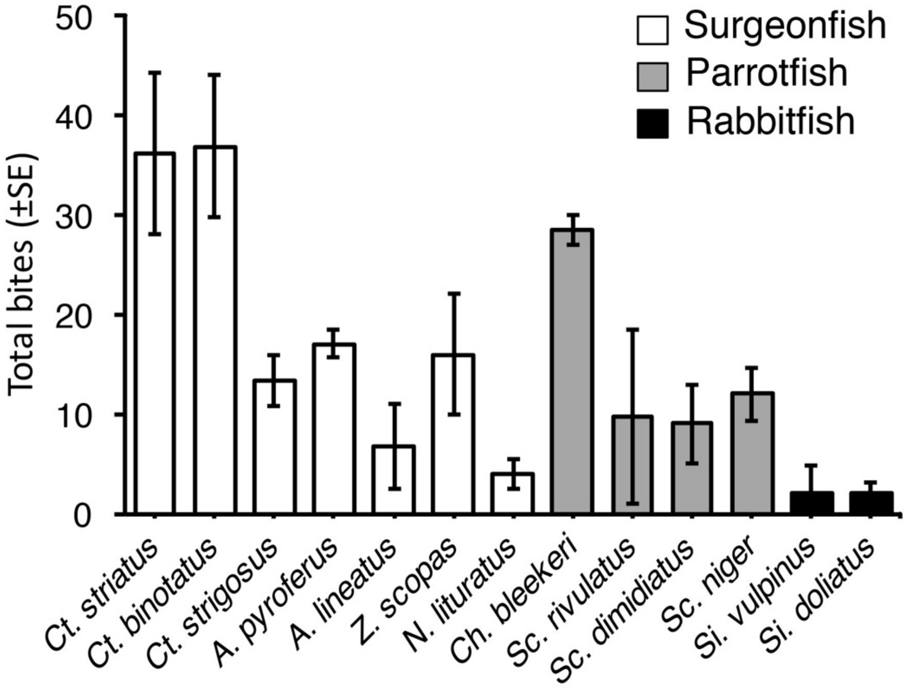

Figure 5.2 Mean total number of bites per species per 5 min trial (± SE, n = 60). Species genus names; *Ct.*: *Ctenochaetus, A.*: *Acanthurus, Z.*: *Zebrasoma*, *N.*: *Naso, Ch.*: *Chlorurus*, *Sc.*: *Scarus*, and *Si.*: *Siganus.*

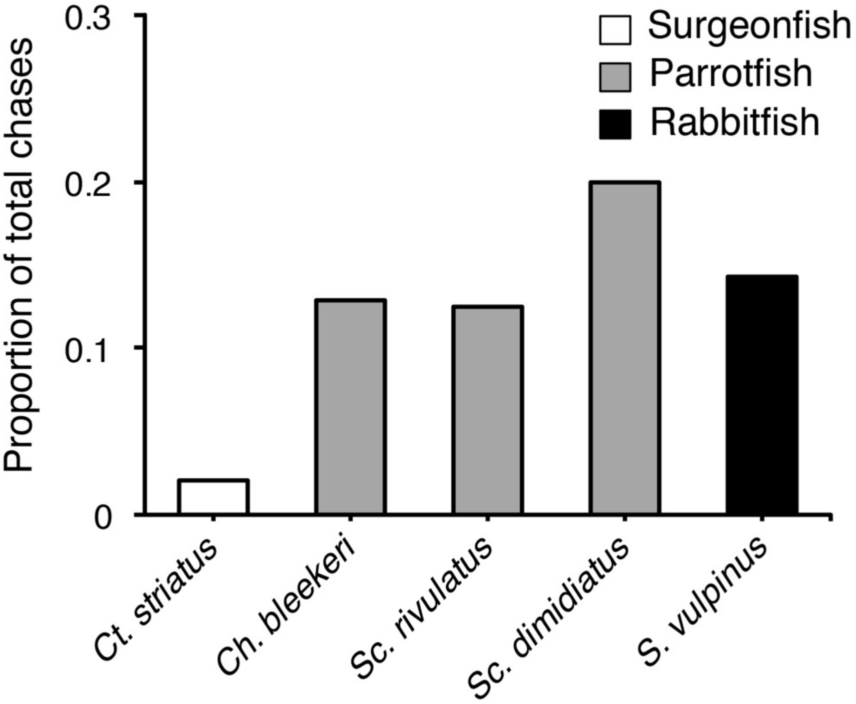

Figure 5.3 Aggressive interactions from *Pomacentrus adelus* displayed as proportion of total chases (n = 60). Species genus names; *Ct.*: *Ctenochaetus*, *Ch.*: *Chlorurus*, *Sc.*: *Scarus*, and *Si.*: *Siganus.*

Herbivore abundance

The prediction that roving herbivore abundance would increase following *P. adelus* removal was not supported. There were no significant differences in roving herbivore relative abundance following the removal of *P. adelus* for both the removal and control plots (Table 5.1). Surgeonfish (Fig. 5.4; $p = 0.979$), parrotfish (Fig. 5.4; $p = 0.493$), and rabbitfish (Fig. 5.4; $p = 0.096$) did not increase in abundance after the agonistic release on the removal plots. No significant difference was observed between locations within treatment type (X^2 (1) = 0.249, $p = 0.883$).

Change in foraging patterns

The hypothesis that foraging activity would increase following the removal of the intermediate territorial damselfish was also rejected. For the control plots, there were no significant differences in foraging activity for surgeonfish, parrotfish, and rabbitfish between treatment periods (Table 5.2). On the contrary, surgeonfish foraging in the removal plots significantly decreased following the removal of *P. adelus* (Table 5.2; Fig. 5.5; $p = 0.002$). Parrotfish (Fig. 5.5; $p = 0.349$) and rabbitfish (Fig. 5.5; $p = 0.261$) foraging was not significantly affected by the removal of *P. adelus* (Table 5.2). No significant difference was observed among locations within treatment type (X^2 (1) = 0.206, $p = 0.902$).

Benthic habitat

The experimental removal of *P. adelus* had little impact on the overall benthic habitat structure. The benthic habitat did not change significantly over time when comparing removal and control plots (Fig. 5.6; Appendix: Table S5.1). Macroalgal cover increased significantly on both the removal ($p < 0.0001$) and control plots ($p < 0.0001$). Conversely, turf cover decreased significantly on both the removal ($p < 0.0001$) and control plots ($p < 0.0001$). Of the 9 habitat types, the only significant change between treatment periods not replicated on the control plots was sediment cover. Sediment increased following the removal of *P. adelus* on the removal plots ($p = 0.018$), but did not differ among period on the control plots ($p = 0.215$). All other habitat categories remained consistent throughout the removal experiment.

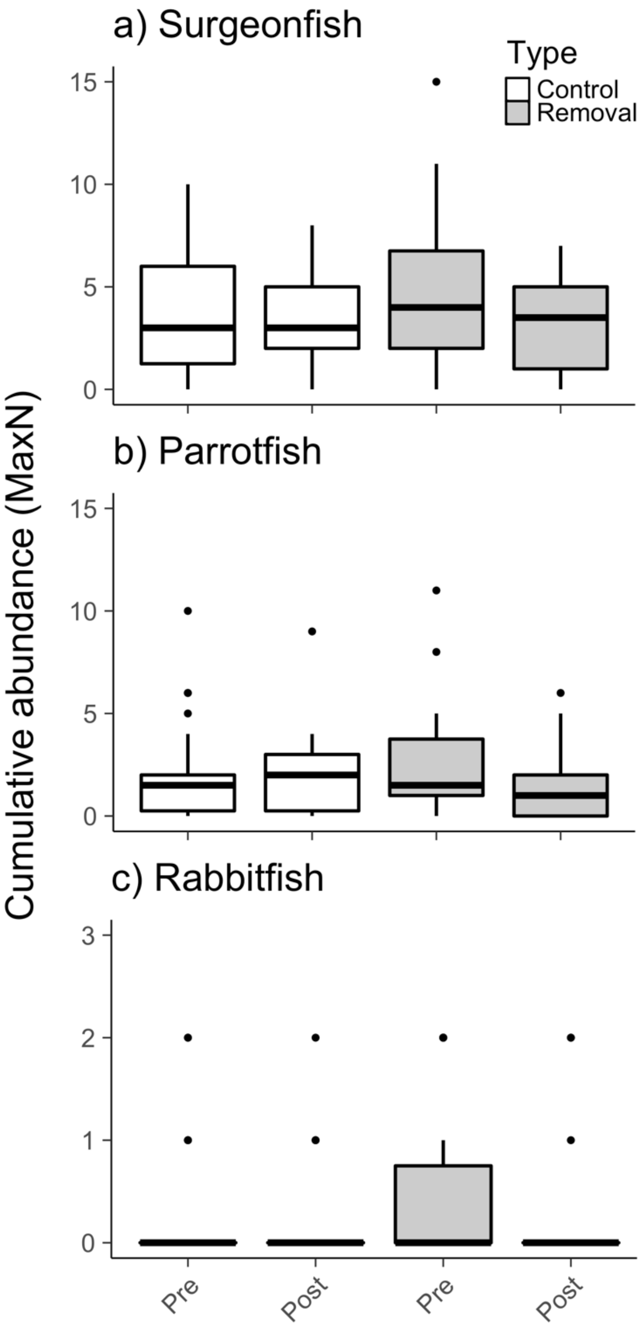

Figure 5.4 Cumulative abundance of (a) surgeonfish, (b) parrotfish, and (c) rabbitfish for control reefs (white) and removal reefs (gray) pre-and post-removal of *Pomacentrus adelus* (n = 30 per group). Box and whisker plot displays lowest and highest values, with the box showing interquartile range, the median represented by a bold line, and outliers represented as black dots. Vertical axes are not comparable.

Source	t ratio	df	p
Surgeonfish			
Removal	-0.026	1	0.979
Control	0.235	1	0.815
Parrotfish			
Removal	0.692	1	0.493
Control	-1.483	1	0.147
Rabbitfish			
Removal	2.921	1	0.096
Control	0	1	1.000

Table 5.1 Conclusions of post-hoc tests (Tukey's HSD) on differences in relative abundance (MaxN) between period (pre- and post-removal) by treatment type.

