# The role of territorial grazers in coral reef trophic dynamics from microbes to apex predators

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Jordan Marie Casey

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- Tracy Ainsworth: design of study, writing of manuscript
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## Abstract

Territories of grazing fishes in the family Pomacentridae have been documented to cover a substantial proportion of shallow coral reefs, and these fishes can have profound effects on benthic dynamics. By cultivating palatable filamentous algae, excluding fleshy macroalgae, and aggressively defending their resources, territorial damselfishes indirectly impact coral-algal competition and play a substantial role in shaping benthic community composition, including the recruitment and post-settlement survival of scleractinian corals. Marine microbes are known to be important drivers of environmental change, and microbial community structure on coral reefs is strongly influenced by coral-algae interactions; however, the extent to which this influence is mediated by territorial grazers is unknown. Territorial damselfishes occur in distinct behavioural guilds ranging from indeterminate territorial grazers with thin algal turfs and low rates of territorial aggression to intensive territorial grazers with thick turfs and high rates of aggression. Members of the genus *Stegastes* are intensive territorial grazers and are known to play a major role in coral-algal dynamics. Further, most previous studies of territorial grazer effects on corals have focused on back-reef habitats although the reef crest is a highly productive environment with elevated rates of coral recruitment and settlement. Lastly, removal of marine predators via fishing is often theorized to alter community structure through trophic cascades, but empirical evidence for this phenomenon is often circumstantial on coral reefs. Given declines of predators on the Great Barrier Reef (GBR), trophic cascade theory would predict ecosystem repercussions to lower trophic levels, but it is unknown how a predator density gradient impacts the distribution of territorial damselfishes. Thus, the overall objective of this thesis was to examine the role of territorial grazers in shaping the structure and dynamics of benthic communities and the extent to which this may be mediated by higher-level trophic interactions across a gradient of fishing pressure.

To achieve this objective, I employed a variety of microbial sampling regimes and survey methods to reveal the role of territorial grazers in trophic dynamics on the GBR, Australia. To elucidate how *Stegastes apicalis* and *S. nigricans* may alter benthic microbial assemblages and coral health, I determined the benthic community composition (epilithic algal matrix (EAM) and prokaryotes) and coral disease prevalence inside and outside of damselfish territories. To determine the impact of territorial grazers on coral microbial assemblages, I established a coral transplant inside and outside of *Stegastes*' territories. Over the course of one year, the percent mortality of transplanted corals was monitored and coral samples were collected for microbial analysis. To assess the impact of territorial grazers on the establishment of juvenile corals, I surveyed the reef crest habitat of Lizard Island using fixed transects to assess the effects of indeterminate and intensive territorial grazers on juvenile coral abundance and taxonomic composition. In addition, the turnover of territorial pomacentrids was monitored, as well as the effects of turnover on juvenile coral assemblages. To examine trophic cascade theory and potential effects of predator removal on lower-trophic levels such as territorial damselfishes, I quantified fish and benthic assemblages across a fishing-induced predator density gradient on Australia's Great Barrier Reef. I evaluated whether the observed patterns in community structure fit the theoretical predictions of trophic cascades, and I assessed the impact of region and management zones across trophic levels.

Microbial analyses and experimental results exposed new findings on the effects of territorial grazers on marine microbial communities. 16S rDNA sequencing revealed distinct bacterial communities associated with turf algae and a two to three times greater relative abundance of phylotypes with high sequence similarity to potential coral pathogens inside *Stegastes'* territories. These potentially pathogenic phylotypes (totalling 30.04% of the community) were found to have high sequence similarity to those amplified from black band disease (BBD) and disease affected corals worldwide. Disease surveys further revealed a

significantly higher occurrence of BBD inside *S. nigricans*' territories. In addition, as compared to outside damselfish territories, *Stegastes* were associated with a higher rate of mortality of transplanted corals. However, 16S rDNA sequencing revealed that territorial grazers do not differentially impact the microbial assemblage of corals exposed to the EAM. Regardless of *Stegastes* presence or absence, coral transplantation resulted in a shift in the coral-associated microbial community and an increase in coral disease associated potential pathogens. Further, transplanted corals that suffer low to high partial mortality undergo a microbial transition from a microbiome similar to that of healthy corals to that resembling the EAM.

Ecological surveys also yielded new insights into the role of small-bodied herbivorous fishes on coral reef trophic dynamics. Intensive territorial grazers were associated with a significantly lower juvenile coral abundance (34% decrease), but neither intensive nor indeterminate grazer territories impacted juvenile coral taxonomic composition. Over the course of one year, there was a high rate of territorial turnover (39.7%). Turnover from control plots to intensive damselfish territories was accompanied by a 44% decrease in juvenile corals; conversely, turnover from intensive damselfish territories to control plots coincided with a 48% increase in juvenile corals. However, although outer reef surveys indicated that protected areas enhance predator populations, we found no cascading effects from predators to lower trophic levels, such as a loss of apex predators leading to higher levels of mesopredators, which suppress mobile herbivores, followed by algal proliferation. Likewise, we found no effects of mesopredators on lower trophic levels, such as a decline of mesopredators causing higher levels of territorial grazers, resulting in lower coral and higher algae cover.

Hence, the results from this thesis reveal that territorial damselfish play a significant role in shaping coral disease dynamics and patterns of juvenile coral abundance on the reef

crest, but predator density does not substantially shape the distribution of territorial grazers or other herbivorous fishes across the outer GBR. Among the microbial results, the findings demonstrate the first link among fish behaviour, reservoirs of potential coral disease pathogens and the prevalence of coral disease. Although damselfish do not seem to alter the microbial community of transplanted corals, coral transplantation significantly impacts coral microbial communities, and transplantation may increase susceptibility to coral disease. Further, damselfish substantially impact the macro-benthos: the association between damselfish territories and the abundance and spatial turnover of juvenile corals strongly implies that territorial grazers have a negative effect on juvenile coral populations. The unexpectedly high temporal turnover of damselfish territories indicates that damselfish-coral-algae linkages are highly dynamic, may be extensively influenced by local-scale effects, and have the potential to impact the structure of coral assemblages on coral reef fronts. Finally, large-scale trophic surveys indicate that top-down forces are weak on coral reefs, implying that densities of most community members, including territorial grazers, are regulated by abiotic indirect factors that vary through space. We conclude that predator-mediated trophic cascades are probably the exception rather than the rule in this ecosystem.

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# Chapter 1: General Introduction

In 1859, Charles Darwin described a “web of complex relations” that bound plants and animals, which laid the foundation for ecosystem-based trophic theory. The concept of trophic dynamics was developed to explain how energy flows through an ecosystem, incorporating sequences of consumption among organisms as well as interactions with abiotic components (Lindeman 1942). Thus, the concept of trophic dynamics is twofold, including (1) predator-prey interactions that directly involve energy transfer through prey consumption, and (2) biological interactions that mediate the structure of biotic and abiotic resources and subsequently alter the availability of energy in an ecosystem (Lindeman 1942). This concept has been widely used across terrestrial and aquatic ecology and is often embedded within other ecological concepts and phenomena. For example, the concept of community stability was founded on the basis that the complexity of energetic pathways, or trophic interactions, increases the stability of a community (Paine 1969). Trophic cascade theory is based on reciprocal predator-prey interactions, which cause alternating increases and decreases in the biomass of trophic levels throughout a food web (Hairston 1960).

On coral reefs, the role of small-bodied herbivorous fishes in coral reef trophic dynamics is especially important due to their high turnover rates and large contribution to energy flows (Depczynski et al. 2007). Within the family Pomacentridae, territorial damselfishes are widespread and abundant across shallow reef environments from the reef crest to back reefs and lagoons (Klumpp et al. 1987; Choat 1991). Due partly to sheer abundance, the structure and composition of damselfish territories plays a large role in benthic dynamics on coral reefs (Ceccarelli et al. 2001; Hata & Kato 2004; Ceccarelli et al. 2006). Territorial damselfishes, also known as territorial grazers, engage in several key behaviours within their territories: feeding on palatable filamentous algae, weeding fleshy

macroalgae, pecking coral polyps to further propagate filamentous algae, and maintaining constant aggression against intruders to protect resources (Kaufman 1977; Hinds & Ballantine 1987; Klumpp & Polunin 1989; Letourneur et al. 1997). As a result, damselfish territories are dominated by the epilithic algal matrix (EAM), a benthic conglomeration of filamentous turf algae, juvenile macroalgae, cyanobacteria, detritus, invertebrates, and microbes (Wilson and Bellwood 1997; Wilson et al. 2003; Fricke et al. 2011; Barott and Rohwer 2012). While certain trophic links involving territorial damselfishes have been relatively well studied, such as the role of territorial damselfishes in promoting turf algae (Hata & Kato 2004) and shaping grazing patterns of mobile herbivorous fishes (Ceccarelli et al. 2011), other components have been predominantly neglected, such as energetic pathways from territorial damselfishes to detritus and microbial communities (Whitman et al. 1998; Moore et al. 2004). In the face of coral reef declines worldwide, it is essential to garner a more concrete, holistic understanding of trophic dynamics involving territorial damselfishes on coral reefs, from predatory fishes to bacterial assemblages.

Although it is known that territorial grazers play a role in shaping benthic dynamics on coral reefs, it is unclear whether these effects extend to the microbial level. Microbial processes on coral reefs influence ecosystem functioning, particularly via nutrient cycling (dissolved organic carbon) and coral disease dynamics (Ainsworth et al. 2009). Thus, an understanding of benthic microbial community structure on coral reefs has the potential to provide forewarning of macro-ecological change (Garren & Azam 2012). However, the role of microbial communities in coral reef trophic dynamics has rarely been investigated beyond fine-scale benthic dynamics (McDole et al. 2012). While patterns of microbial communities on coral reefs are strongly influenced by ecological interactions of corals and algae (Barott & Rohwer 2012; Vega Thurber et al. 2012), it is unclear how territorial grazers may mediate coral-algae-bacteria linkages. Within territorial grazers, there are large discrepancies among

territory characteristics, as each damselfish species farms a unique turf assemblage with highly variable turf biomass per unit area (Ceccarelli 2007). The consequences of territorial variations on coral, algal and microbial assemblages are largely unknown.

In addition to the impact of territorial grazers on microbial assemblages, the role of territorial damselfishes in benthic dynamics over time is predominantly unknown. It has been reported that territorial damselfishes, which effectively exclude grazers and corallivorous fishes, increase coral recruitment (Sammarco and Carleton 1981; Gleason 1996) and facilitate adult coral survival (Wellington 1982; Glynn and Colgan 1988; Done et al. 1991; Suefuji and van Woesik 2001; White and O'Donnell 2010; Gochfeld 2010). Conversely, due to high turf algae biomass in their territories, territorial grazers have been shown to inhibit coral recruitment (Arnold et al. 2010), suppress acroporid growth rates (Potts 1977), and cause mortality across coral genera (Kaufman 1977; White and O'Donnell 2010). However, the majority of previous studies consider the impact of territorial damselfishes on coral ecology on back reefs as a snapshot in time or over short periods of less than one month (Done et al. 1991; Sammarco and Carleton 1981; Suefuji and van Woesik 2001; White and O'Donnell 2010). Thus, it is unclear whether the impact of territorial grazers can be seen across coral assemblages over time, especially in highly dynamic environments such as the reef crest.

Aside from assessing the effects of territorial grazers on benthic dynamics, it is important to gauge the relative impact of predator density on the large-scale distribution of territorial grazers. In a global meta-analysis of fishing effects on herbivorous fishes, significant reductions in the biomass of mobile herbivores was reported in fished areas, while territorial grazers increased in abundance and biomass under fishing pressure (Edwards et al. 2014). However, mobile herbivorous fish extractions and other human impacts may have confounded the potential top-down impacts of apex predator removal. Unlike other coral reef systems, fishers almost exclusively extract top-predators and mesopredators on the Great

Barrier Reef (GBR); there is virtually no fishing for herbivorous fishes (Bellwood et al. 2004). Consequently, the GBR provides an ideal system to examine the impact of predatory fish populations on lower trophic levels among management zones. Although no strong top-down effects from apex predators to mobile herbivores have been found on the outer GBR (Rizzari et al. 2014), no study has cohesively considered the impact of a mesopredator density gradient on territorial grazers and benthic communities in a system where fishing is almost exclusively confined to predatory fishes, such as the coral reefs of the GBR.

The primary aim of this thesis is to investigate the role of territorial damselfishes in trophic dynamics, with a focus on how their behaviour and community structure shape microbial and macro-benthic community composition as well as an analysis of their response to a predator density gradient. This aim was accomplished with a variety of methods, from algal sampling for microbial analyses to large-scale visual surveys of predatory fishes, which provided a comprehensive assessment of trophic interactions on coral reefs in relation to territorial grazers. All studies occurred on the GBR, one of the world's largest and best protected reef systems (Pandolfi et al. 2003; Russ et al. 2008). The majority of work took place on the mid-shelf reefs surrounding Lizard Island in the northern GBR, but Chapter 5 examines patterns across the outer GBR, including the Ribbon Reefs in the northern GBR and the Swains Reefs in the southern GBR.

In **Chapter 2**, I examine the effects of territorial damselfishes in the genus *Stegastes* on benthic microbial assemblages in the EAM. By quantifying *Stegastes*' farming behaviours, identifying algal assemblages, analyzing the microbial communities in the EAM, and running coral disease surveys inside and outside damselfish territories, I demonstrate that *Stegastes* increase the relative abundance of potential pathogens linked to black band disease and promote the prevalence of coral disease. These results have major implications for coral

health in marine systems and elucidate an important trophic link between territorial grazers and microbes.

**Chapter 3** is a direct extension of the microbial study from the previous chapter. Here, I analyze the impact of territorial grazers in the genus *Stegastes* on coral microbial communities, the consortium of bacteria that occupy the tissue, skeleton, and gut of corals. To achieve this, I monitored the survivorship and microbial communities of transplanted corals inside and outside *Stegastes*' territories over one year. While territorial grazers increase the rate of mortality of transplanted corals, *Stegastes* do not have a differential impact on coral microbial communities. However, this study demonstrates that coral transplantation results in an increase in coral disease associated potential pathogens, indicating that coral transplantation may increase susceptibility to coral disease.

In **Chapter 4**, I examine the dynamics of territorial grazers and juvenile corals on the reef crest. With fixed transects on the reef crest, I assessed the effects of two behavioural guilds of territorial grazers on juvenile coral abundance and taxonomic composition over one year. I also monitored the turnover of damselfish territories to determine how shifting territorial distributions may impact juvenile corals. I found that territorial damselfish have a negative effect on the abundance of juvenile corals, and there is a surprisingly high rate of territorial turnover, revealing that damselfish-coral-algal linkages are highly dynamic and have the potential to alter the structure of coral assemblages on the reef crest.

Finally, **Chapter 5** is a large-scale trophic study to test for the existence of cascading trophic effects on territorial damselfishes on the outer GBR. I surveyed territorial grazers in relation to other trophic groups, including apex predators, mesopredators, mobile herbivores, and benthic composition to analyze the relative impacts of region and management zone (fishing pressure) across trophic levels and to evaluate whether territorial grazers respond to a predator density gradient via cascading trophic effects. Although protected areas enhance

apex predator density, I found no evidence of cascading effects to territorial grazers or other lower trophic levels, emphasizing the importance of indirect regional effects on herbivorous fishes and benthic composition in complex marine environments.

Although territorial grazers play a major role in shaping benthic microbial communities and have a dynamic influence on juvenile corals, the spatial distribution of territorial damselfishes is not substantially affected by a human-induced predator density gradient on the GBR. The findings in this thesis highlight the importance of territorial grazers as engineers of benthic community structure, with linkages to coral disease dynamics, and demonstrate the need to consider microbial assemblages in trophic interactions on coral reefs.

At present, Chapter 2 has been published in *Proceedings of the Royal Society B*, Chapter 3 has been published in *Scientific Reports*, Chapter 4 has been published in *Coral Reefs*, and Chapter 5 is in preparation for publication.