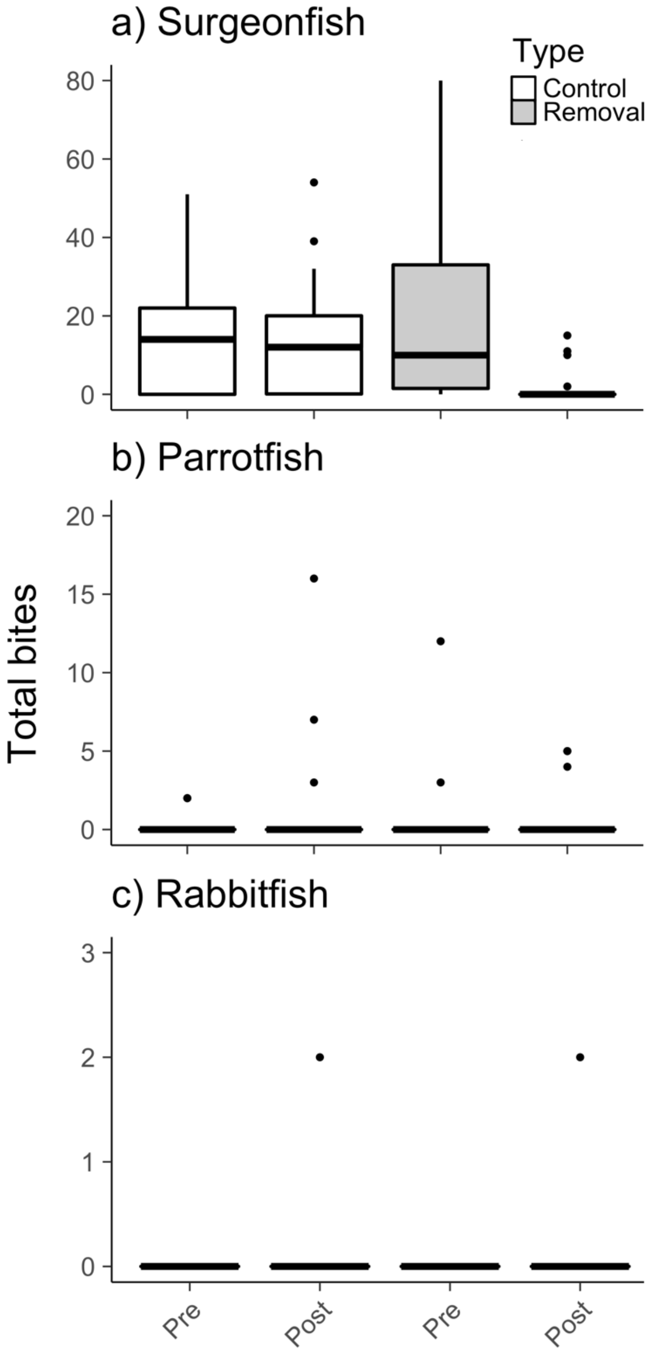

Figure 5.5 Average (a) surgeonfish, (b) parrotfish, and (c) rabbitfish foraging on control reefs (white) and removal reefs (gray) pre-and post-removal of *Pomacentrus adelus* per 5 min trial (n = 30 per group). Box and whisker plot displays lowest and highest values, with the box showing interquartile range, the median represented by a bold line, and outliers represented as black dots. Vertical axes are not comparable.

Source	t ratio	df	p
Surgeonfish			
Removal	-3.283	1	0.002
Control	-0.473	1	0.639
Parrotfish			
Removal	-0.950	1	0.349
Control	-0.652	1	0.519
Rabbitfish			
Removal	1.143	1	0.261
Control	1.143	1	0.261

Table 5.2 Conclusions of post-hoc tests (Tukey's HSD) on differences in foraging between period (pre- and post-removal) by treatment type.

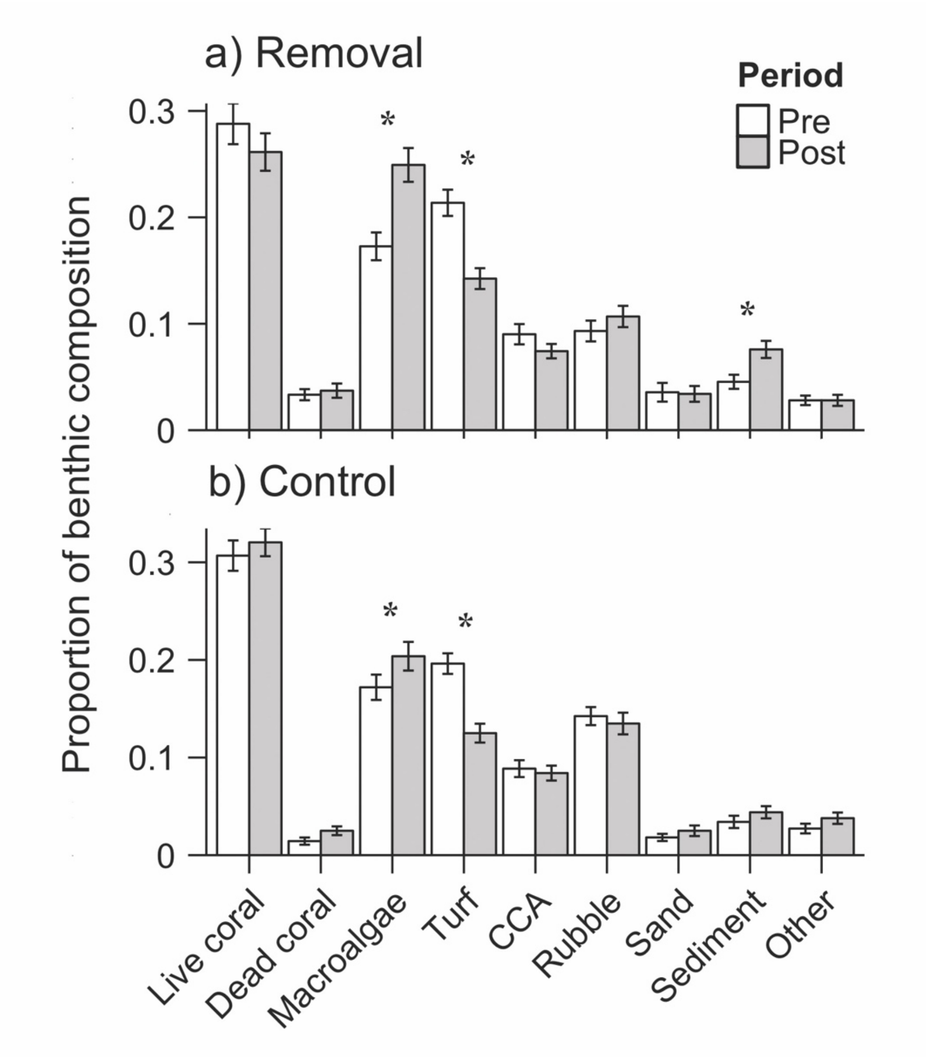

Figure 5.6 Benthic composition pre- (white) and post-removal (gray) of *Pomacentrus adelus* by treatment type: (a) removal and (b) control. The proportion represents an average (± SE) across locations. Statistical significance denoted by an asterisk.

5.5 Discussion

This study indicates that *Pomacentrus adelus* does not have a major influence on the relative abundance and foraging activity of all roving herbivorous fishes or any major direct effect on the benthic substratum, but may play a role in sediment dynamics indirectly through surgeonfish interactions and territory maintenance. None of the three central hypotheses posed were fully supported by the experimental removal of the intermediate farming damselfish *P. adelus*: (1) the overall relative abundance of roving herbivores was unaffected by the large-scale removal of *P. adelus*; (2) parrotfish and rabbitfish foraging activity was not influenced by the removal despite access to undefended resources; and (3) *P. adelus* had no major impact, either directly or indirectly, on the cover of either algae or corals. Hence, the emerging paradigm of a strong interaction between roving herbivores and all types of territorial damselfish is not supported by the findings of the present study. The effects observed were unexpected, including a positive influence of *P. adelus* on the foraging intensity of surgeonfish and a negative effect on the amount of sediment in territories. We argue that in this system, *P. adelus* modifies the benthic composition in a way that benefits surgeonfish foraging and without the presence of *P. adelus* surgeonfish are less apt to forage, which directly impacts reef sediment dynamics.

We argue that aggressive charges by *P. adelus* may represent an annoyance rather than an effective deterrent to the roving herbivores. Overall, aggressive interactions were rare and accounted for only 0.027% of observed incursions. Previous research has documented that *P. adelus* is highly territorial and aggressive on the reef flat and reef crest to other territorial damselfishes (Eurich et al. 2018a), but few chases observed in the present study were directed at herbivores. Of the interactions observed, parrotfish were attacked more frequently than surgeonfish and rabbitfish. This contradicted the assumption that surgeonfish would be targeted more frequently, as it is known that surgeonfish and territorial damselfish overlap in space use and diet (Robertson and Polunin 1981, Russ 1987, Castano et al. 2014). However, it is likely that parrotfish pose a larger threat due to the significant disruption of the benthos by scraping and excavating algae (Bellwood and Choat 1990, Bellwood 1995, 1996, Morgan and Kench 2016). Aggression is expensive because it imposes energy and time costs and increases the risk of injury (Clutton-Brock and Parker 1995). Therefore, individuals will be more aggressive to the species that structurally influence and damage the benthos and resources within their territorial boundaries. However, despite parrotfish sustaining the highest number of aggressive interactions proportionate to other roving herbivores, no behavioural changes were observed once the agonistic release was initiated.

The overall lack of aggression likely reflects *P. adelus* belonging to the guild of intermediate territorial damselfish (Hata and Kato 2004, Ceccarelli 2007). Previous studies have suggested that both rate of attacks and success of attacks by damselfish increase with body size (Foster 1985b). *P. adelus* is a relatively small bodied species compared to other intensive and extensive farming species, which is one explanation for why fewer aggressive interactions were observed. We present an important finding as all territorial damselfish are occasionally assumed to have an equally strong external influence on herbivory through their aggression. Intensive and extensive farming species (e.g., *Stegastes* spp.) that maintain conspicuous algal mats are known to defend their territories aggressively (Ceccarelli et al. 2001, Hoey and Bellwood 2010, Emslie et al. 2012). However, these species tend to occur in patches and are less abundant than intermediate farming species (Pratchett et al. 2016). In Kimbe Bay *P. adelus* is abundant over multiple reef zones in high densities where no intensive and extensive farming species are present (Ceccarelli 2007). Despite the lower quality and quantity of aggressive interactions *P. adelus* may represent a larger impact due to a higher volume of attacks due to the population size and distribution (Eurich et al. 2018a). Therefore, we suggest caution generalising the effects of territorial damselfish aggression as it pertains to roving herbivore foraging dynamics without species-specific behavioural observations.