# Chapter 2: Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease

## Introduction

Microbes are abundant across terrestrial and marine environments and have prominent roles in community dynamics, yet there remains considerable unexplored complexity within microbial communities, particularly within marine environments (Whitman et al. 1998; Arrigo 2005). The forefront of marine microbial ecology emphasizes the role of microbial processes on ecosystem functioning and the ecology of microbial diseases (Ainsworth et al. 2009). Thus, an understanding of benthic microbial community structure on coral reefs has the potential to provide forewarning of macro-ecological change (Garren & Azam 2012). Patterns of microbial communities on coral reefs are strongly influenced by the presence, physiological activity and ecological interactions of corals and algae (Barott & Rohwer 2012; Vega Thurber et al. 2012); however, it is largely unknown how fishes mediate these links between microbes and the macro-benthos. There is strong evidence that territorial grazers, particularly territorial damselfishes, play a key role in benthic dynamics on coral reefs (Ceccarelli et al. 2001; Hata & Kato 2004; Ceccarelli et al. 2006). Territorial grazers engineer benthic structure in their territories by grazing turf algae, coral-pecking (biting coral polyps at the base of coral colonies to further propagate turf algae) and weeding undesirable species of turf algae and fleshy macroalgae (Hinds & Ballantine 1987; Klumpp & Polunin 1989). They also engage in frequent and sustained aggression toward intruders to defend food resources within their territories (Newton 1994; Letourneur et al. 1997), which are comprised of microbes, detritus, filamentous algae, corals, and macroinvertebrates (Horn 1989; Choat

1991; Wilson & Bellwood 1997). Along with shaping benthic community structure, territorial grazers are abundant and widespread, and it is estimated that up to 77 percent of the substratum of shallow reef flats (~2 m depth) may be covered with damselfish territories (Klumpp et al. 1987; Choat 1991; Meekan et al. 1995). Here, I aim to determine the role of territorial grazers in structuring coral-algal-bacteria linkages on the reef benthos.

Territorial grazers' behaviour markedly increases the productivity of palatable filamentous algae and dramatically decelerates the succession of macroalgae on coral reefs (Ceccarelli et al. 2005a; Ceccarelli et al. 2011). Among territorial grazers, there is a spectrum of guilds from extensive to intensive grazers (Emslie et al. 2012). Extensive grazers have large territories with unclear or overlapping boundaries, highly diverse algae turfs and low levels of territorial aggression. In contrast, intensive grazers have more distinct territorial boundaries, monocultures or low-diversity algae turfs with higher algal biomass per unit area and prompt aggressive responses to intruding species (Hata & Kato 2002; Hata et al. 2002; Hata & Kato 2004; Hoey & Bellwood 2010). Within intensive grazers, there are large discrepancies among territory characteristics, as each damselfish species farms a unique turf assemblage with highly variable turf biomass per unit area (Ceccarelli 2007). However, the consequences of territorial variations on coral, algal and microbial assemblages within the defined guilds are largely unknown.

The dominant benthic component of damselfish territories is the epilithic algal matrix (EAM), which is comprised of a conglomeration of living and non-living components, including filamentous turf algae, juvenile macroalgae, cyanobacteria, detritus, invertebrates and a consortium of microbes (Wilson & Bellwood 1997; Wilson et al. 2003; Fricke et al. 2011; Barott & Rohwer 2012). The effects of turf algae on corals are largely detrimental, and many of these interactions are attributed to the microbiota associated with turfs. In addition to inhibiting coral recruitment (Birrell et al. 2005), retarding coral growth (Quan-Young &

Espinoza-Avalos 2006; Barott et al. 2011) and stressing coral physiology (Vermeij et al. 2010; Wangpraseurt et al. 2012), turf algae also enhance microbial activity and coral mortality by releasing dissolved compounds that are harmful to corals (Vega Thurber et al. 2012; Smith et al. 2006; Haas et al. 2011). Previously, both macroalgae and benthic turf algae have been shown to harbour pathogens that are associated with coral disease (Nugues et al. 2004; Sweet et al. 2013). Yet, the microbial communities of damselfish territories are virtually unexplored. While select communities of turf algae may harbour potential pathogens, the indirect effects of territorial grazers on benthic microbial communities, including the prevalence of potentially pathogenic bacteria and the consequential manifestation of coral disease, remain unresolved.

This chapter aims to determine how the cultivation of turf algae-dominated territories by intensive territorial grazers in the genus *Stegastes* influences the structure of the microbial community and the prevalence of coral disease. Specifically, I characterized the algal assemblages inside and outside *Stegastes apicalis* and *Stegastes nigricans'* territories to determine which algae were cultivated or excluded by these fish species, assessed and compared associated differences of microbial communities in the EAM inside and outside of *Stegastes'* territories and ran coral disease surveys inside and outside of *S. nigricans'* territories. The results reveal that microbial assemblages and coral disease prevalence are considerably different inside *Stegastes*' territories and have substantial implications for coral health in reef systems, elucidating an important ecological link between microbes and macro-organisms in the marine environment.

## Methods

### Study site and species

This study took place at Lizard Island in the northern GBR, Australia (14°41'5"S, 145°26'55"E) from February to August of 2013. The main study site was on the back reef in the lagoon between Palfrey and South Island (Palfrey; Figure 2.1), at a depth of 1-3 m. For the coral disease surveys, there were four study sites on the back reef in the lagoon around Lizard Island (Palfrey, Bird, Loomis and Horseshoe; Figure 2.1).

*Stegastes nigricans* and *Stegastes apicalis* (f. Pomacentridae), two intensive territorial grazers (Hata & Kato 2004; Ceccarelli 2007; Emslie et al. 2012), were the study species. *S. apicalis* occurs at a depth of 1-15 m and reaches up to 15 cm (total length). *S. nigricans* occurs at the depth of 1-12 m and reaches up to 14 cm (total length). Both species form social groups (termed "colonies") made up of several contiguous territories, each territory belonging to an individual adult damselfish (Randall et al. 1991). *S. apicalis* form colonies on the reef flat in association with crevices, coral rubble, sparse acroporids and soft corals, whereas *S. nigricans* form colonies in staghorn coral outcrops dominated by *Acropora muricata* (J. M. Casey, personal observation). Both damselfish species are aggressive territorial grazers that are not easily perturbed by human observers (Newton 1994).

All algal composition surveys and EAM sampling were conducted on SCUBA on two colonies of *S. apicalis* (comprised of 12 and 20 territories, respectively) and two colonies of *S. nigricans* (comprised of 30 and 38 territories, respectively). I mapped each colony, and I used the minimum convex polygon (MCP) method to estimate the territory size of each individual fish (Mohr 1947). I observed each individual for a five-minute period then placed four flagged fishing weights around the extremities of the individual's territory. The longest and shortest diameters were measured to the nearest centimeter of the elliptical territory, and the average diameter was used to calculate territory area.

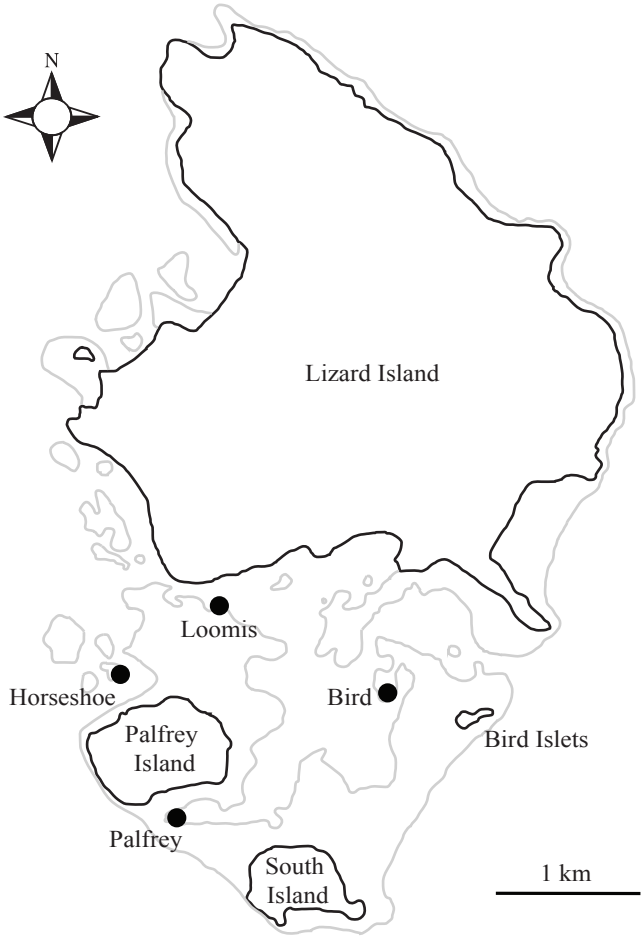



**Figure 2.1** Map of Lizard Island and fringing reefs showing the microbial sampling site in the lagoon by Palfrey Island (Palfrey) and the four black band disease (BBD) survey sites (Palfrey, Bird, Loomis and Horseshoe).

**Cultivation behaviour and territorial defense**

For each species, two observers monitored resource-related behaviours and defense for a total of 500 minutes of observation over four days. Each day, damselfish (n=10) were monitored for five 90 minutes observational periods between 700 and 1630 h (700-830, 900-1030, 1100-1230, 1300-1430, 1500-1630 h). During each 90-minute period, ten individuals were observed per observer for five minutes, which was an adequate time period to establish territorial boundaries. The number of bites (grazing turf algae, coral- pecking, weeding of undesirable species) and defecations were recorded per minute during each five-minute period. Observers also noted aggressive interspecific and intraspecific interactions (territorial defense), including the species, size of the intruder, and the frequency of the attack during the observational period (Newton 1994). To compare the maximum bite- rates of turf algae, weeding, and coral-pecking between *S. apicalis* and *S. nigricans*, I used paired two-tailed t-tests.

**Algal composition**

To assess the algal communities inside *S. apicalis*' and *S. nigricans*' territories, I surveyed twenty territories from each study species. After estimating territory size, percent coverage of algae in each territory was assessed visually and photographically. To assess the exclusion of macroalgae from *Stegastes*' territories, ten 1-$m^2$ quadrats were placed on the benthos to identify the macroalgae taxa that did not appear in damselfish territories. Algae were identified to genus level and, when possible, to species level (Price 1992; Cribb 1996). For the two damselfish species' territories, I quantified differences in algal species richness, evenness, and Shannon Diversity.

**Epilithic algal matrix microbial communities**

To determine the impact of territorial damselfish on microbial communities, I examined the bacterial composition of the EAM inside and outside damselfish territories. In the field using gloves, ten EAM samples were collected in 50 mL tubes from control plots outside of *Stegastes*' territories, inside *S. apicalis'* territories and inside *S. nigricans'* territories. For the collections from *S. apicalis'* and *S. nigricans'* territories, samples were taken across two damselfish colonies, and each sample came from a different damselfish territory. Samples were immediately snap-frozen in liquid nitrogen, stored at -80℃ (Witt et al. 2011) and transported to James Cook University (JCU) for processing and DNA extractions.

Samples were homogenized under liquid nitrogen, DNA was isolated using a PowerPlant DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, USA) following the manufacturer's instructions and DNA quality was checked using a nanodrop. 27f and 519r univeral reverse primers and the V1-V3 region of the 16S rDNA gene were used for amplification with a single-step 30 cycle PCR using a HotStarTaq Plus Master Mix Kit (Qiagen, Valencia, CA, USA). MR DNA, a next generation sequencing and bioinformatics provider (Shallowater, TX, USA), performed the PCR (under the following conditions: 94℃ for 3 minutes, 28 cycles of 94℃ for 30 seconds, 53℃ for 40 seconds and 72℃ for 1 minute; 72℃ for 5 minutes). All amplicon products were mixed in equal concentrations and purified using Agencourt ampure beads (Agencourt Bioscience Corporation, MA, USA) and sequenced with Roche 454 FLX titanium instruments and reagents according to manufacturer's guidelines. The sequence data were processed using a proprietary analysis pipeline at MR DNA and further analyzed with Quantitative Insights Into Microbial Ecology (QIIME; Caporaso et al. 2010). Sequences were depleted of barcodes and primers, and short sequences (< 200 bp) and sequences with homopolymer runs exceeding 6 bp were removed.

The average read length was 431 bp after primer and barcode removal. The sequences were denoised and chimeras were removed using Acacia (Bragg et al. 2012). After normalization, operational taxonomic units (OTUs) were defined with clustering at 3 percent divergence (97 percent similarity) (Dowd et al. 2008a; Dowd et al. 2008b; Edgar 2010; Capone 2011; Dowd et al. 2011; Eren et al. 2011; Swanson et al. 2011). Taxonomy was assigned to OTUs in QIIME, using SILVA (Quast et al. 2013) and BLASTN (Zhang et al. 2000) against a curated GreenGenes database (DeSantis et al. 2006).

I assessed the beta-diversity of the EAM microbial communities inside and outside of damselfish territories with QIIME using a weighted UniFrac analysis. An unweighted pair group method using average linkages (UPGMA) clustering and a principal coordinates analysis (PCoA) were generated from the UniFrac distances (Lozupone & Knight 2005). The PCoA was generated from weighted UniFrac distances and plotted in two dimensions. Individual OTUs (generated using the proprietary pipeline analysis) were then assigned into three categories: autotrophs, heterotrophs and potential pathogens, based on literature reviews (see Appendix A: Table A1). All genera with a less than two percent relative abundance were excluded from the analyses. The data included five genera that are considered potential pathogens for a broad array of hosts; however, among these five genera, only two have previously been linked to coral disease. These two coral-specific potential pathogens made up 95 percent of the potential pathogen category, therefore I only investigated the coral-specific potential pathogens in the analyses. Kruskal-Wallis one-way analyses of variance were used to analyze the differences in the relative abundances of these components of microbial communities in the EAM outside of *Stegastes*' territories as compared to inside *S. apicalis'* territories and *S. nigricans*' territories.

**Coral disease surveys**

To assess the prevalence of coral disease inside and outside of damselfish territories, I determined coral disease presence in *A. muricata* outcrops, a common staghorn coral in the lagoon of Lizard Island. I ran six 10 m transects at each of the four study sites: Palfrey, Bird, Loomis and Horseshoe (Figure 2.1), for a total of 24 transects. At each transect, a 1-$m^2$ quadrat was attached to the transect every 2 m, for a total of five quadrats per transect. Of the six transects at each site, three transects were in *A. muricata* outcrops that were occupied by *S. nigricans*, and three transects were in *A. muricata* outcrops with no territorial damselfish. Since *A. muricata* is common in the lagoon of Lizard Island and *S. nigricans* typically form colonies around *A. muricata* outcrops, it was straightforward to survey comparable *A. muricata* outcrops outside damselfish territories. In contrast, *S. apicalis'* territories and their associated habitat have very heterogeneous coral assemblages (see Chapter 4). Since the prevalence of coral disease varies substantially among coral taxa (Carpenter et al. 2008) and there is evidence that coral composition differs inside and outside damselfish territories (Ceccarelli et al. 2001), this substantially complicates the attribution of differences in coral disease prevalence to the behaviour of *S. apicalis* rather than differences in coral species composition. Therefore, *S. apicalis* territories were not included in this component of the study.

To analyze the effect of damselfish territories on coral disease presence, I used a generalized linear mixed-model (GLMM) with a binomial error distribution and logit-link function. The response variable was binary (coral disease present in quadrat / absent in quadrat). The fixed effect was the presence or absence of *S. nigricans*' territories. I included transect nested within site (Palfrey, Bird, Loomis and Horseshoe) as random factors. This analysis was conducted with the packages *lme4* (Bates et al. 2012) and *arm* (Gelman & Su 2013) using the software program R (R Core Team 2012).

## Results

### Cultivation behaviour and territorial defense

Maximum bite rates were significantly higher for *S. nigricans* than *S. apicalis* for grazing turf algae and weeding undesirable species (Table 2.1; Figure 2.2a,b), suggesting that *S. nigricans* is a more intensive territorial grazer than *S. apicalis*. The maximum bite-rate of turf algae for *S. nigricans* is approximately 30% higher than the maximum bite-rate for *S. apicalis* (Figure 2.2a). Although *S. nigricans* has a smaller average territory size than *S. apicalis* (approximately 0.5 $m^2$ and 1 $m^2$, respectively), turf algae in *S. nigricans'* territories are substantially thicker and obtain a higher biomass via cultivation on branching acroporids as opposed to barren flat regions on the benthos (Figure 2.3), as was described in the algal composition surveys. *S. nigricans* appear to engage in higher rates of grazing or 'farming' turf algae to sustain and further propagate thick turf algal mats within their territories. Rates of coral-pecking do not differ significantly between *S. apicalis* and *S. nigricans* (Table 2.1) and remain low throughout the day, suggesting that territorial grazers play a minimal role in damaging coral colonies (Figure 2.2c).

*S. apicalis* and *S. nigricans* pugnaciously chase away a wide array of intruders across all feeding guilds (Figure 2.4; Figure 2.5). For both species of *Stegastes*, no aggressive interactions were observed with lutjanids, serranids and adult scarids that were greater than 40 cm. However, *S. apicalis* did not react aggressively to territory invasions by holocentrids, scorpaenids and *Dischistodus melanotus*. Assuming that these species do not actively avoid *S. apicalis*' territories relative to *S. nigricans*' territories, this suggests that *S. apicalis* is aggressive to a smaller array of intruders than *S. nigricans*. *Stegastes*' defense against species across feeding guilds shows that they not only guard turf algae from herbivores and omnivores (including detritivores), they opportunistically protect all their resources, including invertebrates and corals from carnivores and corallivores (Figure 2.5).

**Table 2.1** T-value, degrees of freedom (df) and p-value results of a paired two-tailed t-test comparing the maximum bite-rates of grazing turf-algae, weeding undesirable species and coral-pecking between *S. apicalis* and *S. nigricans*. "Time of day" indicates the time of day at which bite-rates of the respective resource-related behaviour reaches a maximum. Shaded cells contain statistically significant values ($p < 0.05$).

| Bite-rates | Time of day | t-value | df | p-value |
|---|---|---|---|---|
| Turf algae | 1300-1430 h | -3.818 | 35 | < 0.001 |
| Weeding | 900-1030 h | 4.792 | 35 | < 0.001 |
| Coral pecking | 900-1030 h | -0.407 | 35 | 0.686 |

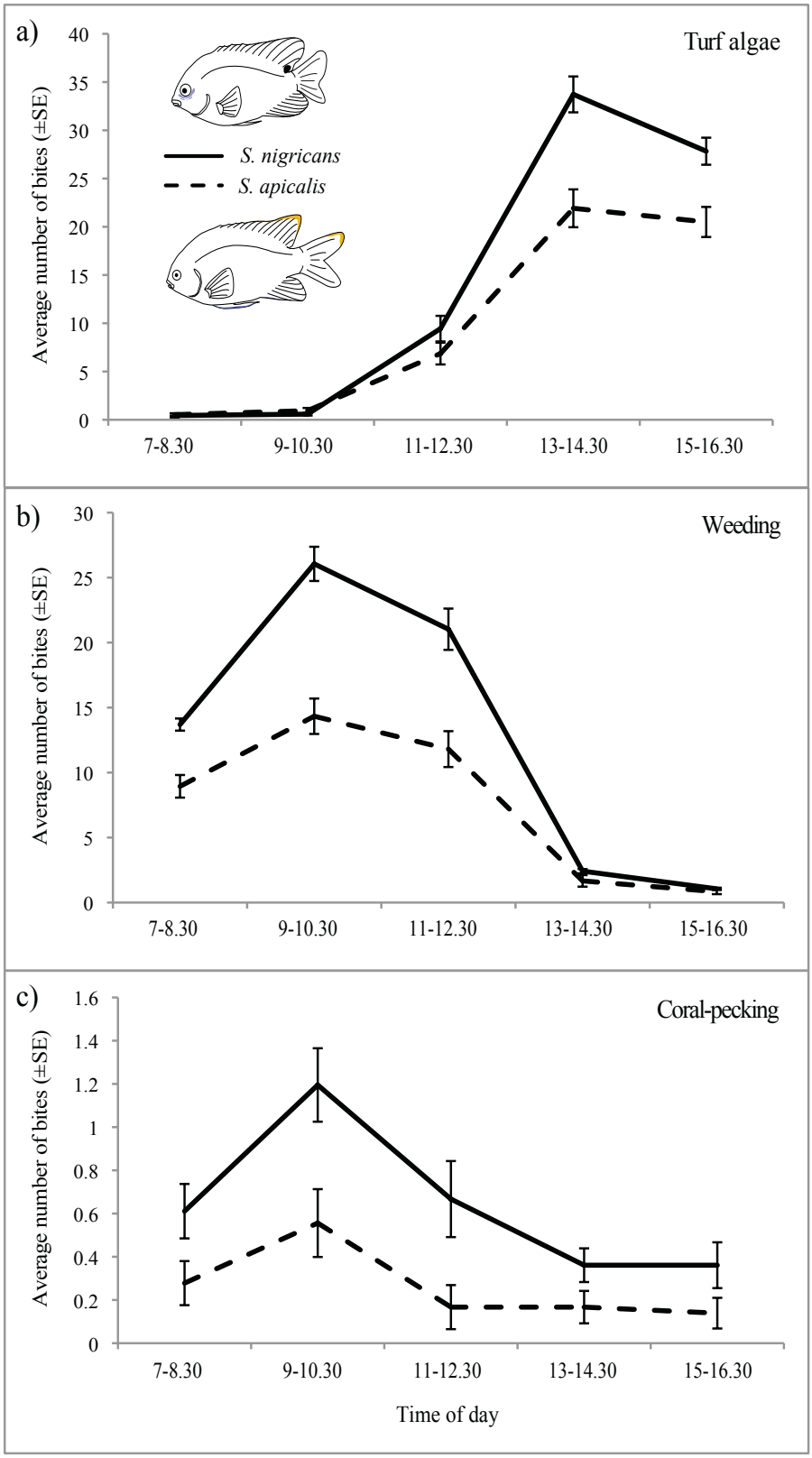



**Figure 2.2** Three resource-related behaviours: (a) grazing turf algae, (b) weeding undesirable species and (c) coral-pecking of *S. apicalis* and *S. nigricans.* The number of bites for each resource-related behaviour was averaged across observational periods (five-minute periods).

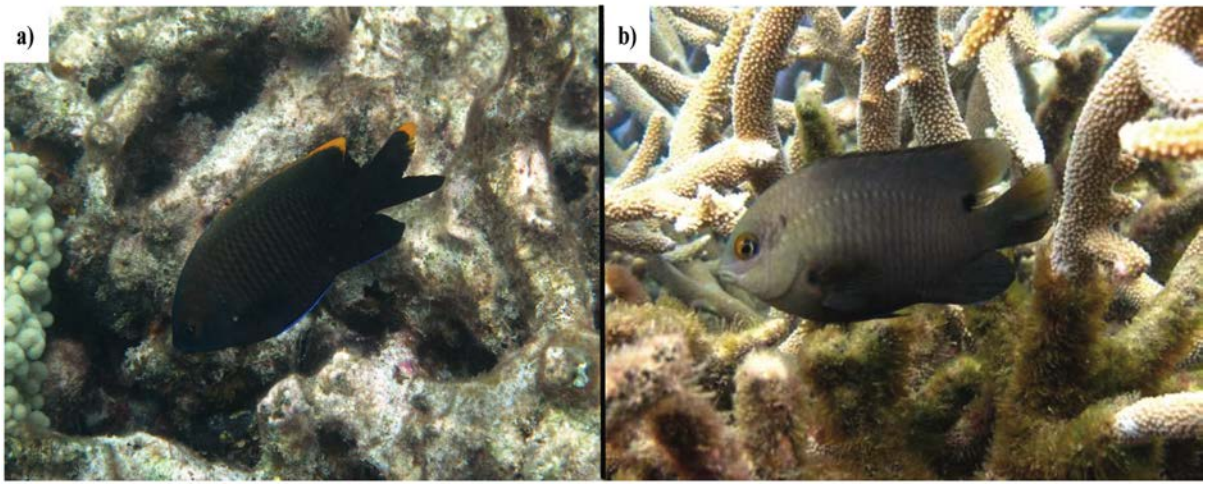



**Figure 2.3** The differential effects of (a) *S. apicalis* and (b) *S. nigricans* on the epilithic algal matrix. *S. apicalis* cultivates a thin layer of turf algae on barren regions and coral rubble on the benthos, whereas *S. nigricans* cultivates a thick turf on the branches of acroporids.

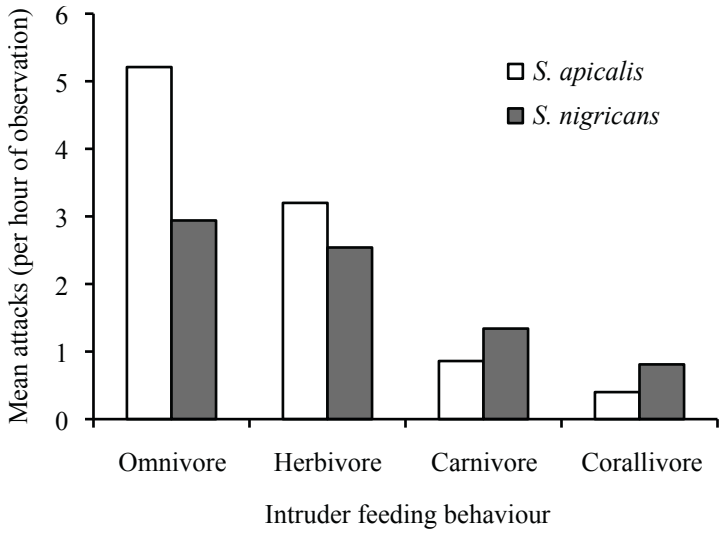



**Figure 2.4** Territorial defense of *S. apicalis* and *S. nigricans* by intruder feeding guild.

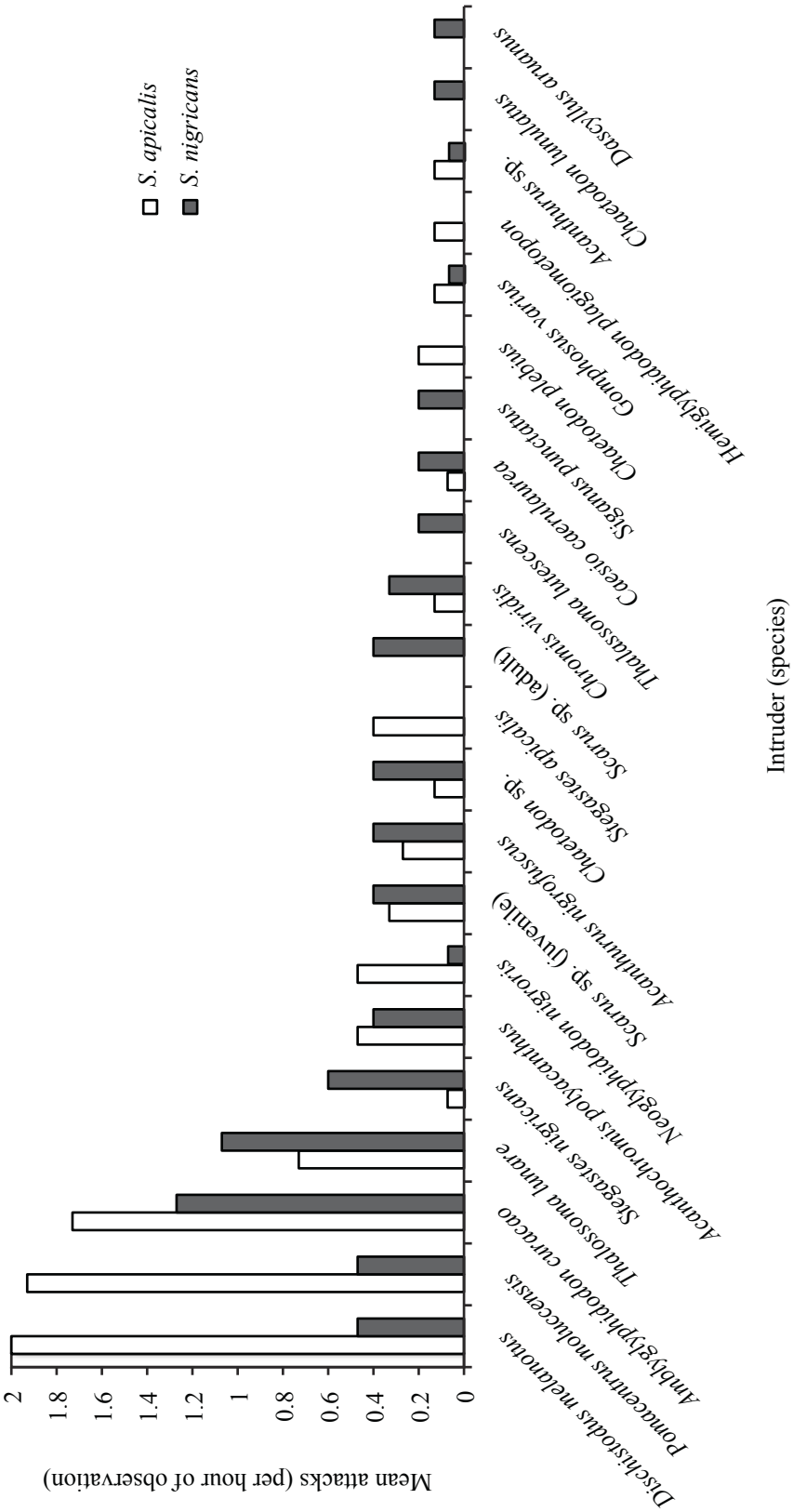



**Figure 2.5** Territorial defense of *S. apicalis* and *S. nigricans* by intruding species.

**Algal composition**

In the northern GBR around Lizard Island, *S. apicalis'* territories have a more diverse assemblage of turf algae than *S. nigricans'* territories (ten versus five species of turf algae; Table 2.2). The species richness, evenness, and Shannon diversity index indicate that the algal community diversity of *S. apicalis*' territories is significantly higher than *S. nigricans*' territories (Table 2.3). The three dominant turf algae genera in *S. apicalis* and *S. nigricans'* territories are *Polysiphonia*, *Amphiroa*, and *Ceramium*, all of which are rhodophytes. *Polysiphonia* sp. is the most abundant turf in both *S. apicalis'* and *S. nigricans'* territories; it comprises over 50 percent of turf algae coverage across all territories. Both damselfish species actively exclude macroalgae (except for *Halimeda*, which occurs in very low frequencies in *S. apicalis'* territories) that commonly occur in the lagoon around Lizard Island and were observed in the control plots. Despite the more diverse algal assemblage in *S. apicalis'* territories, *S. apicalis'* territories have a thinner layer of turf algae cultivated on barren flat regions and coral rubble on the benthos as opposed to *S. nigricans'* territories, which are characterized by a thicker turf (largely composed of *Polysiphonia* sp.) cultivated on the branches of acroporids (Figure 2.3). The thicker turf algae in *S. nigricans'* territories may be attributable to their more intensive farming behaviours (Figure 2.2; Table 2.1) and greater aggression than *S. apicalis* (Figure 2.4; Figure 2.5).

**Table 2.2** Average percent composition of turf algae and macroalgae found inside *S. apicalis'* territories, inside *S. nigricans*' territories and excluded from *Stegastes'* territories in the lagoon around Lizard Island in the northern GBR (A = abundant, 50-100 percent cover; O = occasional, 20-50 percent cover; R = rare, 0-20 percent cover).

| **Turf Algae/Macroalgae** | ***S. apicalis'* territories** | | | ***S. nigricans'* territories** | | | **Excluded from territories** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **A** | **O** | **R** | **A** | **O** | **R** | **A** | **O** | **R** |
| *Polysiphonia* sp. | X | | | X | | | | | |
| *Amphiroa foliacea* | | | X | | | X | | | |
| *Ceramium* sp. | | | X | | | X | | | |
| *Hormothamnion* sp.* | | X | X | | X | X | | | |
| *Dictyosphaeria cavernosa* | | | X | | | | | | |
| *Lithophyllum moluccense* | | | X | | | | | | |
| *Lithophyllum kotschyanum* | | | X | | | | | | |
| *Cladophora socialis* | | | X | | | | | | |
| Crustose coralline algae | | | X | | | | | | |
| *Halimeda opuntia* | | | X | | | | | X | |
| *Sargassum crassifolium* | | | | | | | | X | |
| *Turbinaria ornata* | | | | | | | | X | |
| *Padina* sp. | | | | | | | | | X |
| *Ventricaria* sp. | | | | | | | | | X |

**Hormothamnion* sp. is highly seasonal (occasional in the summer months and rare in the winter months in *S. apicalis* and *S. nigricans'* territories).