Due to the limited aggressive behaviours observed in the present study the overall relative abundance of roving herbivores was not affected by the removal of *P. adelus*. We observed no change in abundance for parrotfish, rabbitfish, or surgeonfish despite approximately 300 less territorial damselfish on the reef flat and reef crest. This contradicted our hypothesis, as it is known that territorial damselfish defend benthic resources from roving herbivores (Foster 1985b, Hixon and Brostoff 1996, Catano et al. 2014). However, Ceccarelli et al. (2005b) also found that territorial damselfish in the same region as the present study were fairly inefficient at excluding roving herbivores from their territories. Furthermore, no effect of the exclusion of roving herbivores by territorial damselfish could be detected. Therefore, in Kimbe Bay it appears that territorial damselfish do not have a strong influence on the habitat structure by reducing the local abundance of roving herbivores through aggressive defence.

Additionally, we found no significant differences in parrotfish foraging activity following the removal of *P. adelus* in the present study. Previous research has demonstrated conflicting results when examining the impacts of territorial damselfish aggression on roving herbivore foraging. Some studies suggest that territorial damselfish limit the ability of roving herbivores to access desirable algae, which is in higher concentration within the territorial boundaries (Klump et al. 1987), and thus causes a decrease in grazing intensity (Hixon and Brostoff 1996). The territorial defence has also been documented to influence parrotfishes diet in the Caribbean. Bruggemann et al. (1994a) provided evidence that territorial damselfish aggression can lead to parrotfishes ingesting higher proportions of inferior food types. Parrotfishes were more likely to forage outside the damselfish territories to avoid energetically expensive interactions despite superior food resources. Further, experimental removals of territorial damselfish have also led to increased grazing rates of roving herbivores and a rapid reduction in turf cover (Mahoney 1981, Hourigan 1986). Contrastingly, our results show that parrotfish foraged at the same rate and intensity following the removal of *P. adelus* and do not corroborate the previously described studies. The present study instead supports the findings of two herbivore exclusion experiments, where no evidence was obtained that territorial damselfish influence the benthic impacts of parrotfish (Ceccarelli et al. 2005b, Ceccarelli et al. 2006). In these studies, some algal taxa increased in cover suggesting that foliose macroalgae and even some filamentous algae are suppressed when territorial damselfish are present. While variation in foraging behaviours of parrotfish is well established in the literature (Bellwood and Choat 1990, Bruggemann et al. 1994b, Bonaldo et al. 2005, Francini-Filho et al. 2010), patterns observed in Kimbe Bay are now confirmed and thus cannot be explained by behavioural variability.

Rabbitfish occupied the study zone but were less abundant than the other families and thus were rarely observed foraging. The lack of an agonistic influence from *P. adelus* was likely due to their low abundance and the limited observed aggression from *P. adelus*. However, the morphological specializations and foraging behaviour of rabbitfish may have also played a role. Fox and Bellwood (2013) revealed that rabbitfish feed to a greater degree than other herbivores from reef crevices and interstices, which are not common microhabitats in *P. adelus* territories (Eurich et al. 2018a). In addition, rabbitfish feed in pairs, with one fish frequently assuming an upright vigilance position in the water column while the partner forages in the reef substratum (Brandl and Bellwood 2015). Thus, no changes in abundance or foraging rates were detected, as the most common observation was non-feeding pairs swimming through *P. adelus* territories. A more detailed study targeting the movement of rabbitfish pairs is required to further assess the influence of territorial damselfishes on the removal of macroalgae by siganids (Fox and Bellwood 2008).

Unexpectedly, the removal of *P. adelus* resulted in a significant decrease in surgeonfish feeding despite overlap in resource use and competitive interactions (Robertson et al. 1979). We argue a higher foraging activity prior to the removal of *P. adelus* indicates that *P. adelus* may modify the benthic composition in a way that benefits surgeonfish. Ceccarelli et al. (2001) reviewed the benthic influence of territorial damselfish and found that the guild influences the algal matrix by removing unwanted sediment from the epilithic algal matrix. This is corroborated by other intermediate territorial damselfish work (Hata and Kato 2004, Ceccarelli 2007, Hata and Ceccarelli 2016). Our results suggest that *P. adelus* did not have a strong influence on the algae and coral cover in Kimbe Bay, but did influence sediment dynamics on the reef flat and reef crest. The removal plots had a significantly higher proportion of sediment compared to controls and the pre-removal surveys. Increased benthic sediment loads within the algal turf matrix can suppress herbivory and detritivory (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Tebbett et al. 2017b). In the present study, the increase in sediment following the decrease of *P. adelus* likely decreased the foraging patterns of surgeonfish, which selectively target detritus and avoid sediment (Purcell and Bellwood 1993, Goatley and Bellwood 2010, Tebbett et al. 2017a). Tebbett et al. (2017b) used feeding trials with *Ctenochaetus striatus*, a focal species in the present study, to show that detritivorous surgeonfish can also distinguish sediment grain sizes within algal turfs and selectively feed to avoid fine sediments. Recent research confirms that total sediment loads can mediate feeding selectivity of some surgeonfish but that species-specific differences are present (Tebbett et al. 2017c). Together, this suggests that *P. adelus* contributes to the overall sediment dynamics and benthic herbivory and detritivory patterns in Kimbe Bay.

Conclusions

In conclusion, our research indicates that the paradigm that all territorial damselfish negatively impact roving herbivores through territorial behaviour is not always the case. In Kimbe Bay, *P. adelus* did not have a major impact on parrotfish and rabbitfish abundance and foraging activity and did not influence the algae and coral assemblages. Instead, *P. adelus*, an intermediate territorial damselfish, positively influenced surgeonfish foraging and reef sediment dynamics. This finding adds to the growing view that the interactions between these families of fishes is complex. Previous studies suggesting that all territorial damselfish reduce foraging rates of roving herbivores may not be applicable in all systems, or for all species. We suggest that this particular damselfish does not influence the feeding rates of surgeonfish through direct aggressive interactions, but instead contributes indirectly by removing sediment from algal turfs. Understanding how guilds of fishes interact with one another and their environments is important in the face of increasing anthropogenic and climate change associated impacts. As sediment inputs onto coral reefs continue to increase globally through terrestrial runoff, dredging, and other coastal land use practices, understanding the interactions and ecological processes among fishes on coral reefs is critical.

Chapter 6

General Discussion

A central aim of community ecology is to understand how communities are spatially and temporally organized by identifying, interpreting, and explaining general patterns that underlie the structure of animal assemblages. Patterns and differences in species distributions have been explained in a variety of ways: one species may exclude a subordinate through interference competition or, alternatively, the partitioning of resources may reduce direct interactions and facilitate coexistence. Certainly, the abundance and quality of a resource is a primary driver for shaping ecological communities. Species interactions further govern population distributions across space and gradients in the natural environment. Field ecologists have measured the potential effects of resource partitioning and competition on the coexistence of ecologically similar species by manipulations of competing species and/or essential resources. Decades of research have demonstrated that the nature and availability of finite resources (e.g., habitat and food) influences the abundance and diversity of animals. However, the ongoing debate on the mechanisms of coexistence of coral reef fishes has been largely pursued in the absence of detailed information on the extent of fine-scale partitioning or knowledge of species-level interactions (Gravel et al. 2011, Connolly et al. 2014). Increasing habitat degradation will directly and indirectly intensify competitive interactions over limited resources, with the loss of specialised species through local extinction posing a severe threat to coral reefs, one of the world's most biodiverse ecosystems. Thus, the species-specific differences are particularly important when considering the functional role and coexistence of a taxa that is abundant and important to the overall community.

This thesis investigated the mechanisms that drive species distributions and ecological partitioning along gradients in the natural environment as a precursor to the long-term ecological changes on coral reefs. **Chapter 2** first established the fine-scale partitioning of territorial damselfishes at Kimbe Bay, Papua New Guinea, which provided the context for the following chapters to explore the mechanisms of coexistence. **Chapter 3** supplemented the habitat partitioning research by assessing the diet of the 7 species. These chapters together provided evidence that microhabitat selectivity and dietary diversification facilitate the co-habitation of species within a reef zone. The Chapter 2 'bottle experiment' further confirmed that interspecific aggression maintains the distributional boundaries between neighbours and limits population overlap. In order to substantiate how competitive interactions and resource partitioning influence species coexistence in a complex ecosystem a large-scale field experiment was conducted. **Chapter 4** demonstrated that when exploring coexistence in reef fish communities, the more traditional niche mechanisms (i.e., Chapter 2 and Chapter 3) operate alongside direct and indirect competitive dynamics, and within highly diverse systems these ecological processes are magnified. Moreover, the thesis highlights the importance of challenging common generalisations and paradigms. By examining the functional role of territorial damselfishes in Chapter 3, this research provides evidence of novel dietary diversification and planktivory in a guild that was previously categorised as strictly reef-based feeders. Lastly, **Chapter 5** challenged the generalisation that all territorial damselfish negatively impact the foraging behaviour of roving herbivores. Results indicate that territorial damselfish may instead contribute to surgeonfish foraging indirectly through the removal of sediment. These chapters provide compelling evidence of the importance of addressing ecological theory with a multifactorial perspective of the processes and mechanisms that govern coexistence within a community and the functional role of key species.

6.1 Coexistence of territorial damselfishes

Resource partitioning is refined by interactions among neighbouring species which regularly come into contact with one another (MacArthur 1958). Further, ecologically similar animals facilitate coexistence by acting as generalists or specialists when resource availability is limited (MacNally 1995). On coral reefs where habitat is limited, neighbouring fishes with overlapping distributions may coexist if they have contrasting patterns of habitat selectivity and versatility. These concepts have been well studied by coral reef fish ecologists and sparked the first real debate of reef fish coexistence (Smith and Tyler 1972, 1973, Sale 1976, 1977, Talbot et al. 1978). This thesis was not motivated to challenge early theory, resurrect old ideas stemming from methodological limitations or revisit debates that were never resolved. Driven by an astonishing subdivision of ecologically similar species, this thesis set out to theoretically explain a striking pattern, previously undescribed at the present scale. By applying theoretical ecology from terrestrial science and the early reef fish coexistence literature, this thesis highlights two thoroughly documented founding principles: 1) Ecosystems are dynamically interacting systems of organisms, the communities they make up, and the abiotic components of their ecosystems; and 2) Few complex ecological patterns can be described exclusively by one mechanistic process. Results from this thesis provide evidence that components of each founding theory are valid and suggest that coexistence of the 7 intermediate territorial damselfish is a multi-factorial process of traditional niche partitioning coupled with competitive dynamics (Hixon 2011, Pereira et al. 2015).