**Table 2.3** Diversity metrics describing algal community composition, including average value and standard error (SE) for *S. apicalis*' territories and *S. nigricans*' territories as well as the t-value, degrees of freedom (df) and p-value results of a paired two-tailed t-test. Shaded cells contain statistically significant values ($p < 0.05$).

| **Diversity metrics** | ***S. apicalis*** | | ***S. nigricans*** | | **t-value** | **df** | **p-value** |
|---|---|---|---|---|---|---|---|
| | **Average** | **SE** | **Average** | **SE** | | | |
| Species richness | 6.4 | 0.4 | 3.2 | 0.172 | 6.839 | 19 | < 0.0001 |
| Evenness | 0.712 | 0.015 | 0.553 | 0.024 | 9.967 | 19 | < 0.0001 |
| Shannon Index (H′) | 1.301 | 0.072 | 0.632 | 0.048 | 9.272 | 19 | < 0.0001 |

**Epilithic algal matrix microbial communities**

Bacterial 16S rDNA gene amplicon sequencing retrieved 102,038 high-quality sequence reads from 24 EAM samples. Sequence reads were normalised to 1050 reads per sample to allow for comparison between samples and bacterial community patterns. All sequences were submitted to the NCBI Sequence Read Archive (SAMN02808132-SAMN02808155).

The microbial community of the EAM is distinct among *S. apicalis'* territories, *S. nigricans'* territories and control plots outside of damselfish territories (Figure 2.6). There is some overlap between territories of *S. apicalis* and *S. nigricans,* suggesting that these two damselfish territories have similar microbial communities. *Polysiphonia* sp. is the dominant taxon in both damselfish species' territories, so this may explain the clustering between *S. apicalis'* and *S. nigricans'* territories (Figure 2.6; Figure 2.7). Further, there is some similarity between control plots outside of damselfish territories and *S. apicalis'* territories. Since *S. apicalis* cultivates algae on flattened regions of the benthos, which is a similar substrate to the control plots, whereas *S. nigricans'* cultivates algae on the branches of acroporids (Figure 2.3), microbial assemblages within control plots outside of damselfish territories cluster with *S. apicalis*' territories (Figure 2.6; Figure 2.7).

Assigning bacterial phylotypes into broad groupings of autotrophs, heterotrophs and potential coral pathogens (see Appendix A: Table A1) further reveals that damselfish territories have distinct microbial consortia (Figure 2.8). The relative abundance of autotrophs is significantly lower inside *S. apicalis*' territories (Kruskal-Wallis, $\chi^2 = 6.615$, p = 0.010) as is the relative abundance of heterotrophs inside *S. apicalis'* territories (Kruskal-Wallis, $\chi^2 = 3.84$, p = 0.050) and *S. nigricans*' territories (Kruskal-Wallis, $\chi^2 = 8.218$, p = 0.004) as opposed to outside *Stegastes*' territories (Figure 2.8; Table 2.4). The relative abundances of potential coral pathogens is two to three times greater inside *Stegastes*' territories as opposed to outside *Stegastes*' territories (Figure 2.8); there are significantly

higher relative abundances of potential opportunistic coral pathogens inside of *S. apicalis'* (Kruskal-Wallis, $\chi^2 = 4.335$, p = 0.037) and *S. nigricans'* (Kruskal-Wallis, $\chi^2 = 7.471$, p = 0.006) territories than outside of *Stegastes*' territories (Table 2.4). The coral-specific potential pathogen communities are comprised of the genera *Leptolyngbya* and *Oscillatoria*, key cyanobacteria associated with the pathogenicity of black band disease (BBD) (Myers et al. 2007).

I compared the identified OTUs with high sequence similarity to potential coral pathogens (cyanobacterial genera, *Leptolyngbya* and *Oscillatoria*) to the entire BLAST nucleotide collection (Swanson et al. 2011). The highest abundant *Oscillatoria* sequences from the current study yielded 34 BLAST hits (> 95% sequence identity) from two previous studies of BBD (Sekar et al. 2008; Klaus et al. 2011). Within the overlapping region of the amplified sequence, the most abundant *Leptolyngbya* sequences from the current study showed 97% sequence similarity to a *Leptolyngbya* sequence reported in a previous BBD study (Gantar et al. 2009) and to uncultured bacterial clones amplified from BBD corals (see Appendix B: Table B1). The taxonomy of these cyanobacterial potential coral pathogens is likely unresolved, which reflective of the complex phylogeneny of the cyanoprokaryote and supports previous calls for a re-evaluation of the taxonomy of the genus *Leptolyngbya* (Stoyanov et al. 2014). I also aligned the four most abundant uncultured cyanobacterial potential pathogen sequences to the unidentified bacterium clone sequence associated with the highest similarity from the BLAST results, which was the top match for 46.61% of the OTUs and associated with BBD affected corals (see Appendix B: Table B1; Figure 2.9).

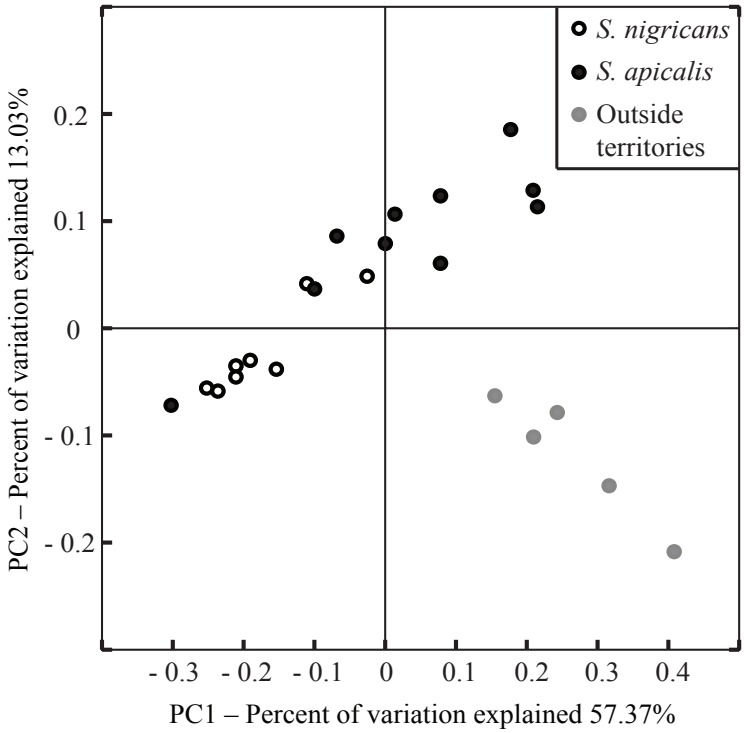



**Figure 2.6** Principal coordinates analysis (PCoA) plot showing the percent of variation in the microbial community of the EAM explained among *S. nigricans'* territories, *S. apicalis'* territories and outside of *Stegastes*' territories.

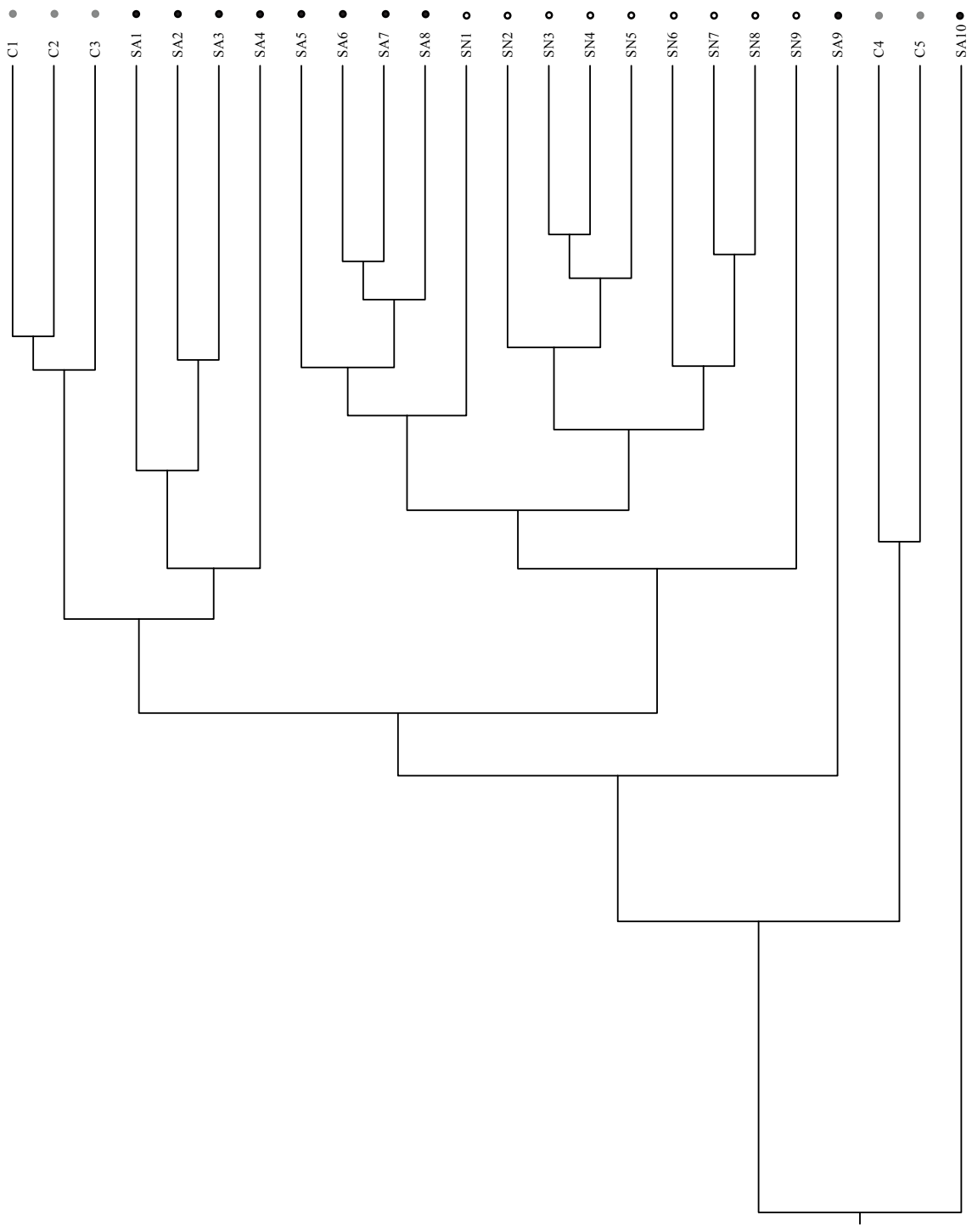



**Figure 2.7** UPGMA cluster of EAM microbial community samples (C = control, EAM outside of damselfish territories; SA = EAM inside *S. apicalis*' territories; SN = EAM inside *S. nigricans*' territories). The circular symbols with which the sample is represented on figure 2.6 is included after the sample name.

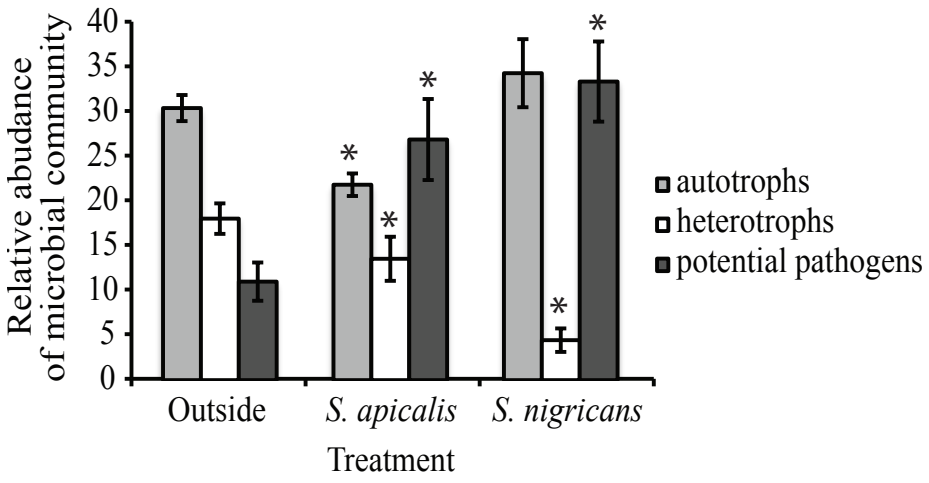



**Figure 2.8** Relative abundances of autotrophs, heterotrophs and coral-specific potential pathogens in the EAM in control plots outside of *Stegastes*' territories, inside *S. apicalis'* territories and inside *S. nigricans'* territories. Asterisks represent significant differences ($p < 0.05$) between the control plot (outside *Stegastes*' territories) and respective *Stegastes'* territories (Kruskal-Wallis one-way analysis of variance; see Table 2.4).

**Table 2.4** Kruskal-Wallis one-way of analysis of variance chi-squared ($\chi^2$) and p-value results for the relative abundances of autotrophs, heterotrophs and coral-specific potential pathogens in the EAM in control plots outside of *Stegastes*' territories as compared to the relative abundances autotrophs, heterotrophs and coral-specific potential pathogens in the EAM in *S. apicalis'* territories and in *S. nigricans'* territories. Shaded cells contain statistically significant values ($p < 0.05$).

| **Microbial Community** | ***S. apicalis*** | | ***S. nigricans*** | |
|---|---|---|---|---|
| | $\chi^2$ | p-value | $\chi^2$ | p-value |
| Autotrophs | 6.615 | 0.010 | 0.111 | 0.739 |
| Heterotrophs | 3.84 | 0.050 | 8.218 | 0.004 |
| Potential pathogens | 4.335 | 0.037 | 7.471 | 0.006 |

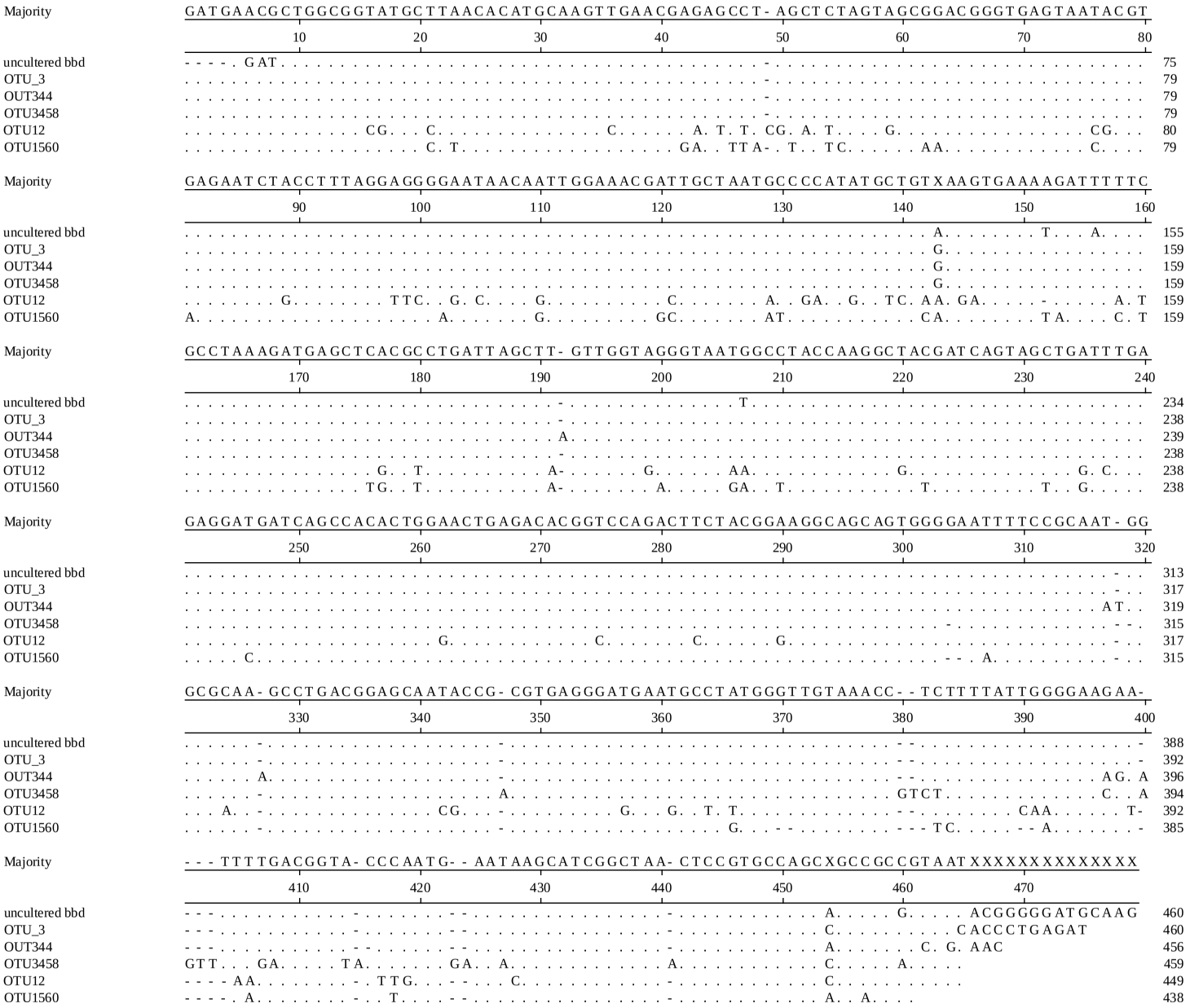



**Figure 2.9** Alignment of our four most abundant uncultured cyanobacterial potential pathogen sequences (that were assigned to *Leptolyngbya*) to the unidentified bacterium clone sequence (see Appendix B: Table B1, S41) with the highest similarity from the BLAST results.

**Coral disease surveys**

In *A. muricata* outcrops inside of *S. nigricans'* territories, I detected an average of 3.17 ± 1.41 occurrences of BBD per transect, whereas in *A. muricata* outcrops outside of *S. nigricans'* territories, there were zero occurrences of BBD (Figure 2.10). The GLMM revealed that *A. muricata* inside *S. nigricans'* territories have a significantly higher occurrence of BBD than *A. muricata* outside of *S. nigricans'* territories ($z = 2.670$, $p = 0.008$; Table 2.5; Figure 2.10).

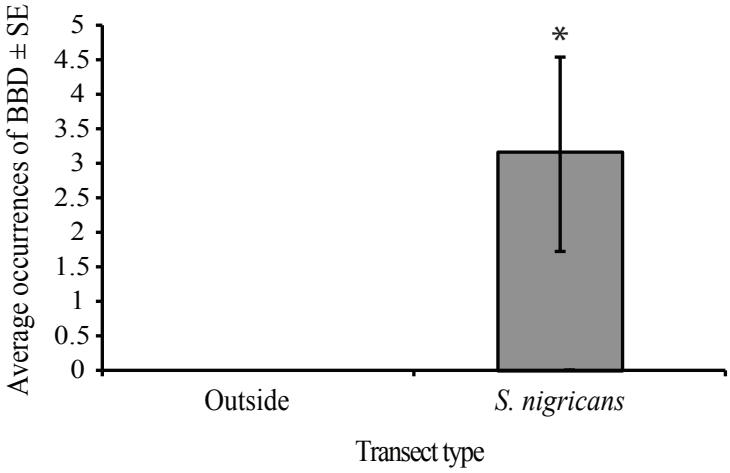



**Figure 2.10** Average occurrences of black band disease in *A. muricata* outcrops outside damselfish territories (n = 60) and inside *S. nigricans'* territories (n = 60; GLMM: p = 0.008). The asterisk represents a significant difference ($p < 0.05$).

**Table 2.5** Summary of GLMM statistics showing the effects of *S. nigricans*' territories on the presence of black band disease in *Acropora muricata* outcrops. Shaded cells contain statistically significant values ($p < 0.05$).

| | **Estimate** | **Std. Error** | **z-value** | **p-value** |
|---|---|---|---|---|
| Intercept | -4.482 | 1.230 | -3.645 | <0.001 |
| *S. nigricans* present | 3.462 | 1.297 | 2.670 | 0.008 |

## Discussion

This study shows how the modification of benthic habitat by a macro-organism can influence microbial assemblage structure, with potentially broad implications for ecosystem health. Specifically, on coral reefs, territorial grazers strongly influence both algal and microbial community structure, with potential implications for the dynamics of coral disease. Intensive territorial grazers in the genus *Stegastes* demonstrably shape turf algae communities by excluding macroalgae and cultivating low-diversity, high-density communities of rhodophytes (Klumpp & Polunin 1989; Ceccarelli et al. 2005a). These behaviours also result in a shift of the microbial communities associated with the EAM in damselfish territories to communities with a high prevalence of potential opportunistic pathogens linked to coral disease. Moreover, at least for *S. nigricans*, these differences in microbial community structure are associated with a higher occurence of coral disease relative to corals outside of damselfish territories. This provides the crucial first link between fish behaviour, reservoirs of potential coral disease pathogens and the occurrence of coral disease. In light of territorial grazers' extensive space occupation on many shallow coral reefs (Klumpp et al. 1987; Meekan et al. 1995), territorial damselfish may have a large role in coral disease dynamics via their extensive manipulation of the marine benthos.

Although both study species cultivate turf-dominant territories, I found considerable differences between the study species. *S. nigricans* have a less diverse assemblage of turf algae than *S. apicalis*, suggesting that *S. nigricans* should be classified as a more intensive territorial grazer than *S. apicalis*. This inference is supported by direct behavioural observations, which indicate more active cultivation of algae and greater aggression in *S. nigricans* as opposed to *S. apicalis* (Figure 2.2). It is likely that *S. nigricans* have a less diverse assemblage of turf algae because they cultivate a thick mat of *Polysiphonia* sp. (Figure 2.3), a highly filamentous turf that readily retains detritus and is one of the main food

sources of *Stegastes* (Galetto & Bellwood 1994; Ceccarelli et al. 2005b; Jones et al. 2006; Hata & Kato 2006; Hata & Umezawa 2011). When cultivated to reach high densities, such as inside *S. nigricans'* territories, *Polysiphonia* sp. may outcompete some of the more delicate turf algae present in *S. apicalis*' territories (Table 2.2) due to *Polysiphonia*'s advantageous lateral vegetative propagation and resilience to disturbance (Airoldi 1998; Airoldi 2000).

The most striking finding is that damselfish have a marked effect on benthic microbial communities and increase the prevalence of BBD, at least in *S. nigricans*' territories. *Oscillatoria*, an opportunistic pathogen associated with BBD (Myers et al. 2007), and uncultured cyanobacterial potential pathogens with homology to those isolated from BBD were strongly associated with the EAM inside damselfish territories. *Oscillatoria* and the uncultured cyanobacterial potential pathogens are both cyanobacteria, which is consistent with previous studies that show that diseased corals, particularly those with BBD, have elevated levels of cyanobacteria (Frias-Lopez et al. 2004; Sato et al. 2009; Mouchka et al. 2010). The prevalence of these phylotypes has major implications for coral reefs, suggesting that through altering benthic structure and preventing the establishment of macroalgae, territorial grazers may increase the incidence of microbes associated with coral disease. Intensive territorial grazers cultivate turf algae and detritus as food resources (Wilson & Bellwood et al. 1997), which appear to harbour potential pathogens linked to BBD and may act as a coral disease pathogen reservoir. Turf algae have previously been shown to harbour pathogens that are associated with coral disease (Barott et al. 2011; Sweet et al. 2013). However, fish behaviour has not previously been directly linked to reservoirs of potential pathogens that may cause coral disease or the actual increased prevalence of coral disease.

Identifying reservoirs for marine disease is a major priority within the realm of ocean disease research because knowledge of the rates of spread and modes of transmission of pathogens are limited (Harvell et al. 1999; Harvell et al. 2004; Bourne et al. 2009), yet no

study has closely examined the role of coral reef fishes in the transmission of coral disease. A previous study argued for a negative link between reef fish diversity and coral disease, and this was attributed to the fact that chaetodontids, which are typically not fished, remain on reefs disturbed by fishing and may play a role in the transmission of disease (Raymundo et al. 2009). If a link between fish diversity and coral disease does exist, it requires a more focused analysis of reef fish activities and associated disease prevalence. As the results suggest, coral reef fishes, especially herbivores and detritivores that strongly impact benthic dynamics, may play an important role in the formation of reservoirs of coral disease due to their feeding behaviours and territoriality. Consequently, there is a need to further examine widespread and abundant groups with strong benthic interactions, such as territorial pomacentrids, to determine their relationship to coral disease.

By actively cultivating benthic assemblages and within their territories, territorial pomacentrids function as ecosystem engineers (Jones et al. 1994). This study demonstrates that in the course of structuring habitat and modulating the availability of resources, ecosystem engineers may induce substantial alterations to microbial assemblages, with repercussions for microbial processes that influence disease ecology. On coral reefs, connections between fish populations, behaviour, disease reservoirs and coral health are of potentially substantial importance in regions where damselfish abundances are increasing, a phenomenon that may be associated with overfishing. Recent studies have reported up to a sixty-fold increase in damselfish abundances across a gradient of human impact (e.g., Hawaiian Islands (Friedlander & DeMartini 2002); Line Islands (Sandin et al. 2008)). Although large-scale patterns in fish community structure are influenced by numerous factors, including historical biogeography, reef geomorphology and human activities unrelated to fishing (Pinca et al. 2011; Taylor 2014), a global meta-analysis of local-scale studies has found a positive relationship between fishing pressure and damselfish abundance

that is consistent with the earlier studies (Edwards et al. 2014). Regardless of the specific mechanism that underlies this relationship, this study indicates that an increase in intensive territorial grazers will likely have substantial implications for the structure of the benthic microbial community on coral reefs, potentially increasing reservoirs of opportunistic pathogens linked to coral disease as well as the occurrence of coral disease. Consequently, understanding the mechanistic links among fishing pressure, damselfish abundances, shifts in microbial assemblages and the dynamics of associated coral communities may be important for anticipating and managing ongoing changes to the structure and functioning of coral reef ecosystems.

# Chapter 3: Coral transplantation triggers shift in microbiome and promotion of coral disease associated potential pathogens

## Introduction

Microbial diversity is essential for the functioning and resilience of terrestrial and marine ecosystems (Garren & Azam 2012). On coral reefs, microbial communities influence biogeochemical and ecological processes such as nutrient cycling and larval recruitment (Webster et al. 2004; Ainsworth et al. 2009). Reef-building corals are host to well-studied obligate symbionts in the genus *Symbiodinium*, but less is known about the diverse assemblages of bacteria that associate with corals (Knowlton & Rohwer 2003). Microbial communities are hypothesized to confer many benefits to their coral hosts, such as energy provision, photosynthesis, nitrogen fixation, and the prevention of infection. However, under disturbances and stressful environmental conditions, shifts in the coral microbiome have been linked to the degradation of coral reefs (Vega Thurber et al. 2009). Yet, current research does not adequately address the potential impacts of trophic interactions on microbial communities on coral reefs.

In the marine environment, benthic microbial communities are influenced by an array of abiotic and biotic factors, including nutrient fluxes and benthic-feeding organisms (Alongi 1994; Casey et al. 2014). Territorial damselfishes are abundant and important engineers of the reef benthos and play a key role in benthic dynamics (Choat 1991; Ceccarelli et al. 2001; Hata & Kato 2004). These fishes exhibit several key behaviors that extensively modify benthic structure in their territories: grazing turf algae, weeding unpalatable macroalgae, coral-pecking to further propagate turf algae, and engaging in constant aggression to protect their algal resources from intruders (Kaufman 1977; Hinds & Ballantine 1987; Klumpp &

Polunin 1989). Although turf algae is omnipresent across the reef benthos, territorial damselfishes cultivate a notably thicker turf inside their territories, and damselfishes in the genus *Stegastes* maintain low-diversity algal turfs on the benthos and coral skeletons (Hata et al. 2002; Hata & Kato 2004). Thus, damselfish territories are dominated by the epilithic algal matrix (EAM), a conglomeration of turf algae, juvenile macroalgae, detritus, invertebrates, and bacterial assemblages (Wilson & Bellwood 1997; Wilson et al. 2003; Fricke et al. 2011; Barott & Rohwer 2012).

The EAM is known to have negative effects on coral growth and survival both inside and outside of damselfish territories (Quan-Young & Espinoza-Avalos 2006; Smith et al. 2006; Barott et al. 2011; Haas et al. 2011; Vega Thurber et al. 2012; Sweet et al. 2013); therefore, due to their cultivation of a thick EAM, the impact of territorial grazers on corals is largely negative. Territorial grazers have been shown to inhibit coral recruitment (Arnold et al. 2010), negatively impact the abundance of juvenile corals (Casey et al. 2015), and cause mortality in adult corals (Kaufman 1977). The EAM inside *Stegastes*' territories has also been shown to harbour potential pathogens linked to black band disease (BBD; Casey et al. 2014). Due to the elevated levels of potential coral disease pathogens in the EAM, territorial grazers may indirectly promote disease and mortality in corals inside their territories. Direct contact-mediated coral-algal interactions may cause toxicity or hypoxia in coral tissues, thus facilitating the invasion of opportunistic pathogens. This stress-induced increase in potential pathogens may ultimately lead to coral disease or death (Barott & Rohwer 2012).

Although corals and algae have a highly antagonistic relationship on coral reefs, they are known to harbour distinct microbial communities (Barott et al. 2011), and corals can outcompete turf algae in areas of low anthropogenic disturbance (Barott et al. 2012). While territorial damselfishes in the genus *Stegastes* have been shown to negatively impact corals, the relationship between damselfishes and corals is variable depending on region and habitat,

and damselfishes have also been reported to increase coral recruitment (Gleason 1996) and facilitate adult coral survival (Glynn & Colgan 1988; Done et al. 1991; Suefuji & van Woesik 1998; White & O'Donnell 2009; Gochfeld 2010). Therefore, the high occurrence of coral disease-associated bacteria in the EAM inside *Stegastes*' territories is not necessarily indicative of the composition of neighboring coral microbial assemblages. Thus, this study aims to determine the coral survivorship and the microbial composition of corals within territories of damselfishes in the genus *Stegastes.* Specifically, I determined the impact of *Stegastes* on the survival of transplanted corals and analyzed how coral transplantation inside and outside of *Stegastes*' territories affects coral microbial communities.

## Methods

### Study site and species

This study took place at Lizard Island in the northern GBR, Australia (14°41'5"S, 145°26'55"E) from February 2012 to August 2013. The study site was on the back reef in the lagoon between Palfrey and South Island at a depth of 1-3 m (Figure 3.1).

*Stegastes nigricans* and *Stegastes apicalis* (f. Pomacentridae), two intensive territorial grazers, were the damselfish study species. *S. apicalis* occurs at a depth of 1-15 m and reaches up to 15 cm (total length). *S. nigricans* occurs at the depth of 1-12 m and reaches up to 14 cm (total length). Both species form social groups (termed "colonies") made up of several contiguous territories, where each territory belongs to an individual adult damselfish.

*Acropora muricata* was the coral study species. It is a common staghorn coral with aborescent branching in shallow reefs around Lizard Island, especially lagoon and back reef habitats. *Stegastes* typically form colonies within or around outcrops of *A. muricata.*

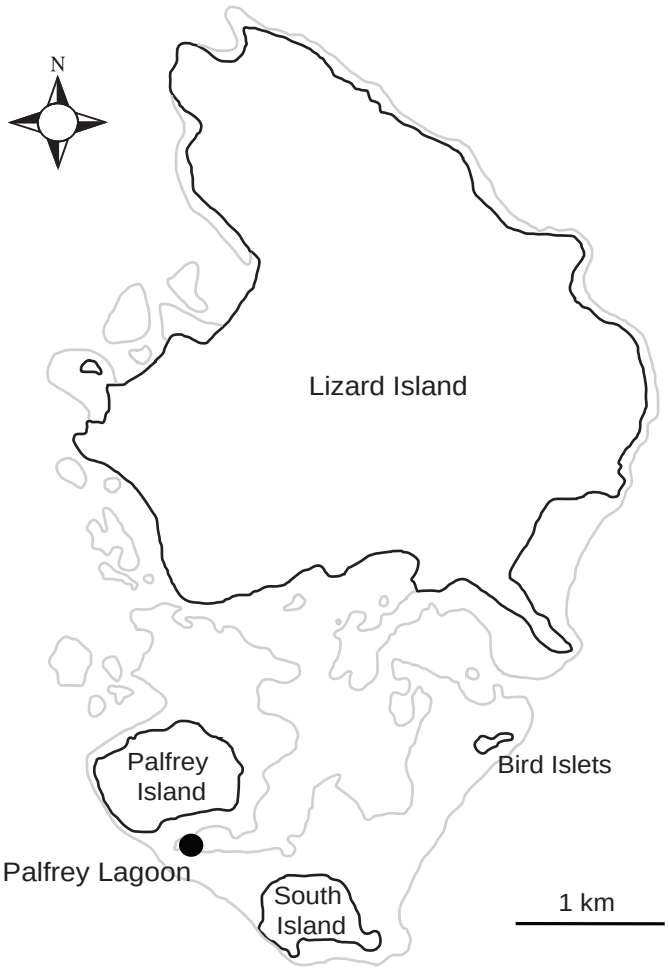



**Figure 3.1** Map of Lizard Island and fringing reefs showing the study site in the lagoon by Palfrey Island.

**Coral baseline samples**

To determine the impact of territorial damselfishes on coral microbial communities, I first collected coral branches from outside and inside damselfish territories. In the field, ten 15 cm coral branches were collected from control plots outside damselfish territories, ten from inside *S. apicalis*' territories, and ten from inside *S. nigricans*' territories. For the collections from *S. apicalis*' and *S. nigricans*' territories, branches were taken across two damselfish colonies, and each branch came from a different damselfish territory.