Habitat partitioning

Ecosystems with exceptionally high biodiversity require fine partitioning and competitive interactions among sympatric species. These multi-species competitive networks are rare. This thesis was conducted in Kimbe Bay on the northern coast of West New Britain in PNG following preliminary surveys (J. G. Eurich) and a decade of exploratory research (G. P. Jones, M. I. McCormick, P. L. Munday, M. Srinivasan, and M. C. Bonin). Kimbe Bay lies within the Coral Triangle of the Indo-Pacific, the region recognized for the highest coral reef biodiversity (Roberts et al. 2002). Over 800 species of reef fishes and some 300 species of corals are recorded in this region (Spalding et al. 2001, Maniwavie et al. 2000). The specific study sites used in this thesis have a particularly high density and diversity of intermediate, shallow-water territorial damselfish and provided the foundation of the studies (Ceccarelli 2007). Damselfish within each reef zone revealed partitioning of space with distinct distributions over a distance of 1 − 2 m. Chapter 2 represents the finest scale of habitat partitioning yet documented for this guild. This level of partitioning may reflect the high species diversity of territorial damselfish within the Coral Triangle. Where species richness is high, ecologically similar species partition resources to a greater extent and are more specialized (Schoener 1974, Ross 1986, Bellwood et al. 2006, Holbrook et al. 2015). I hypothesise that in other regions with a lower abundance of territorial damselfishes, space occupancy, and diversity (e.g. Great Barrier Reef), the fine-scale spatial partitioning observed in this study will not be as prevalent or ecologically necessary (Ceccarelli 2007). Therefore, if any readers are presented with the opportunity to visit Kimbe Bay, please do. The spatial partitioning of the territorial damselfish populations are so fine an observer can see the division among species while swimming along the natural reef profile. The fascinating zonal distributions and distinct population boundaries encourage further exploration.

Microhabitat use and selectivity

Ecological partitioning along natural resource gradients has been found in plants (Grace and Wetzel 1981), reptiles (Schoener 1974), birds (Burger et al. 1977), rodents (Ziv et al. 1993), and many other taxa. On coral reefs, live and dead corals provide the majority of structural complexity, and reef fishes are strongly associated with the structure for shelter (Ehrlich 1975, Fishelson 1980, Sale 1980, Jones et al. 2004, Munday 2004, Pratchett et al. 2008, McCormick and Weaver 2012). Species that overlap in resource use partition the available habitat and associated foods in ways that will minimize interspecific competition and increase their fitness. Habitat partitioning has been widely described for a variety of reef fishes across multiple tropical regions (Doherty 1983, Robertson and Gaines 1986, Wainwright 1988, Shpigel and Fishelson 1989, reviewed by Williams 1991). Therefore, I hypothesised in Kimbe Bay where habitat is limited, neighbouring fishes with overlapping distributions may coexist if they have contrasting patterns of habitat selectivity and versatility. I first investigated the habitat use and availability across the environmental gradient, as previous work had clearly shown that fishes partition space along depth gradients (McGehee 1994, Nanami et al. 2005, Jankowski et al. 2015, MacDonald et al. 2016). In Chapter 2, I demonstrated that species within the same reef zone exhibited differences in microhabitat selectivity. While there was some overlap in microhabitat use among the 7 species, with all commonly associated with rubble substrata, there were distinct differences in the substrata used. Moreover, Chapter 2 established the pairing of a species with generalist microhabitat use to a species with specialist microhabitat use within each zone, despite all habitats being relatively abundant across reef zones. The difference in ecological versatility among neighbouring species therefore facilitates coexistence through the partitioning of microhabitats.

Trophic diversification among species

After addressing habitat partitioning I examined the second most important resource on coral reefs: food. When assessing trophic niche partitioning in Chapter 3 subtle differences among the diet of neighbouring species was established, which reinforced Chapter 2's original hypotheses of coexistence. The isotopic distributions were linked to distribution patterns along the reef profile gradient. Where the distribution of species overlapped, these species were characterised by differences in source contributions. Adjacent species exhibited high to intermediate trophic niche partitioning when examining pelagic versus reef-based (benthic) dietary sources. The dietary diversification observed was likely refined by differences in ecological versatility between adjacent species. While opportunistic feeding has been previously documented, neighbouring territorial damselfish individuals exploited different feeding strategies over long-term diet trends during mutually inclusive time periods. Bearhop et al. (2004) discriminated between different types of generalists within a population, with species either all taking a wide range of food types (type A) or specializing in a different but narrow range of food types (type B). The large variation of $\delta^{13}C$ values with little difference in trophic position in the present study could be related to perpetual intra-population variability in prey choice (i.e., type B), thus promoting coexistence (Frédérich et al. 2016).

Competitive dynamics

Together, this suggests that neighbouring damselfish are constraining their microhabitat use and diet to facilitate the co-habitation of reef zones. However, microhabitat selectivity and dietary diversification alone was insufficient in explaining the distinct zonation and limited distributional overlap. I argue diet and habitat partitioning play a supplementary role to competitive interactions in reinforcing the patterns of spatial partitioning and coexistence among ecologically similar species. Chapter 2 examined the aggression between neighbouring species using a ‘bottle’ experiment. The levels of aggression elicited by neighbouring species were significantly higher for all 7 species compared with non-adjacent species, suggesting that interference competition contributes to a sharp transition from one species to another along the reef profile. Species that did not commonly come into contact with one another received little or no aggression despite occupying relatively similar niche breadths. These findings support the logic of animal conflict and competition theory (Maynard Smith and Price 1973, Connell 1983, Schoener 1983, Maynard Smith and Harper 1988). Aggression is expensive because it imposes energy and time costs and increases the risk of injury (Clutton-Brock and Parker 1995, Tibbetts and Dale 2004). Individuals do not need to be aggressive to all species, just the ones that pose a direct threat. Within a reef zone, damselfish showed higher aggression towards a neighbouring species due to the increased competition for space and habitat. Thus, interspecific aggression helps maintain the distributional boundaries between neighbouring populations.

Early coral reef studies stressed intense interspecific competition for living space as the main driver behind niche partitioning (Smith and Tyler 1972, 1973, Smith 1978, Jones 1991). A large body of literature has since confirmed that interspecific aggression results in the spatial segregation of many fishes (Ebersole 1977, 1985, Robertson and Gaines 1986, Robertson 1996, Bay et al. 2001, Jones and McCormick 2002, Boström-Einarsson et al. 2014). Chapter 2 provided additional evidence that agonistic interactions among species within the guild can explain the high degree of resource partitioning and limited distributional overlap. However, an experimental removal of a dominant competitor was necessary to understand if interference competition is present and if subordinate distributional shifts would occur. In Chapter 4, I employed a large-scale removal experiment to examine the extent to which the most abundant species influenced the distribution and abundance of neighbouring and non-neighbouring species in the guild. The findings indicated that the distinct distribution patterns among the reef crest species were linked to levels of interspecific agonistic behaviour. The competitive release following the removal of a superior competitor resulted in comprehensive direct and indirect effects, with the subordinate neighbour shifting into the newly available space, followed by successive shifts in species responding to the change in the distributions of their immediate neighbours. Similar to the classical Connell (1961) intertidal experiments on *Balanus* and *Chthamalus*, this field experiment demonstrated territorial damselfishes have a fundamental niche that extends to the reef crest, but naturally occupy a smaller realised niche when in competition with more dominant species (Whittaker et al. 1973). In Chapter 4, I demonstrated that competitive networks within a community can operate directly, by interference competition, and indirectly through a competitive release among ecologically similar species. In addition, Chapter 4 expands on competitive interaction networks by providing insight into the mechanisms of indirect effects in a multi-species comparison, which have previously received little attention (Bonin et al. 2015).

This thesis supports the conclusion that interference competition contributes to explaining the spatial structure and abundance in a multi-species guild of territorial damselfish. The distinct distribution patterns characterised by a high degree of fine-scale partitioning among the main reef-crest species were linked to levels of agonistic behaviour and niche partitioning (both habitat and food). I provided additional strong evidence that species with similar resource requirements coexist through direct and indirect competitive mechanisms. Lastly, the habitat use, diet, and agonistic behaviours of the 7 territorial damselfish species previously were poorly understood as the literature is biased towards larger-bodied species.

Table 6.1 Summary of Kimbe Bay, PNG territorial damselfish niche breadth from Chapter Two, Three, and Four. Species: *Pomacentrus tripunctatus, Chrysiptera unimaculata, Pomacentrus bankanensis, Pomacentrus adelus, Plectroglyphidodon lacrymatus, Neoglyphidodon nigroris, Pomacentrus burroughi*.