**Coral transplant**

To determine the effects of EAM exposure and damselfish farming behaviours on coral fragments over time, I set up a coral transplant outside and inside damselfish territories. Due to the higher success rate of coral transplantation of *A. muricata* when medium to large-sized fragments (10-20 cm) are used (Okubo et al. 2005), I sourced 120 15-cm fragments of *A. muricata* from outside damselfish territories. To minimize handling time, coral fragments were briefly transported to large seawater bins for labeling at the field site, then immediately transplanted using marine epoxy. Coral fragments were directly transplanted rather than allocating a recovery period in holding tanks because placing corals in holding tanks after fragmentation can substantially alter bacterial assemblages (Ainsworth & Hoegh-Guldberg 2009) and experimental injuries (such as wounding from fragmentation) have been shown to have a limited impact on the coral immune response (van de Water et al. 2015). Forty fragments were transplanted in control plots outside of damselfish territories, forty fragments were transplanted inside *S. apicalis*' territories, and forty fragments were transplanted in *S. nigricans*' territories. Coral fragments were distributed randomly across treatments with respect to the source colonies. Two transplanted corals were placed in each *Stegastes*' territory, and the transplanted corals were distributed across two *S. apicalis*' colonies and two

*S. nigricans*' colonies, which were the same colonies that were used for baseline sample collections.

After six months, the percent mortality (percentage of tissue loss) of each coral fragment was estimated, and ten coral fragments (only one fragment from each territory) were sampled from each treatment for microbial analyses. Percent mortality estimates and microbial sampling (ten coral fragments from each treatment) were repeated after one year. Thus, I sampled a total of 90 coral fragments: 30 baseline samples, 30 samples after six months of transplantation, and 30 samples after one year of transplantation. Of each 30 samples, ten were from control plots outside of damselfish territories, ten were from *S. apicalis*' territories, and ten were from *S. nigricans*' territories.

**Microbial processing**

After collection, coral fragments were immediately snap-frozen in liquid nitrogen, stored at -80℃, and transported to James Cook University for processing and DNA extractions. Samples were homogenized under liquid nitrogen. When tissue fragments suffered partial to high mortality, care was taken to homogenize only live tissue sections of the coral fragments (dead tissue and algae coverage was excluded). See Casey et al. (2014) for methods of DNA isolation, quality control, PCR, and 16S rDNA sequencing.

**Coral mortality data analysis**

To analyze the effect of intensive territorial grazers on the mortality of transplanted corals, I used Akaike's Information Criterion (AIC) to compare the fit of three generalized linear models (GLM) to the data. Due to preferential removal of coral fragments with low mortality for microbial analysis after six months of transplantation, I focused on mortality over the first six month period only to avoid biases associated with sample removal. For each model, the

response was multinomial (low mortality, partial mortality, and high mortality in transplanted coral): low mortality was defined as 0-20% loss of tissue from the coral branch, partial mortality was defined as 20-80% loss of tissue from the coral branch, and high mortality was defined as 80-99% loss of tissue from the coral branch (Figure 3.2). In the first GLM, the fixed effect was the presence or absence of a damselfish territory, separating the effects of damselfish species (control plots with no damselfish territory *versus S. apicalis*' territories and *S. nigricans*' territories). In the second GLM, the fixed effect was also the presence or absence of a damselfish territory, without separating the effects of damselfish species (control plots with no damselfish territory *versus* damselfish territories). The third GLM was an intercept-only model with no treatment effects. The analysis was conducted with the package *nnet* (Venables & Ripley 2002) using the software program R (R Core Team 2015).

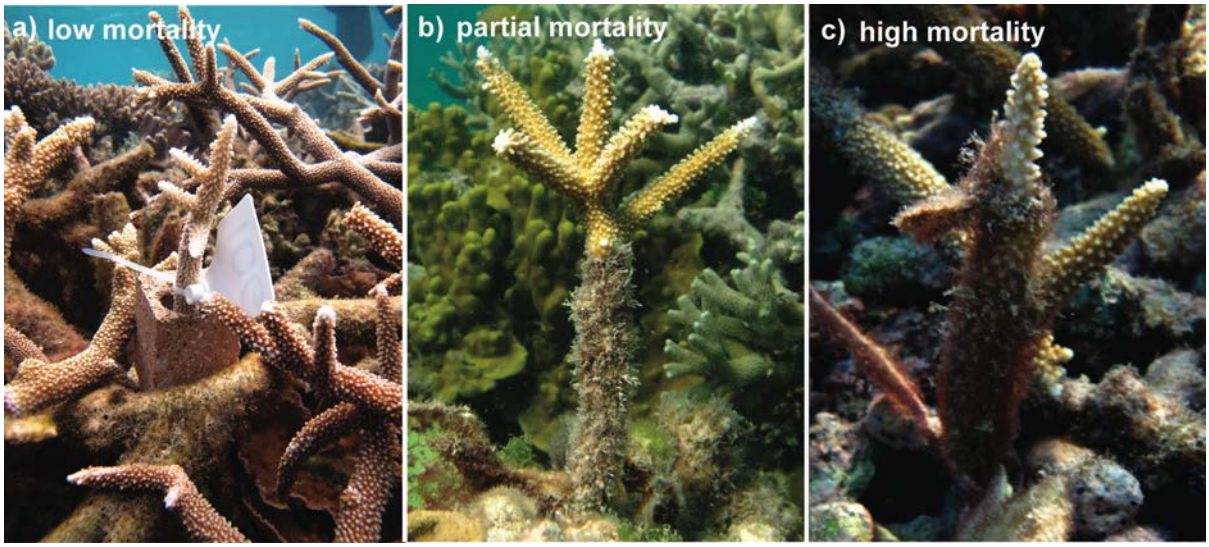



**Figure 3.2** Mortality of transplanted corals in *Stegastes*' territories after six months. (a) Low (0-20%) mortality, (b) partial (20-80%) mortality, and (c) high (80-99%) mortality. Photographs taken by J.M.C.

**Microbial data analysis**

The sequence data were processed using a proprietary analysis pipeline at MR DNA and re-analyzed with Quantitative Insights Into Microbial Ecology (QIIME; Caporaso et al. 2005). For both the proprietary analysis pipeline at MR DNA and QIIME, sequences were depleted of barcodes and primers, and short sequences (< 200 bp) and sequences with homopolymer runs exceeding 6 bp were removed. The average read length was 437 bp after primer and barcode removal. See Casey et al. (2014) for further methods of denoising, normalization, definition of operational taxonomic units (OTUs), and taxonomical assignments with QIIME.

We assessed the beta-diversity of the coral and EAM microbial communities (EAM samples were collected concurrently at the same study site; data published by Casey et al. (2014)) inside and outside of damselfish territories with QIIME using a weighted UniFrac analysis. A principal coordinates analysis (PCoA) was generated from the UniFrac distances (Lozupone & Knight 2005). A PCoA was generated from weighted UniFrac distances and plotted in two dimensions.

Individual OTUs were assigned into three categories: autotrophs, heterotrophs and potential pathogens, based on literature reviews (see Appendix C: Table C1). All genera with a less than two percent relative abundance were excluded from the analyses (see Appendix D: Tables D1-D9). Our data included twenty-one genera that are considered potential pathogens for a broad array of hosts; however, among these genera, four are specifically linked to coral disease. These four coral-specific potential pathogens made up 26.4% percent relative abundance of the potential pathogen category, and I focused on these coral disease associated potential pathogens in a further analysis.

We fit GLMs to analyze the differences in the relative abundances of autotrophs, heterotrophs, potential pathogens, and potential coral disease pathogens in coral microbial communities outside of damselfish territories as compared to inside *S. apicalis'* territories

and *S. nigricans*' territories and across the three sampling periods (baseline, six month of transplantation, and one year of transplantation). We used a quasi-binomial error structure to account for the fact that the response variable (relative abundance) varied continuously between zero and one. The fixed effects included treatment (control plots outside of damselfish territories, inside *S. apicalis'* territories, and inside *S. nigricans*' territories) and time (baseline, transplantation after six months, and transplantation after one year) and their interactions. Thus, these models simultaneously analyzed the effects of damselfish presence as well as time of transplantation on the metabolic groupings of coral bacterial assemblages. Since I employed a quasi-binomial error structure in this analysis, likelihood-based model selection, such as AIC, could not be used. Instead, I employed a quasi-likelihood procedure based on adjusted model deviances, which utilizes the standard *F* distribution as the null distribution (see Zuur et al. (2009)). The analysis was conducted with the packages *lme4* (Bates et al. 2014) and *arm* (Gelman & Su 2014) using the software program R (R Core Team 2015).

## Results

### Mortality of transplanted corals

Model selection indicated that the best model of coral mortality included the effects of both damselfish species by comparing control plots with no damselfish territory to *S. apicalis*' territories and *S. nigricans*' territories. Specifically, after six months, corals transplanted inside damselfish territories suffered a higher mortality (loss of tissue) than corals outside damselfish territories, with coral fragments inside *S. nigricans*' territories exhibiting a stronger estimated response than fragments inside *S. apicalis*' territories (Table 3.1, Figure 3.2, and Figure 3.3).

**Table 3.1** Model selection and effect sizes (Coefficients) among three generalized linear models with a multinomial distribution showing the effects of territorial damselfishes on the partial mortality (20-80%) and high mortality (80-99%) of transplanted corals, including a comparison of a) control plots without damselfish present (Control), *S. apicalis*' territories, and *S. nigricans*' territories, b) control plots without damselfish present and damselfish territories (Damselfish), and c) an intercept-only model with no treatment effects. P-values are for individual effects and represent tests of the null hypothesis that the relevant treatment differs from the control. Shaded cells contain statistically significant values ($p < 0.05$).

| Model | Mortality | Variable | Coefficients | Std. Error | p-value | AIC |
|---|---|---|---|---|---|---|
| a) Damselfish species | Partial | Control | -1.897 | 0.619 | -- | 181.74 |
| | | *S. apicalis* | -0.875 | 1.202 | 0.234 | |
| | | *S. nigricans* | 1.609 | 0.822 | 0.027 | |
| | High | Control | -0.798 | 0.401 | -- | |
| | | *S. apicalis* | 0.798 | 0.535 | 0.070 | |
| | | *S. nigricans* | 1.492 | 0.590 | 0.007 | |
| b) Damselfish grouped | Partial | Control | -1.897 | 0.619 | -- | 184.27 |
| | | Damselfish | 0.665 | 0.754 | 0.190 | |
| | High | Control | -0.798 | 0.401 | -- | |
| | | Damselfish | 1.086 | 0.484 | 0.014 | |
| c) Intercept only | Partial | Intercept | -1.481 | 0.350 | <0.001 | 185.66 |
| | High | Intercept | -0.071 | 0.217 | <0.001 | |

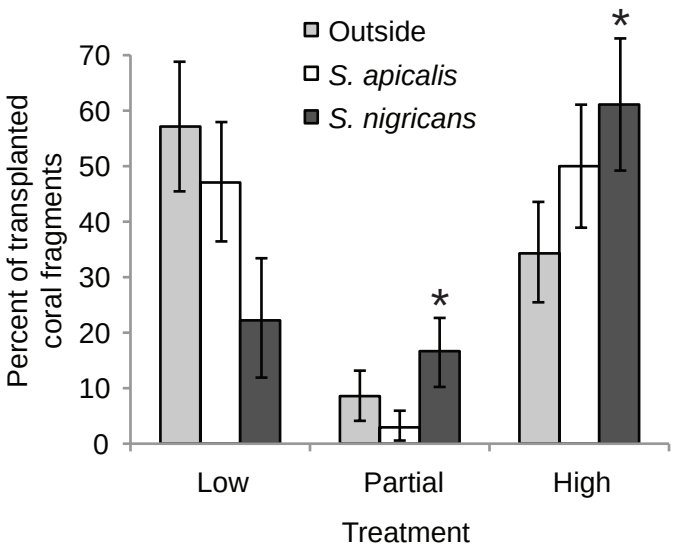



**Figure 3.3** Percent of transplanted coral fragments (± SE) that suffered mortality after six months of transplantation. Mortality is categorized as low mortality (0-20%), partial mortality (20-80%), and high mortality (80-99%). Treatments include control plots outside damselfish territories (35 fragments), inside *S. apicalis'* territories (34 fragments), and inside *S. nigricans'* territories (36 fragments). Bars represent means and standard errors of percentages of fragments in each mortality category across control plots outside damselfish territories and inside different damselfish territories ($n$ = 20 territories in each case). Asterisks indicate significant values ($p < 0.05$).

**Coral microbial communities**

Bacterial 16S rDNA gene amplicon sequencing retrieved 235,388 high-quality sequence reads from 77 coral samples (DNA extractions and sequencing were successful for 77 coral samples out of the 90 collected coral fragments). Sequence reads were normalized to 960 reads per sample to allow for comparison between samples and bacterial community patterns, which further excluded two samples, resulting in 75 coral samples. In an analysis of all bacterial phylotypes, genera were assigned into the metabolic groupings of autotrophs, heterotrophs, and potential pathogens (see Appendix C: Table C1), revealing that microbial communities in the coral fragments shift according to the presence of damselfish territories and over the course of one year of transplantation (Figure 3.4). Model selection indicated that the best model for the relative abundance of autotrophs included the main effects of treatment (damselfish effects) and time, but no interaction (Table 3.2). As compared to baseline coral microbial communities, there were significant increases in the relative abundance of autotrophs after six months ($p = 0.001$) and one year ($p = 0.008$) of transplantation (Figure 3.4). Further, as compared to corals transplanted outside of damselfish territories, corals inside *S. nigricans*' territories had significantly lower relative abundances of autotrophs ($p = 0008$). For heterotrophs, model selection indicated that the best model included the effect of time only (Table 3.2). As compared to baseline coral microbial communities, there were significant decreases in the relative abundance of heterotrophs after six months ($p < 0.001$) and one year ($p < 0.001$) of transplantation (Figure 3.4). Lastly, model selection indicated that the best model for potential pathogens included the full model: effects of treatment (damselfish effects), time, and their interactions (Table 3.2). The relative abundance of potential pathogens was impacted by a significant interaction ($p = 0.002$). Visual inspection suggests that changes in potential pathogens across treatments and time were driven by larger

increases over the first six months in control fragments relative to those in damselfish territories, particularly those of *S. nigricans* (Figure 3.4).

**Potential coral disease pathogens**

Model selection indicated that the best model for the relative abundance of potential coral disease pathogens included the main effects of treatment (damselfish effects) and time, but no interaction (Table 3.2). As compared to baseline coral fragments, acroporid fragments experienced significantly higher relative abundances in potential pathogens associated with coral disease after six months ($p = 0.001$), and to a lesser extent, after one year ($p = 0.008$) of transplantation (Figure 3.5). The potential coral disease pathogens were in the genera *Geitlerinema*, *Leptolyngbya*, *Oscillatoria*, and *Sphingomonas* (Myers et al. 2007; Richardson et al. 1998). Of these coral-disease associated potential pathogens, *Geitlerinema*, *Leptolyngbya*, and *Oscillatoria* are associated with BBD (Myers et al. 2007). Also, as compared to no-damselfish controls, there were significantly lower relative abundances of potential pathogens associated with coral disease in coral fragments inside *S. nigricans*' territories ($p = 0.008$), but the lower abundances inside *S. apicalis*' territories did not differ significantly from controls ($p = 0.073$, Figure 3.5).

**Table 3.2** Model selection for four generalized linear models with quasi-binomial error structures for the relative abundances of autotrophs, heterotrophs, potential pathogens, and potential coral disease pathogens in coral fragments in control plots outside *Stegastes*' territories as compared to coral fragments inside *S. apicalis'* territories and *S. nigricans'* territories (damselfish effects). Sampling periods include baseline coral fragments as compared to transplanted corals after six months and transplanted corals after one year (time effects). The full models include the damselfish effects, time effects, and their interactions. Model selection was performed with a quasi-likelihood procedure based on adjusted model deviances, which utilizes the standard *F* distribution. P-values test the null hypothesis that the simpler model of the two being compared is true; thus, shaded cells ($p < 0.05$) indicate rejection of the simpler model in favor of the more complex one.

| Energetic grouping | Model selection | Difference in deviances | Degrees of freedom | F-value | p-value |
|---|---|---|---|---|---|
| Autotrophs | Full model vs. Main effects only | 0.630 | 4 | 1.460 | 0.224 |
| | Main effects vs. Damselfish effects only | 7.952 | 2 | 35.960 | <0.001 |
| | Main effects vs. Time effects only | 1.312 | 2 | 5.935 | 0.004 |
| Heterotrophs | Full model vs. Main effects only | 0.389 | 4 | 0.272 | 0.895 |
| | Main effects vs. Damselfish effects only | 8.685 | 2 | 12.692 | <0.001 |
| | Main effects vs. Time effects only | 0.354 | 2 | 0.517 | 0.598 |
| Potential pathogens | Full model vs. Main effects only | 1.487 | 4 | 2.958 | 0.026 |
| | Main effects vs. Damselfish effects only | 1.256 | 2 | 4.502 | 0.014 |
| | Main effects vs. Time effects only | 1.228 | 2 | 4.402 | 0.016 |
| Potential coral disease pathogens | Full model vs. Main effects only | 0.629 | 4 | 1.535 | 0.202 |
| | Main effects vs. Damselfish effects only | 4.661 | 2 | 22.103 | <0.001 |
| | Main effects vs. Time effects only | 0.897 | 2 | 4.255 | 0.018 |

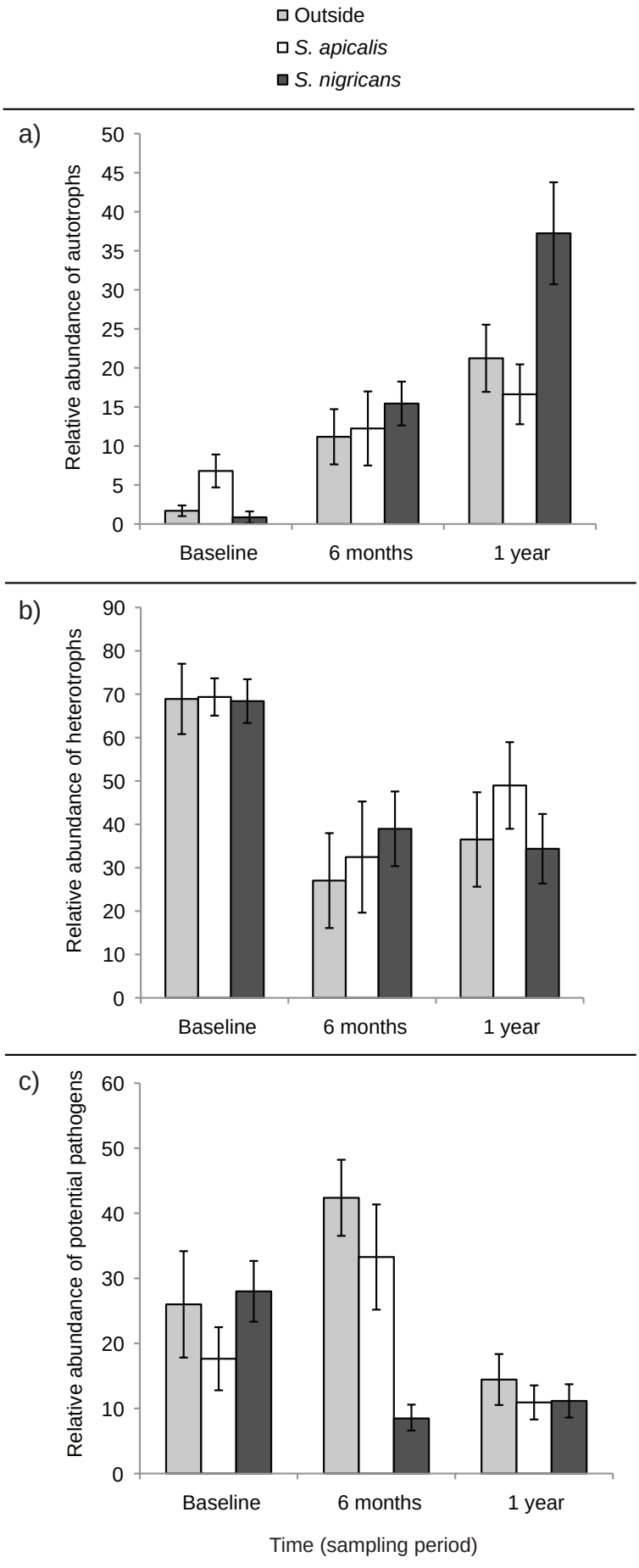

Outside
S. apicalis
S. nigricans
a)
Relative abundance of autotrophs
0
5
10
15
20
25
30
35
40
45
50
Baseline
6 months
1 year
b)
Relative abundance of heterotrophs
0
10
20
30
40
50
60
70
80
90
Baseline
6 months
1 year
c)
Relative abundance of potential pathogens
0
10
20
30
40
50
60
Baseline
6 months
1 year
Time (sampling period)

**Figure 3.4** Relative abundances of autotrophs, heterotrophs, and potential pathogens in coral fragments. The relative abundance (± SE) of (a) autotrophs, (b) heterotrophs, and (c) potential pathogens according to damselfish presence (control plots outside damselfish territories, inside *S. apicalis'* territories, and inside *S. nigricans'* territories) and time after transplantation (baseline coral fragments, transplanted coral fragments after six months, and transplanted coral fragments after one year).

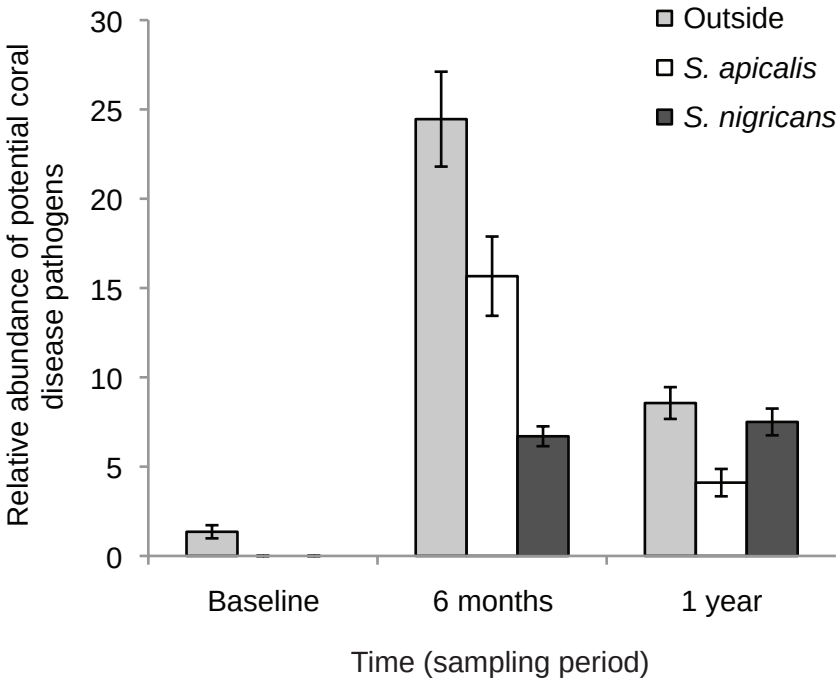



**Figure 3.5** Relative abundances of potential coral disease pathogens in coral fragments. The relative abundance (± SE) of coral disease associated potential pathogens according to damselfish presence (control plots outside damselfish territories, inside *S. apicalis'* territories, and inside *S. nigricans'* territories) and time after transplantation (baseline coral fragments, transplanted coral fragments after six months, and transplanted coral fragments after one year).

## Discussion

This study reveals that the presence of territorial damselfishes increases the rate of mortality of corals relocated to within territories. As compared to benthic plots outside damselfish territories, *S. nigricans* trigger the highest rate of mortality in transplanted corals, with *S. apicalis* causing an intermediate rate of mortality between plots outside of damselfish territories and *S. nigricans*' territories. It has been shown that *S. nigricans* engage in more intensive farming behaviours than *S. apicalis* (Casey et al. 2014); therefore, it is likely that *S. nigricans*' intensive cultivation of the EAM or direct polyp mortality by coral-pecking may outcompete stressed, transplanted corals. Surprisingly, despite these higher rates of mortality, *Stegastes* do not have a differential impact on coral microbial communities. While previous work has shown that there are higher relative abundances of coral disease pathogens in the EAM inside *Stegastes'* territories (Casey et al. 2014), this study demonstrates that shifts in bacterial assemblages in corals after transplantation are not directly related to the impact of territorial damselfishes.

However, the damage caused by coral transplantation is found to impact the microbial community of corals. Six months after coral transplantation, over fifty percent of the coral fragments suffered partial to high mortality. As a result of this high rate of mortality, coral transplantation both inside and outside damselfish territories also triggered a shift in the coral microbiome that is evident up to a year after the initial transplantation. To further analyze how the microbiome of transplanted corals shift over time as a function of percent coral mortality, I examined the similarity of transplanted coral microbial communities to EAM microbial communities (EAM data published by Casey et al. (2014)). This analysis reveals a transition in the microbial community of baseline coral samples and the healthy tissue of transplanted corals with low (0-20%) mortality to transplanted corals with partial (20-80%) mortality to transplanted corals with high (80-99%) mortality (Figure 3.6). The microbial

community of transplanted corals with high mortality is more similar to the EAM microbial community than to the baseline coral microbial community. Exposure to the benthos, and consequently the EAM, has a transformative effect on microbial communities of transplanted corals that suffer partial to high mortality, as the coral tissue undergoes a microbial transition from an association with healthy corals to an association with the EAM. This microbial shift, in which coral microbial communities increasingly resemble the EAM microbial community, has major implications for benthic microbial assemblages. When benthic microbial communities become homogenous, from the EAM to corals, this loss of microbial diversity may lead to decreased resilience against potential coral disease pathogens (Hube 2004; Sunagawa et al. 2010; Apprill et al. 2013).

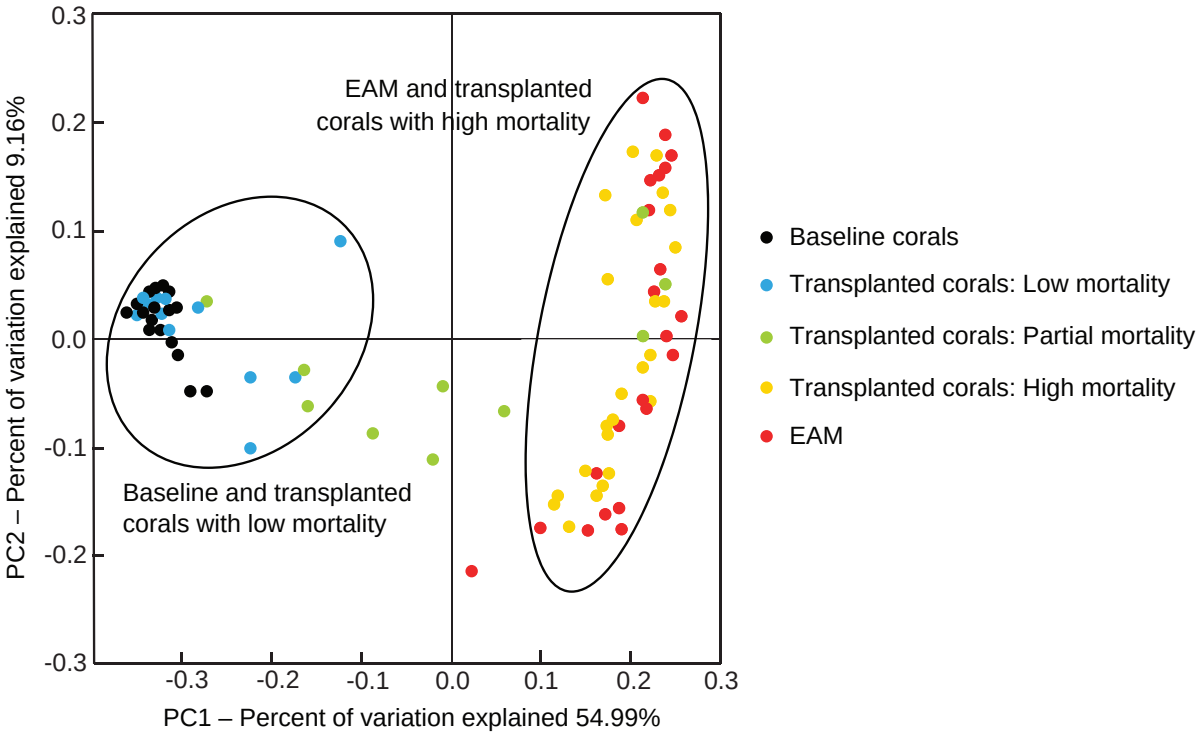



**Figure 3.6** Principal coordinates analysis (PCoA) showing the percent of variation explained in the microbial community. Treatments include baseline coral fragments, transplanted corals with low mortality (0-20%), transplanted corals with partial mortality (20-80%), transplanted corals with high mortality (80-99%), and EAM samples (data published in Casey et al. (2014)) outside damselfish territories, inside *S. apicalis*' territories, and inside *S. nigricans*' territories. The ellipses represent distinct clustering of the baseline corals, transplanted corals, and EAM samples.

Previous work shows that there are higher relative abundances of BBD pathogens in the EAM inside *Stegastes'* territories as well as a higher occurrence of BBD inside *S. nigricans*' territories (Casey et al. 2014). This study reveals that the higher relative abundance of potential coral disease pathogens in the EAM inside *Stegastes*' territories may opportunistically cause BBD in acroporids, but it does not demonstrate nor predict shifts in the overall coral microbial assemblage in *A. muricata* inside *Stegastes*' territories. The fact that BBD pathogens are omnipresent, albeit in lower abundances, across the reef benthos allows them to opportunistically colonize stressed transplanted corals, regardless of *Stegastes* presence or absence. It is known that even healthy corals have potential pathogens in their bacterial assemblages, and under changing environmental conditions, a commensal may transition to a pathogenic state (Hube 2004). Here, I found that one prevalent taxon among the samples has been previously linked to disease in corals. Bacteria in the genus *Ruegeria* were consistently present within 50 percent of all coral fragments and previously have been associated with both healthy corals and coral lesions resulting from Yellow Band Disease (Apprill et al. 2013). *Ruegeria* also undergoes horizontal gene transfer, which may help hosts and microbial associates adapt to environmental challenges in short time periods (McDaniel et al. 2010; McDaniel et al. 2012). Despite the suggestion of a possible link between *Ruegeria* and the promotion of coral disease (Sekar et al. 2008; Sunagawa et al. 2009; Apprill et al. 2013), the common occurrence of *Ruegeria* in baseline and transplanted corals suggests that the role of these bacteria is a commensal in the current study.

A considerable number of studies have investigated the efficacy of coral transplantation as a means for coral reef restoration by examining how transplantation affects coral growth, mortality and physiology (Pulcer-Rosario & Randall 1987; Yap et al. 1998; Ammar et al. 2000; Thornton et al. 2000; Soong & Chen 2003; Raymundo & Maypa 2004; Garrison & Ward 2008). While it is known that environmental stressors (Vega Thurber et al.

2009; Geffen et al. 2009; Littman et al. 2010; Meron et al. 2012; Jessen et al. 2013) and coral disease (Pantos et al. 2003; Pantos & Bythell 2006; Harvell et al. 2007; Sekar et al. 2008; Sunagawa et al. 2009; Kimes et al. 2010; Sato et al. 2013) cause changes in coral microbial communities, no previous study has analyzed the impact of coral transplantation on coral microbial communities. Due to the use of coral transplantation for coral reef restoration (Harriott & Fisk 1988b; Oren & Benayahu 1997; Jaap 2000; Ammar et al. 2000; Thornton et al. 2000; Soong & Chen 2003; Raymundo & Maypa 2004; Rinkevich 2005; Garrison & Ward 2008; Yap 2009; Muko & Iwasa 2011), this paper demonstrates how transplantation may negatively impact the survival and health of corals. Since microbes are key players in coral health, it is imperative to consider microbial communities when examining the utility of conservation measures such as coral transplantation (Garren & Azam 2012).