Species	Reef zone	Microhabitat use	Diet	Aggression
P. tripunctatus	Reef flat	Generalist Rubble and macroalgae	Omnivore	Low
C. unimaculata	Reef flat	Specialist Rubble	Herbivore	Low
P. bankanensis	Reef flat	Specialist Rubble	Planktivore	High
P. adelus	Reef crest	Specialist Rubble	Omnivore	Medium
Pl. lacrymatus	Reef crest	Specialist Turf	Herbivore	Medium
N. nigroris	Reef slope	Generalist Rubble and turf	Planktivore	High
P. burroughi	Reef slope	Generalist Rubble and sediment	Omnivore	Low

6.2 Challenging paradigms

Territorial damselfish have recently been categorised into three guilds based on the effect of the various species on benthic assemblage structure and through interspecific aggression: intensive farmers, extensive farmers, and an intermediate group (Hata and Kato 2004, Ceccarelli 2007, Hata and Ceccarelli 2016). Where intensive farmers weed low diversity algal turfs intensively with aggressive defence, extensive farmers weed and defend larger territories to a lesser extent, and an intermediate group maintains discrete territories of algal turf that are different from the surrounding algae (Emslie et al. 2012, Pratchett et al. 2016). The 7 species of territorial damselfish researched in this thesis are predominantly (though not necessarily exclusively) benthic-feeding ‘intermediate farmers’, with the exception of *Pl. lacrymatus*, which was classified as an ‘extensive farmer’ (reviewed by Pratchett et al. 2016). Intensive and extensive farming species (e.g., *Stegastes* spp.) that maintain conspicuous algal mats are known to defend their territories aggressively (Ceccarelli et al. 2001, Hoey and Bellwood 2010, Emslie et al. 2012). However, these species tend to occur in patches and are less abundant than intermediate farming species (Pratchett et al. 2016). Despite intermediate farmers influencing the environment to a lesser degree, the territories support greater quantities of palatable filamentous algae (Ceccarelli 2007) and reduce coral larvae settlement (Casey et al. 2014). This thesis set out to address these broad functional classifications of territorial damselfishes and shed light on the understudied intermediate group, specifically investigating interspecific differences among similar species. In addition, previous literature presented conflicting evidence that all territorial damselfish, especially intermediate farming species – the most abundant guild (Pratchett et al. 2016), hinder the foraging patterns of roving herbivores through agonistic interactions.

Territorial damselfish feeding strategies

Damselfishes, including known planktivores, corallivores, and territorial herbivorous species, were previously assigned to three trophic groups based on feeding strategies - pelagic feeders zooplanktivores, reef-based feeders corallivores algivores or herbivores, and an intermediate group of omnivores (Frédérich et al. 2009, 2016, Gajdzik et al. 2016). While comparative studies have not focused solely on territorial damselfish, a similar trophic diversity was observed within the guild of territorial damselfish in Chapter 3. The trophic diversity within this group was much higher than expected based on previous literature. Territorial damselfish are commonly classified as herbivorous or omnivorous (Ceccarelli et al. 2001, Frédérich et al. 2016). However, Chapter 3 found evidence of planktivory within the guild. While this is not unique for pomacentrids, as damselfish (e.g., Chrominae) have served as a model for this trophic strategy (Frédérich et al. 2013), territorial damselfish have not previously been described as pelagic feeders. Through the integrated perspective of trophic role provided by stable isotopes, Chapter 3 documents *Pomacentrus bankanensis* and *Neoglyphidodon nigroris* as pelagic feeders (supporting prior J. G. Eurich pers. obs. from Chapter 2 video data) under the suggested criterion of a species to consume ≥ 70% zooplanktonic prey or filamentous algae to not be considered an intermediate omnivore (Frédérich et al. 2016). Chapter 3 represents the first isotopic values for these species and highlights the need for species-specific evidence when assigning a species to broad taxa-related functional classifications.

The effect on roving herbivores

Several experimental studies have shown that the aggressive exclusion of roving herbivores by extensive or intensive farming species affects the benthic assemblage structure (Hixon and Brostoff 1983, Russ 1987, Hixon 1996, Ceccarelli et al. 2005a). The common paradigm is that all territorial damselfishes reduce foraging rates of roving herbivores through aggressive interactions and territorial defence. However, Chapter 5 challenged this generalisation by investigating the effect of intermediate farming species on roving herbivores in Kimbe Bay. Some studies have shown that roving herbivores will actively avoid the territories of territorial damselfish to feed on desirable algae without harassment (Robertson et al. 1976, Hamilton and Dill 2003). Additionally, surgeonfish and parrotfish periodically may use schooling behaviours to overwhelm territorial damselfish and gain access (Robertson et al. 1976, Foster 1985a). However, Ceccarelli et al. (2005b) found that extensive and intermediate territorial damselfish were fairly inefficient at excluding roving herbivores from their territories and roving herbivores had a significant impact on benthic habitat, both with and without the presence of territorial damselfish. Chapter 5 supports these findings as the experimental removal of the intermediate farming damselfish *Pomacentrus adelus* did not influence the overall relative abundance of roving herbivores or the foraging activity of parrotfish and rabbitfish. Contradicting the common generalisation, the removal of *P. adelus* resulted in a significant decrease in surgeonfish feeding despite overlap in resource use and competitive interactions (Robertson et al. 1979). I argued a higher foraging activity prior to the removal of *P. adelus* indicates that *P. adelus* modifies the benthic composition in a way that benefits surgeonfish. Hence, the emerging paradigm of a strong interaction between roving herbivores and all types of territorial damselfish was not supported by the findings of Chapter 5. I suggest that this particular damselfish and other intermediate territorial damselfish species may not influence the feeding rates of surgeonfish through direct aggressive interactions, but instead indirectly contribute by removing sediment from algal turfs. These findings add to the growing view that the interactions between these families of fishes are complex and that common generalisations do not always hold true.

6.3 Ecological implications

Understanding how guilds of fishes interact with one another and their environments is important in the face of increasing anthropogenic and climate change associated impacts. As sediment inputs onto coral reefs continue to increase globally through terrestrial runoff, dredging, and other coastal land use practices, understanding the interactions and ecological processes among fishes on coral reefs is critical. The results from Chapter 5 revealed *P. adelus* contributes to the overall sediment dynamics through territorial maintenance, which influences the benthic herbivory and detritivory patterns of surgeonfish in Kimbe Bay. Recent research confirms that total sediment loads can mediate feeding selectivity of some surgeonfish but that species-specific differences are present (Tebbett et al. 2017c). I have shown that in Kimbe Bay, *P. adelus* modifies the benthic composition in a way that benefits surgeonfish foraging and without the presence of *P. adelus* surgeonfish are less apt to forage, which directly impacts reef sediment dynamics. In Kimbe Bay, *P. adelus* is abundant over multiple reef zones in high densities where no intensive and extensive farming species are present (Ceccarelli 2007). Despite the lower quality and quantity of aggressive interactions *P. adelus* represents a larger impact due to a higher volume of attacks due to the population size and distribution. The research conducted for this thesis distinguishes between the three farming-based classifications of territorial damselfish and in doing so highlights important species-specific differences. These differences are becoming increasingly important as roving herbivorous fishes play a critical role on coral reefs in reducing algal biomass and preventing alternative algal dominated stable states (Mumby et al. 2006, Hughes et al. 2007, Francini-Filho et al. 2010). By understanding the foraging patterns of roving herbivores and territorial damselfishes agonistic interactions, Chapter 5 helps define the mechanistic drivers that underlie reef habitat structure and resilience.

Revealing indirect relationships among ecologically similar species within a complex community remains a formidable challenge, yet it is necessary to gain generality and predictive power (Bonin et al. 2015). Changes to important trophic links between two species can indirectly alter the distribution and abundance of species between trophic levels.

However, they can also have indirect effects on interactions among species within the same trophic levels (Pace et al. 1999, Shurin et al. 2002). Similar knock-on effects of subordinate competitors within trophic levels may be present after the collapse of a primary competitor and have received much less attention (Navarrete et al. 2000, Gosnell and Gaines 2012). This thesis demonstrates that competitive networks within a community operate directly and indirectly and that a competitive release can influence species that are not directly associated. Evidence presented in Chapter 4 suggests that the loss of a species through a removal influences subordinate species and overall spatial assemblage. Cerny-Chipman et al. (2017) addressed this gap among seastars and whelks and found diverging patterns in abundance of the subordinate competitor following the collapse of the keystone species. While no niche expansion was observed, the study highlights the importance of knock-on community effects within adjacent trophic levels. The progressive shifts of subordinate species along a communal resource axis following the removal of a dominant competitor experimentally confirm the observational findings of Cerny-Chipman et al. (2017). In addition, it is known that reduced habitat quality through disturbances, such as ocean acidification and coral bleaching, can alter and even reverse pairwise competitive interactions between species (McCormick 2012, McCormick et al. 2013, Boström-Einarsson et al. 2014). With growing pressures, including climate change, globalization, and migration, on the world ecosystems, we hope these effects do not extend to the progressive loss of species that cannot compete for the dwindling resources.

6.4 Concluding remarks

The outcomes of this thesis demonstrate that it is time to move beyond past debates that have consumed coral reef fish ecologists and embrace the pluralistic notion that competition is one of many factors that shape coral reef community structure. First and foremost, several chapters have examined the importance of partitioning habitat and diet as a means to reduce conflict among sympatric species. Driven by an astonishing subdivision of ecologically similar species, this thesis explained a striking pattern, previously undescribed at the present scale. While microhabitat partitioning and trophic diversification clarify the high degree of resource partitioning and limited distributional overlap, the mechanisms of coexistence were a result of direct and indirect competitive dynamics. The findings of this thesis support Bonin et al. (2015) in that intraspecific and interspecific competitors can alter the patterns of distribution, abundance, and resource use of ecologically similar species. Despite 4 decades of research, this issue was not entirely resolved (see reviews by Hixon 1991, Jones 1991, Hixon and Webster 2002, Jones and McCormick 2002, Forrester 2015, Hixon 2015). Combined, the results from this thesis help close this debate by demonstrating that when exploring coexistence in reef fish communities, the more traditional niche mechanisms (Chapters 2 and 3) operate alongside competitive dynamics (Chapters 4), and within highly diverse systems these ecological processes are magnified. Through a novel multi-species large-scale experiment, this thesis highlights the importance of analysing ecological interactions at the community level to address indirect effects that may otherwise be missed if examining pairwise interactions. In addition, microhabitat use and selectivity (Chapter 2), dietary diversification (Chapter 3), and agonistic interactions with functionally important reef fish families (Chapter 5) of an understudied guild of fishes were investigated. The thesis highlights the importance of challenging common generalisations and paradigms in a changing environment. Clearly, territorial damselfish are not all ecologically equivalent and the classifications of extensive, intensive, and intermediate farmers (Hata and Kato 2004, Ceccarelli 2007, Hata and Ceccarelli 2016) should permanently be used when theorising the impact of territorial damselfish on coral reefs in the future. By examining the functional role of territorial damselfishes this thesis provides evidence of novel dietary diversification (Chapter 3) and demonstrates the complexity of territorial damselfish and roving herbivore interactions (Chapter 5). It is likely that variation in the health of coral reefs will alter these critically important interactions further; however, more research is needed to determine these effects. Only by examining multiple stressors on coral reef fishes over ecologically relevant scales will it be possible to gauge how marine populations will respond to a rapidly changing environment.

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Appendix

Publication list

Publications arising from this thesis

Chapter 2. **Eurich JG**, McCormick MI, Jones GP (2018a) Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes. *Marine Ecology Progress Series.* 587: 201–215. http://dx.doi.org/10.3354/meps12458

Chapter 3. **Eurich JG**, Matley JK, Baker R, McCormick MI, Jones GP (*in press*) Stable isotope analysis reveals trophic diversity and partitioning in territorial damselfishes on a low latitude coral reef. *Marine Biology.*

Chapter 4. **Eurich JG**, McCormick MI, Jones GP (2018b) Direct and indirect effects of interspecific competition in a highly partitioned guild of reef fishes. *Ecosphere.* 9: e02389. https://doi.org/10.1002/ecs2.2389

Chapter 5. **Eurich JG**[1], Shomaker SM[1], McCormick MI, Jones GP (2018c) Herbivore foraging dynamics after the removal of an abundant territorial damselfish in Kimbe Bay, Papua New Guinea. *Journal of Experimental Marine Biology and Ecology.* 506: 155–162. http://doi.org/10.1016/j.jembe.2018.06.009

Publications not arising from this thesis

Richardson LE, Graham NAJ, Pratchett MS, **Eurich JG**, Hoey AS (2018) Mass coral bleaching causes biotic homogenization of reef fish assemblages. *Global Change Biology.* 24: 3117–3129. https://doi.org/10.1111/gcb.14119

Eurich JG, Selden RL, Warner RR (2014) California spiny lobster preference for urchins from kelp forests: implications for urchin barren persistence. *Marine Ecology Progress Series.* 498: 217–225. https://doi.org/10.3354/meps10643

Conference presentations during candidature

Eurich JG (2018) Breaking paradigms: a damselfish and surgeonfish story. *UCSD, Scripps Coral Club*. San Diego, CA, USA.

Eurich JG, McCormick MI, Jones GP (2017) The damselfish domino effect: a competitive release in a highly partitioned guild reveals subordinates versatility. 10th *Indo-Pacific Fish Conference*. Tahiti, French Polynesia.

Eurich JG, Miller AH, McCormick MI, Jones GP (2016) A competitive release in a guild of coral reef fishes reveals subordinates versatility: will other specialists follow suit if resource partitioning is reduced? *13th International Coral Reef Symposium*. Honolulu, HI, USA.

Miller AH, **Eurich JG** (2016) Using spatial statistics to examine damselfish population distributions after a competitive release. *ESRI User Conference*. San Diego, CA, USA.

Miller AH, **Eurich JG** (2016) Using spatial statistics to examine damselfish population distributions after a competitive release. *California GIS Conference*. Anaheim, CA, USA.

Eurich JG (2015) Processes underlying niche partitioning and ecological versatility in an guild of coral reef damselfishes. *ARC Centre of Excellence for Coral Reef Studies, James Cook University*. Townsville, QLD, AU.

Supplementary information Chapter 2

The following supplement accompanies the article

Eurich JG, McCormick MI, Jones GP (2018a) Habitat selection and aggression as determinants of fine-scale partitioning of coral reef zones in a guild of territorial damselfishes. *Marine Ecology Progress Series.* 587: 201–215. http://dx.doi.org/10.3354/meps12458

Text S2.1 Microhabitat availability

The reef flat (RF), reef crest (RC), and reef slope (RS) did not differ significantly in benthic cover in most categories but did show some subtle differences in percent cover (Appendix: Fig. S2.1). Non-biological (3.5 - 7.6%), sediment (3.7 - 4.5%), and other (22.4 - 23.6%) did not differ significantly between zones. Live coral had higher cover on the reef slope than the crest or flat ($p < 0.0001$). Additionally, *Turbinaria* sp. (13.0%) and *Padina* sp. (1.6%) were significant substrates on the reef flat and non-abundant in other zones ($p < 0.0001$ and $p = 0.009$, respectively). Conversely, although turf was a major substratum on all zones, the reef crest had a considerable amount (22.8%), with significantly less on the reef slope (13.5%, $p = 0.009$) and the reef flat (19.1%, $p = 0.004$). Rubble was prevalent on all zones but was a major substrate on the reef slope (RF 7.2%, RC 9.5%, RS 16.5%). However, the comparison was non-significant due to high levels of variance within pooled transect data ($p = 0.488$ and $p = 0.150$). The reef flat and reef crest visually had less rubble but was skewed due to sparse concentrated rubble gutters that ran perpendicular from the flats to the crest through the survey sites (J.G. Eurich pers. observation).

Figure S2.1 Benthic composition by reef zone. The percent cover represents an average across all sites (n = 3) and transects (n = 12).

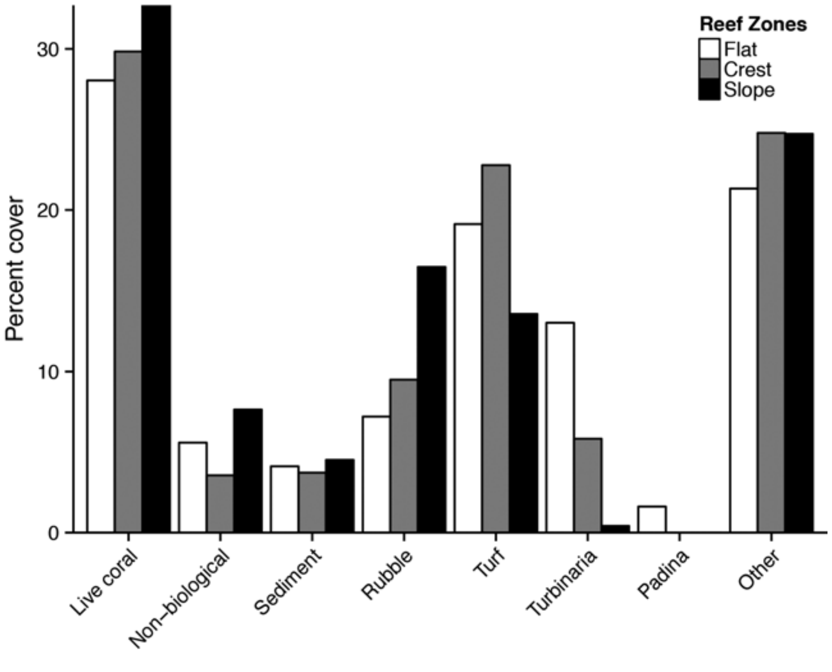


Table S2.1 Generalised linear mixed model coefficients testing for differences in benthic cover between reef zone (reef crest: RC; reef flat: RF; reef slope: RS) and site (Garbuna, Hanging Gardens, and Luba Luba). The parameter estimates and coefficients for the model best fit by maximum likelihood (Appendix: Table S2.2) are indicated.

Habitat	Source of variation	Fixed effects	Est.	SE	z-value	P-value (z)
Live coral	ZoneRC : SiteGarb	*intercept*	-2.200	0.058	-37.527	< 0.0001
		ZoneRF	-0.051	0.083	-0.619	0.535
		ZoneRS	0.356	0.085	4.176	< 0.0001
		SiteLuba	-0.344	0.092	-3.735	0.001
		SiteHGar	-0.466	0.188	-2.486	0.013
		ZoneRF : SiteLuba	0.285	0.127	2.236	0.025
		ZoneRS : SiteLuba	-0.144	0.137	-1.051	0.293
		ZoneRF : SiteHGar	0.345	0.196	1.765	0.077
		ZoneRS : SiteHGar	-0.024	0.176	-0.137	0.891
Non-biological substrate	ZoneRC : SiteGarb	*intercept*	-2.787	0.234	-12.45	< 0.0001
		ZoneRF	0.107	0.261	0.412	0.681
		ZoneRS	0.238	0.298	0.801	0.423
		SiteLuba	0.236	0.283	0.832	0.405
		SiteHGar	0.211	0.305	0.694	0.488
		ZoneRF : SiteLuba	-0.334	0.342	-0.974	0.330
		ZoneRS : SiteLuba	-0.116	0.360	-0.323	0.747
		ZoneRF : SiteHGar	-0.015	0.402	-0.036	0.971
		ZoneRS : SiteHGar	0.128	0.428	0.299	0.765
Sediment	ZoneRC	*intercept*	-2.392	0.128	-18.745	< 0.0001
		ZoneRF	0.144	0.172	0.837	0.402
		ZoneRS	0.052	0.182	0.286	0.775
Rubble	ZoneRC : SiteGarb	*intercept*	-2.188	0.161	-13.620	< 0.0001
		ZoneRF	0.076	0.199	0.380	0.704
		ZoneRS	0.336	0.171	1.970	0.488
		SiteLuba	0.029	0.208	0.139	0.890
		SiteHGar	0.046	0.139	0.331	0.741
		ZoneRF : SiteLuba	0.051	0.249	0.205	0.838
		ZoneRS : SiteLuba	-0.116	0.218	-0.530	0.596
		ZoneRF : SiteHGar	-0.083	0.163	-0.513	0.608
		ZoneRS : SiteHGar	0.169	0.165	1.025	0.305
Turf	ZoneRC	*intercept*	-1.356	0.119	-11.380	< 0.0001
		ZoneRF	0.048	0.151	0.320	0.749
		ZoneRS	-0.477	0.183	-1.609	0.009
Turbinaria	ZoneRC	*intercept*	-2.291	0.314	-7.303	< 0.0001
		ZoneRF	0.484	0.242	2.001	0.045
		ZoneRS	-0.887	0.557	-1.591	0.112
Padina	SiteGarb	*intercept*	-2.344	0.280	-8.380	< 0.0001
		SiteLuba	-0.349	0.367	-0.953	0.341
		SiteHGar	-0.116	0.360	-0.323	0.747
Other	ZoneRC	*intercept*	-2.818	0.141	-19.925	< 0.0001
		ZoneRF	0.342	0.210	1.629	0.103
		ZoneRS	0.221	0.189	1.170	0.242

Table S2.2 Generalised linear mixed model selection results and criteria for examining the relationships between reef zone and site for different types of benthic cover (as used in habitat availability). Coefficients and p-values used (Appendix: Table S2.1) were derived from selected model (*). The minimally adequate model was chosen according to the lowest Akaike information criterion (AIC). Replicates within reef sites (n = 3; Garbuna, Hanging Gardens, and Luba Luba) and replicate transects (n = 4) were included as random effects (RE) in all models + RE: + (1 | SubSite) + (1 | Transect). Proportion of count per transect (n = 20) was used for the weights within the formula (family: binomial ‘logit’). BIC: Bayesian information criterion; logLik: log-likelihood; deviance: null deviance; df.resid: residual deviance.

Source	Candidate models	AIC	BIC	logLik	deviance	df.resid	Model
Live coral	ReefZone*Site + RE	2502.4	2540.1	-1243.2	2486.4	815	*
	ReefZone + Site + RE	2509.4	2537.6	-1248.7	2497.4	817	
Non-biological substrate	ReefZone*Site + RE	522.3	549.2	-253.2	506.3	203	*
	ReefZone + Site + RE	519.5	539.6	-253.7	507.5	205	
Sediment	ReefZone*Site + RE	354.8	377.1	-169.4	338.8	113	
	ReefZone + Site + RE	354.4	371.2	-171.2	342.4	115	
	ReefZone + RE	352.5	366.4	-171.2	342.5	116	*
Rubble	ReefZone*Site + RE	796.8	824.5	-390.4	780.8	230	*
	ReefZone + Site + RE	793.4	814.2	-390.7	781.4	232	
Turf	ReefZone*Site + RE	1023.8	1052.2	-503.9	1007.8	251	
	ReefZone + Site + RE	1023.9	1045.3	-506.0	1011.9	253	
	ReefZone + RE	1022.3	1040.1	-506.1	1012.3	254	*
Turbinaria	ReefZone*Site + RE	492.2	515.4	-238.1	476.2	125	
	ReefZone + Site + RE	489.7	507.1	-238.9	477.7	127	
	ReefZone + RE	487.3	502.4	-239.0	477.9	128	*
Padina	[1]Site + RE	65.4	70.0	-28.7	57.4	19	*
Other	ReefZone*Site + RE	310.0	332.7	-147.0	294.0	117	
	ReefZone + Site + RE	309.3	326.3	-148.6	297.3	119	
	ReefZone + RE	307.5	321.6	-148.7	297.5	120	*

[1] *Padina* only occurs on the reef flat so analysis of zone was not performed due to a one level factor.

Table S2.3 Generalised linear model coefficients from experimental aggression trials.

Species	Source of variation	Fixed effects	Est.	SE	*z*-value	*P*-value (*z*)
Pomacentrus tripunctatus	Conspecific	*intercept*	1.791	0.380	4.713	< 0.0001
		Heterospecific	-1.204	0.419	-2.877	0.004
	Neighbour	*intercept*	1.609	0.244	6.606	< 0.0001
		Non-neighbour	-1.358	0.311	-4370	< 0.0001
Chrysiptera unimaculata	Conspecific	*intercept*	2.208	0.400	5.519	< 0.0001
		Heterospecific	-1.759	0.442	-3.978	< 0.0001
	Neighbour	*intercept*	1.720	0.260	6.616	< 0.0001
		Non-neighbour	-1.617	0.344	-4.695	< 0.0001
Pomacentrus bankanensis	Conspecific	*intercept*	4.006	0.339	11.824	< 0.0001
		Heterospecific	-1.386	0.367	-3.774	< 0.0001
	Neighbour	*intercept*	3.310	0.209	15.875	< 0.0001
		Non-neighbour	-0.712	0.281	-2.534	0.011
Pomacentrus adelus	Conspecific	*intercept*	2.388	0.293	8.166	< 0.0001
		Heterospecific	-0.841	0.319	-2.636	0.008
	Neighbour	*intercept*	2.153	0.169	12.770	< 0.0001
		Non-neighbour	-0.880	0.227	-3.885	< 0.0001
Plectroglyphidodon lacrymatus	Conspecific	*intercept*	3.077	0.404	7.614	< 0.0001
		Heterospecific	-0.937	0.438	-2.140	0.032
	Neighbour	*intercept*	2.694	0.245	11.017	< 0.0001
		Non-neighbour	-0.685	0.318	-2.154	0.031
Neoglyphidodon nigroris	Conspecific	*intercept*	3.512	0.408	8.600	< 0.0001
		Heterospecific	-1.777	0.444	-4.004	< 0.0001
	Neighbour	*intercept*	3.060	0.285	10.741	< 0.0001
		Non-neighbour	-1.527	0.346	-4.419	< 0.0001
Pomacentrus burroughi	Conspecific	*intercept*	2.460	0.181	13.595	< 0.0001
		Heterospecific	-1.291	0.205	-6.305	< 0.0001
	Neighbour	*intercept*	2.116	0.145	14.560	< 0.0001
		Non-neighbour	-1.059	0.185	-5.731	< 0.0001

Table S2.4 Resident species mean aggressive interactions (sum of category 2 display, 3 charge, and 4 bite; category 1 investigations omitted) towards neighbouring and conspecific stimulus species per 4 min trial (± SE, n = 10). No aggressive interactions were made towards the control stimulus. Rare category 1 interactions (investigations, displayed below; ± SE, n = 10) were observed immediately following bag placement.

		Stimulus species				
		Neighbour	Non-neighbour	Conspecific	Heterospecific	Control
Resident species	*P. tripunctatus*	5.0 ± 1.5	1.3 ± 0.3	6.0 ± 1.5	1.8 ± 0.5	0.1 ± 0.1
	C. unimaculata	5.6 ± 1.0	1.1 ± 0.4	9.1 ± 1.7	1.6 ± 0.4	0
	P. bankanensis	27.4 ± 4.9	13.4 ± 2.5	54.9 ± 9.0	13.7 ± 2.0	0
	P. adelus	8.6 ± 1.5	3.6 ± 0.5	10.9 ± 2.3	4.7 ± 0.7	0
	Pl. lacrymatus	14.8 ± 2.9	7.5 ± 1.9	21.7 ± 4.4	8.5 ± 1.7	0
	N. nigroris	21.3 ± 4.4	4.6 ± 1.1	33.5 ± 6.6	5.7 ± 1.2	0.1 ± 0.1
	P. burroughi	8.3 ± 1.2	2.9 ± 0.3	11.7 ± 1.8	3.2 ± 0.3	0

Supplementary information Chapter 3

The following supplement accompanies the article

Eurich JG, Matley JK, Baker R, McCormick MI, Jones GP (*in press*) Stable isotope analysis reveals trophic diversity and partitioning in territorial damselfishes on a low latitude coral reef. *Marine Biology*.

Figure S3.1 Prey contribution of a) territorial damselfish and b) obligates consumers from the multi-source (all prey types) mixing model. Box and whisker plot displays the range between 25% and 75% credibility quantiles, with error bars extending to the maximum and minimal values (97.5% and 2.5%, respectively), and the median represented by the bold line.

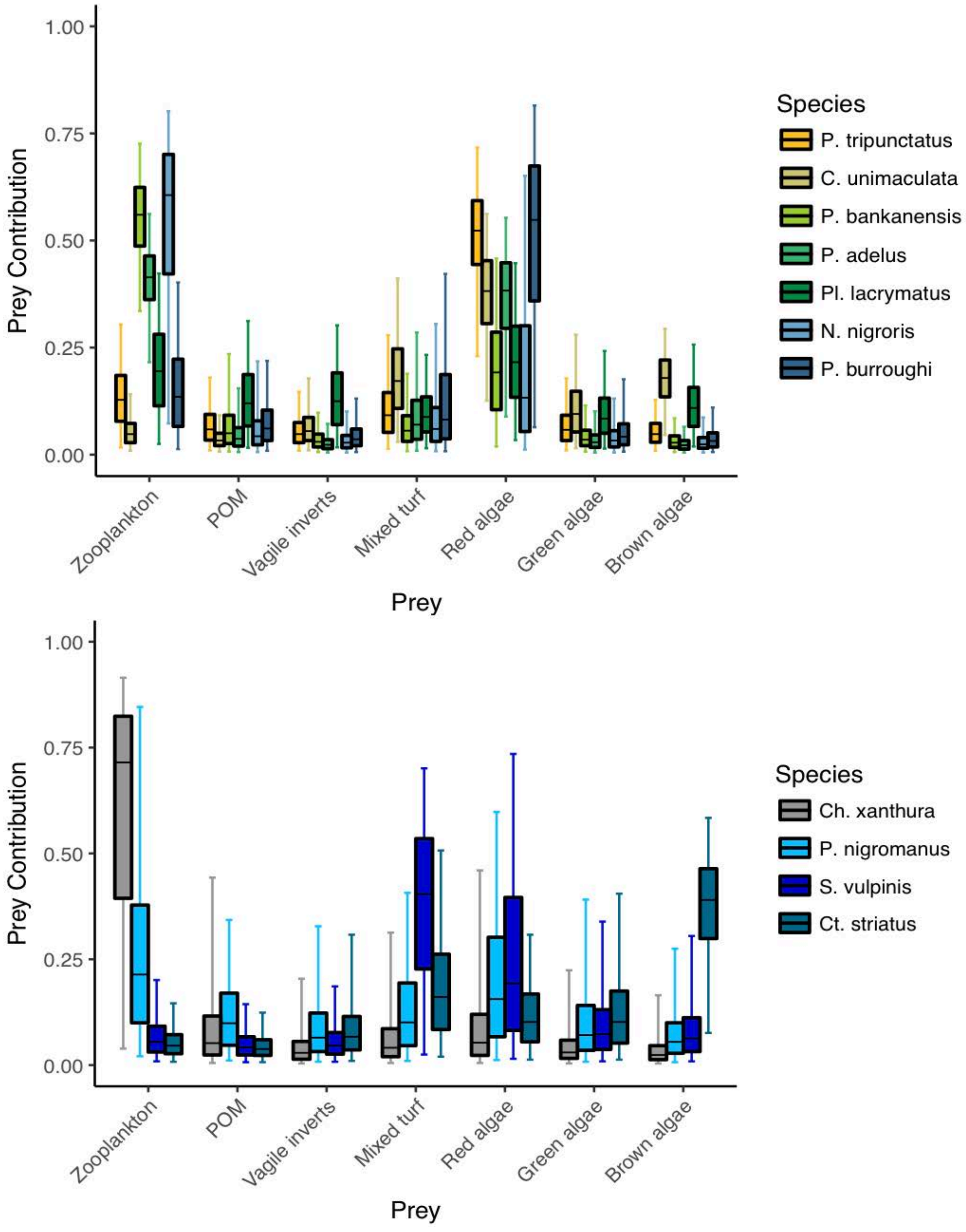
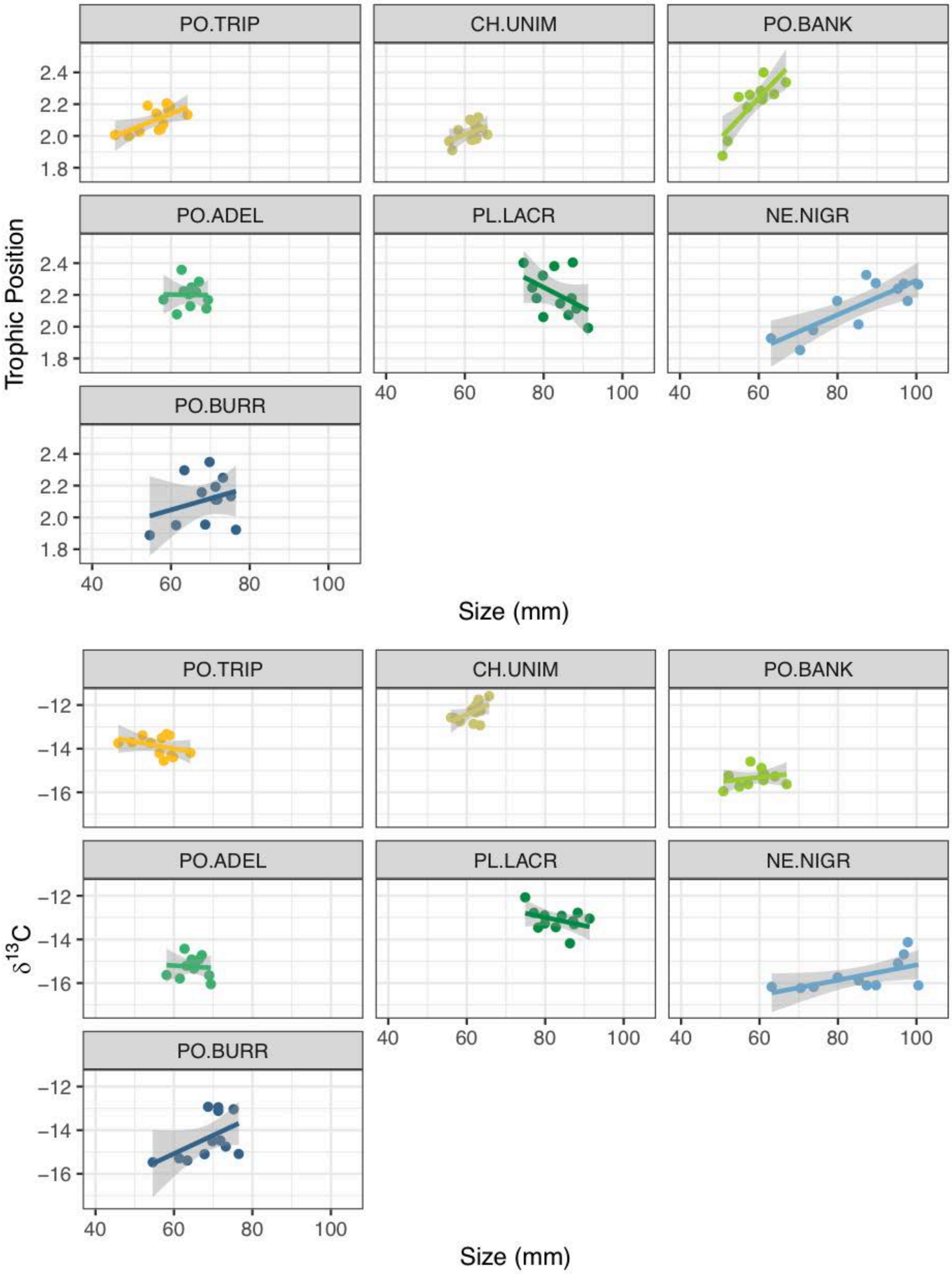


Figure S3.2 Territorial damselfish a) trophic position and b) $\delta^{13}C$ signatures by species size (mm). Data points represent individuals, fit with a linear regression line. Species abbreviations and sample sizes are defined in Table 3.2. Vertical axes are not comparable.



Supplementary information Chapter 4

The following supplement accompanies the article

Eurich JG, McCormick MI, Jones GP (2018b) Direct and indirect effects of interspecific competition in a highly partitioned guild of reef fishes. *Ecosphere.* 9: e02389. https://doi.org/10.1002/ecs2.2389

Table S4.1 Results of Tukey's post-hoc pairwise comparisons on differences of abundance between the pre-removal survey period and the consecutive post-removal survey periods for the three reef flat species.

Pre-removal		Post-removal	Est.	SE	*z*-value	*P*-value (*z*)
Pomacentrus bankanensis						
Pre	-	Post 1 day	0.116	0.158	0.731	0.978
Pre	-	Post 3 days	0.251	0.151	1.669	0.547
Pre	-	Post 1 week	0.426	0.142	3.000	0.032
Pre	-	Post 3 months	0.743	0.129	5.782	<0.0001
Pre	-	Post 6 months	0.827	0.125	6.591	<0.0001
Chrysiptera unimaculata						
Pre	-	Post 1 day	0.711	0.172	4.142	<0.0001
Pre	-	Post 3 days	0.930	0.161	5.772	<0.0001
Pre	-	Post 1 week	1.087	0.155	7.021	<0.0001
Pre	-	Post 3 months	0.902	0.162	5.551	<0.0001
Pre	-	Post 6 months	0.972	0.159	6.096	<0.0001
Pomacentrus tripunctatus						
Pre	-	Post 1 day	1.099	0.447	2.457	0.136
Pre	-	Post 3 days	1.099	0.447	2.457	0.136
Pre	-	Post 1 week	1.361	0.421	3.236	0.015
Pre	-	Post 3 months	1.099	0.447	2.457	0.136
Pre	-	Post 6 months	1.740	0.391	4.455	<0.0001

Table S4.2 Comparison of abundances of damselfishes for plots where *Pomacentrus adelus* were removed (removal) and those where *P. adelus* were not removed (control) across experimental census periods. Results represent the output of a generalised linear mixed effects models with Poisson distribution.

Source	X^2	df	p
Pomacentrus adelus			
Removal	1434.800	7	< 0.0001
Control	4.114	7	0.391
Pomacentrus adelus recruits			
Removal	62.048	7	< 0.0001
Control	11.695	7	0.020
Pomacentrus bankanensis			
Removal	60.483	7	< 0.0001
Control	1.387	7	0.846
Chrysiptera unimaculata			
Removal	74.422	7	< 0.0001
Control	4.622	7	0.328
Pomacentrus tripunctatus			
Removal	24.412	7	< 0.0001
Control	4.370	7	0.358
Plectroglyphidodon lacrymatus			
Removal	0.897	7	0.970
Control	1.518	7	0.823
Neoglyphidodon nigroris			
Removal	0.557	7	0.989
Control	0.501	7	0.973
Pomacentrus burroughi			
Removal	1.277	7	0.937
Control	1.635	7	0.802

Table S4.3 Changes in species distributions 6 months after the removal of *P. adelus* on the removal plots (left, n = 2) and control plots (right, n = 2). Values presented are the change in meters (m) in mean population distribution towards reef crest ± variance (SE). A positive value represents a shift from the reef flat to the reef crest and down the reef slope, with a negative value representing a shift up the reef slope to the reef crest and reef flat. Individual location was recorded to the nearest 0.25 m. Asterisk represent significantly different values ($p \leq 0.05$) from the pre-removal abundance levels.

	Removals	**Controls**
P. adelus	– 0.22 ± 0.16	0.25 ± 0.18
P. tripunctatus	0.37 ± 0.15	– 0.11 ± 0.15
C. unimaculata	0.75 ± 0.13	0.07 ± 0.13
P. bankanensis	1.32 ± 0.28 *	– 0.01 ± 0.28
Pl. lacrymatus	– 0.04 ± 0.27	0.37 ± 0.29
N. nigroris	0.38 ± 0.31	0.25 ± 0.42
P. burroughi	0.27 ± 0.08	0.03 ± 0.14

Supplementary information Chapter 5

The following supplement accompanies the article

Eurich JG[1], Shomaker SM[1], McCormick MI, Jones GP (2018c) Herbivore foraging dynamics after the removal of an abundant territorial damselfish in Kimbe Bay, Papua New Guinea. *Journal of Experimental Marine Biology and Ecology.* 506: 155–162. http://doi.org/10.1016/j.jembe.2018.06.009

Table S5.1 Results of ANOVAs on differences between percent cover of different habitat categories by period (pre and post 3 months removal) and location (Garbuna and Luba Luba) for both treatment types. No significant interactions were observed between factors.

Habitat	Treatment	Source	X^2	df	p
Live coral	Removal	Period	2.468	1	0.116
		Location	30.886	1	< 0.001
	Control	Period	0.576	1	0.448
		Location	33.261	1	< 0.001
Dead coral	Removal	Period	0.259	1	0.611
		Location	0.499	1	0.480
	Control	Period	3.687	1	0.055
		Location	3.687	1	0.055
Macroalgae	Removal	Period	24.017	1	< 0.001
		Location	0.195	1	0.659
	Control	Period	2.912	1	0.035
		Location	19.213	1	< 0.001
Turf	Removal	Period	22.741	1	< 0.001
		Location	0.093	1	0.760
	Control	Period	20.303	1	< 0.001
		Location	5.394	1	0.005
CCA	Removal	Period	2.279	1	0.131
		Location	3.225	1	0.073
	Control	Period	0.168	1	0.682
		Location	0.280	1	0.584
Rubble	Removal	Period	1.404	1	0.236
		Location	18.380	1	< 0.001
	Control	Period	0.319	1	0.572
		Location	0.013	1	0.910
Sand	Removal	Period	0.051	1	0.822
		Location	9.564	1	0.002
	Control	Period	1.352	1	0.245
		Location	0.014	1	0.907

Sediment	Removal	Period	5.609	1	0.018
		Location	0.725	1	0.395
	Control	Period	1.535	1	0.215
		Location	0.729	1	0.393
Other	Removal	Period	0.000	1	0.999
		Location	0.480	1	0.488
	Control	Period	1.791	1	0.181
		Location	1.005	1	0.316