Here, I show that coral fragments undergo higher rates of mortality inside damselfish territories, but territorial grazers do not differentially affect the microbial communities of transplanted corals. Rather, the damage caused by coral transplantation leads to a shift in the microbial community toward an increase in potential coral disease pathogens, especially those linked to BBD (Myers et al. 2007), which is independent of territorial grazer presence or absence. The increase in potential pathogens in transplanted corals suggests that transplanted corals may be more susceptible to coral disease under certain stressful environmental conditions, such as an increase in sea surface temperature or nutrient fluxes. This study highlights the importance of examining ecological interactions beyond trends of macro-organisms and demonstrates how microbial communities provide essential information about coral health and resilience (Knowlton & Rohwer 2003; Teplitski & Ritchie 2009; Garren & Azam 2012).

# Chapter 4: Coupled dynamics of territorial damselfishes and juvenile corals on the reef crest

## Introduction

Coral recruitment and post-settlement survivorship have profound effects on reef structure (Vermeij 2005; Ritson-Williams et al. 2009). However, scleractinian coral settlement is highly variable (Wallace 1985; Connell et al 1997; Hughes et al. 1999) and is often poorly related to adult coral community structure (Hughes et al. 1999; Edmunds 2000; Trapon et al. 2013a). This disjunct between coral recruits and subsequent adult coral communities may be the result of new recruits' selectivity for certain conditions and differences in post-settlement dynamics over large spatial scales (Hughes et al. 1999). Post-settlement survival is largely determined by coral spat selection of substratum, which is dependent on light conditions and the presence of only a select few species of crustose coralline algae (CCA; Babcock & Mundy 1996; Harrington et al. 2004; Price 2010; Ritson-Williams et al. 2010). Thus, coral recruits experience low rates of survivorship post-settlement, with 67-99% mortality in their first year (Babcock 1985; Smith 1992; Babcock & Mundy 1996; Dunstan & Johnson 1998; Wilson & Harrison 2005; Graham et al. 2013).

Coral recruits that survive to the juvenile coral life history stage, defined as colonies from 1 to 5 cm in diameter (Penin et al. 2010; Rylaarsdam 1983), have an increasing chance of survival with an increasing colony size (Hughes 1984). However, there are large differences in growth rates of juvenile corals (van Moorsel 1988) and persisting high rates of mortality (19-56% mortality over 14 months) within this life stage (Babcock & Mundy 1996; Vermeij 2006; Penin et al. 2010), which have important effects on the subsequent establishment of adult colonies. The current literature provides a mixed picture of coral

settlement, growth, and survival, with both negative and positive impacts attributed to mobile grazers, such as scarine labrids, acantharids, siganids, and echinoids. Juvenile coral mortality is often attributed to indirect predation by grazing fishes and echinoids (Sammarco 1980; Sammarco 1985; Christiansen et al. 2009; Baria et al. 2010; Penin et al. 2010; Trapon et al. 2013b); however, these grazers may also provide benefits to juvenile corals by reducing algal coverage and ameliorating coral-algae space competition (Birkeland 1977; Brock 1979; Edmunds & Carpenter 2001; Hughes et al. 2007b). In addition, there is also evidence that the selection of cryptic microhabitats may effectively enhance survivorship of juvenile corals, presumably through protection from grazing (Bak & Engel 1979; Harriott & Fisk 1988a; Brandl et al. 2014). Given the complex array of processes that determine patterns of coral recruitment and survival to adult populations, studies that distinguish between competing explanations are particularly valuable. This is especially true for habitats in which the maintenance of coral growth is important to the integrity of reef structure, such as the reef crest.

Territorial damselfishes have the potential to substantially influence the recruitment and post-settlement dynamics of corals. They cultivate specific algal assemblages within their territories, which are maintained by pugnacious defense against other grazing species, and thus may have a profound effect on benthic reef biota (Ceccarelli et al. 2001; Hata & Kato 2004; Ceccarelli et al. 2006; Ceccarelli 2007). Moreover, although territorial damselfishes occur in a wide variety of reef habitats, they are abundant on shallow crests and the growing margins of coral reefs and may adversely or favourably affect the establishment of juvenile corals (Klumpp et al. 1987; Choat 1991). Territorial damselfish engage in several key behaviours within their territories: grazing turf algae, pecking coral polyps to further propagate algae, weeding unpalatable algae species, and constant aggression against intruders to protect resources (Kaufman 1977; Hinds & Ballantine 1987; Klumpp & Polunin 1989;

Letourneur et al. 1997). Within the spectrum of territorial grazers, there are several behavioural guilds, including indeterminate grazers, extensive grazers, and intensive grazers (Emslie et al. 2012). Indeterminate grazers have diverse algal turfs with unclear or overlapping territorial boundaries and the lowest rates of territorial aggression. In contrast, intensive grazers have low-diversity algal turfs with high biomass per unit area, distinct territories, and high rates of territorial aggression (Hata & Kato 2004; Hoey & Bellwood 2010; Emslie et al. 2012).

Due partly to sheer abundance, the structure and composition of damselfish territories plays a large role in benthic dynamics on coral reefs. Across behavioural guilds, damselfish territories are dominated by the epilithic algal matrix (EAM), a benthic conglomeration of filamentous turf algae, juvenile macroalgae, cyanobacteria, detritus, invertebrates, and microbes (Wilson & Bellwood 1997; Wilson et al. 2003; Fricke et al. 2011; Barott & Rohwer 2012). The effects of the EAM, and most specifically of turf algae, on corals are believed to be largely negative. When exposed to turf algae, corals suffer from recruitment inhibition (Birrell et al. 2005; Penin et al. 2011), declines in growth (Quan-Young & Espinoza-Avalos 2006; Barott et al. 2011), physiological stress (Vermeij et al. 2010; Wangpraseurt et al. 2012), and mortality (Smith et al. 2006; Haas et al. 2011; Vega Thurber et al. 2012; Sweet et al. 2013). While turf algae exposure is clearly detrimental to corals, the indirect effects of territorial grazers on corals are ambiguous. It has been reported that the territoriality of intensive damselfishes, which effectively excludes grazing fishes, corallivorous fishes, and echinoids, increases coral recruitment (Sammarco & Carleton 1981; Gleason 1996) and facilitates adult coral survival (Wellington 1982; Glynn & Colgan 1988; Done et al. 1991; Suefuji & van Woesik 2001; White and O'Donnell 2010; Gochfeld 2010). Intensive grazers have also been reported to increase the diversity of coral spat genera by causing high mortality of dominant coral spat genera while providing refuge to rare genera (Sammarco &

Williams 1982). Conversely, due to high turf algae biomass in their territories, intensive territorial grazers have been shown to inhibit coral recruitment (Arnold et al. 2010), suppress acroporid growth rates (Potts 1977), and cause mortality across coral genera (Kaufman 1977; White & O'Donnell 2010).

To date, the majority of studies that examine the effects of territorial damselfish on juvenile and adult corals have been conducted on sheltered back reefs (Kaufman 1977; Potts 1977; Sammarco & Williams 1982; Done et al. 1991; Suefuji & van Woesik 2001; White & O'Donnell 2010). However, damselfish territories may also occupy a considerable proportion of the substrate on reef crests, with studies reporting territory coverage as high as 40% on exposed reef fronts (Klumpp et al. 1987). There are several reasons why territorial grazers may have different effects on exposed reef fronts as compared to sheltered back reefs. Due to the high level of water flow, there is a significantly lower biomass of algae, detritus, and sediment on the reef crest as compared to back reefs (Purcell & Bellwood 2001). Reef crest environments are also characterized by a high turnover of algae and detritus, which may be a significant source of nutrition for roving herbivores and detritivores that intensively graze reef fronts, and the feeding patterns of these grazing fishes may indirectly impact corals (Bellwood 1995; Purcell & Bellwood 2001). Along with high algal and detrital turnover rates, the reef crest is a dynamic system for coral communities with the highest levels coral recruitment on reefs (Huston 1985). All of these differences between reef zone habitats may plausibly lead to distinct impacts of territorial grazers on exposed reef crests as compared to back reefs.

Further, the majority of previous studies consider the impact of territorial damselfishes on coral ecology as a snapshot in time or over short periods of less than one month (Done et al. 1991; Sammarco & Carleton 1981; Suefuji & van Woesik 2001; White and O'Donnell 2010; Gochfeld 2010). While simulation models have predicted how spatial shifts in

herbivory may affect coral recruitment and growth in reef systems over time (Sandin & McNamara 2012), no current empirical study has documented the extent of turnover of damselfish territories or its effects on the reef crest benthos.

A recent review called for studies of how territorial grazers affect the abundances and taxonomic assemblages of juvenile corals across large spatial scales on coral reefs (Ceccarelli et al. 2001), particularly from the context of distinct behavioural guilds (i.e., indeterminate territorial grazers versus intensive territorial grazers). Given the relative lack of information about the impacts of territorial grazers on benthic dynamics of exposed reef fronts, this study focuses on how territorial grazers shape juvenile coral communities in this important and highly productive habitat. Specifically, I aimed to: (1) determine the effects of indeterminate and intensive territorial damselfishes on the abundance of juvenile corals on the reef crest; (2) assess how indeterminate and intensive damselfish territories shape the taxonomic composition of juvenile coral communities; and (3) analyze how the spatial turnover of indeterminate and intensive damselfish territories affect juvenile corals on the exposed reef front.

## Methods

### Study site and species

This study took place around Lizard Island, a mid-shelf reef in the northern Great Barrier Reef (GBR), Australia (14°41’5”S, 145°26’55”E) from July 2012 to August 2013. The study sites were on the exposed reef crest at Palfrey Crest, Lizard Head, and Bommie Bay (Figure 4.1) at a depth of 1 to 3 m. Using semi-quantitative visual estimates, live coral cover was approximated at 30-35% at each study site. *Pomacentrus bankanensis* and *Pomacentrus chrysurus* (f. Pomacentridae) represented “indeterminate territorial grazers” and *Stegastes apicalis* (f. Pomacentridae) represented “intensive territorial grazers” because they

were the most abundant territorial grazers in each respective behavioural guild at the study sites. Whenever other territorial grazer species were detected (e.g. *Pomacentrus wardi*, *Pomacentrus grammorhynchus, Plectroglyphidodon lacrymatus, Plectroglyphidodon dickii, Plectroglyphidodon johnstonianus*, *Neoglyphidodon nigroris*, *Dischistodus melanotus*, or *Dischistodus perspicillatus*), they were recorded but excluded from the analyses.

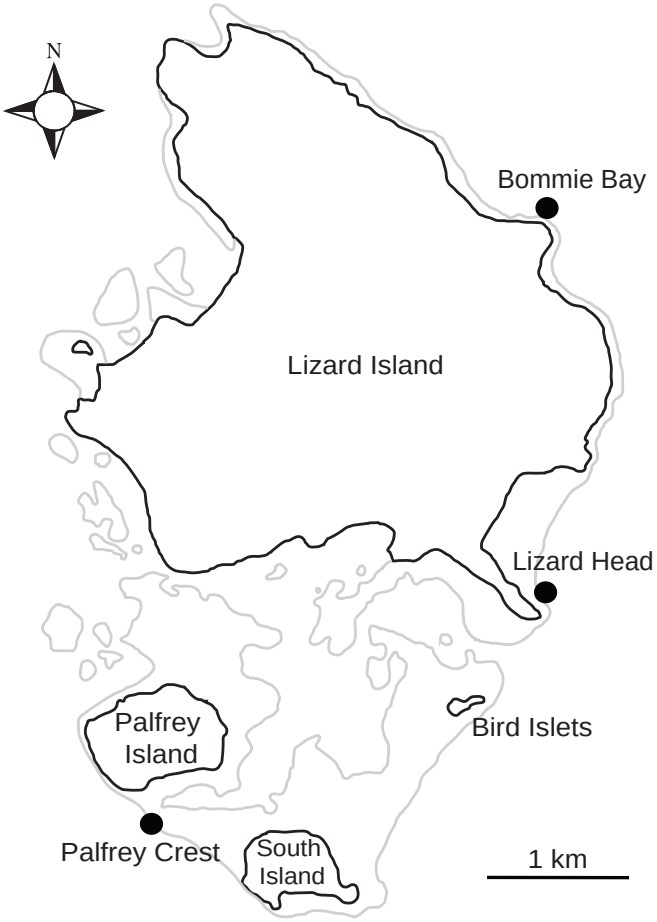



**Figure 4.1** Map of Lizard Island and fringing reefs showing the study sites on the reef crest at Palfrey Crest, Lizard Head, and Bommie Bay.

**Fish and coral transects**

Juvenile corals and damselfish territories were mapped using permanent 10 m high-tension wires as transects on the reef crest. I defined juvenile scleractinian corals as any coral with a minimum diameter of 1 cm and a maximum diameter of 5 cm (Rylaarsdam 1983; Roth & Knowlton 2009; Penin et al. 2010). To the best of my ability, colonies that resulted from fission or fragmentation of older colonies were excluded (Trapon 2013a). There were three transects at Palfrey Crest, six transects at Lizard Head, and three transects at Bommie Bay (total: n = 12). There were an additional three transects at Lizard Head compared to the other sites to increase our sample size of *S. apicalis* territories. Each 10 m transect was secured to the reef using permanent 50 cm steel stakes. A 1-$m^2$ quadrat was attached to the wire transect every 2 m, for a total of five quadrats per transect, giving a total of 60 quadrats per sampling period. In each quadrat, observers first recorded the presence or absence of damselfish territories, including identification to species, behavioural guild, and approximate length of each territorial grazer. The quadrat was further divided into 10 x 10 cm blocks, for a total of one hundred 10 $cm^2$ blocks, with high-tension string secured at 10 cm intervals along the horizontal and vertical axes. This permitted observers to map the location of each individual juvenile coral to the nearest 10 cm. Observers recorded all juvenile corals, including identification to genus, spatial positioning within the quadrat, and approximate maximum and minimum diameters (to the nearest 0.5 cm) of each coral. Photographs were taken of the juvenile corals when identification was uncertain, and corals were subsequently identified to genus with Coral Finder (Kelley 2010) and Corals of the World (Veron 2000). Surveys were conducted every six months for one year (sampling periods: July 2012, February 2013, and August 2013).

**Data analysis**

To assess the effects of territorial grazers on juvenile coral abundances, the library *nlme* (Pinheiro et al. 2012) in R (R Core Team 2012) was used to fit linear mixed-effects (LME) models (Table 4.1a). Territorial grazer presence or absence (no territorial grazer, indeterminate grazer, or intensive grazer) was set as the fixed effect. As random effects, I used month (July 2012, February 2013, or August 2013), nested within transect, nested within site (Palfrey Crest, Lizard Head, or Bommie Bay). A Shapiro-Wilk test revealed a non-normal distribution of the juvenile coral abundances ($W = 0.9612$, $p < 0.001$), so square root transformations were applied. After transformations, residual plots were approximately normally distributed and did not reveal deviations from homoscedasticity.

A canonical correspondence analysis was used to determine any differences in juvenile coral taxonomic composition of the four most abundant coral groups (*Porites*, *Acropora*, *Pocillopora*, and Faviidae) outside of damselfish territories, inside indeterminate damselfish territories, and inside intensive damselfish territories. Relative abundance plots of the ten most abundant coral genera outside of damselfish territories, inside indeterminate damselfish territories, and inside intensive damselfish territories were used to assess evenness of coral genera outside and inside damselfish territories. To further analyze the effect of damselfish territories on the abundance of the four most abundant coral groups, the libraries *MASS* (Venables & Ripley 2002) and *nlme* (Pinheiro et al. 2012) in R (R Core Team 2012) were used to fit generalized linear mixed-models (GLMM) using penalized quasi-likelihood (PQL) with a quasi-Poisson error distribution (Table 4.1b). Territorial grazer presence or absence (no territorial grazer, indeterminate grazer, or intensive grazer) was set as the fixed effect. As random effects, I used month (July 2012, February 2013, or August 2013), nested within transect, nested within site (Palfrey Crest, Lizard Head, or Bommie Bay).

To determine how spatial turnover of territorial grazers affects juvenile corals, I first used a contingency table to determine whether there were differences between the two six-

month periods in the relative proportions of different territory turnover events. The contingency table revealed no association (Fisher's exact test, two-tailed, $p > 0.99$); therefore, the two six-month periods were combined for all further analyses. To analyze the relationship between territorial grazer turnover and the resulting gain or loss of juvenile corals over two six-month periods, LME models were used (Table 4.1c). Turnover (no turnover, control plots to indeterminate damselfish territories, indeterminate damselfish territories to control plots, control plots to intensive damselfish territories, and intensive damselfish territories to control plots) was set as the fixed effect. As random effects, I used transect nested within site (Palfrey Crest, Lizard Head, or Bommie Bay). Residual plots did not reveal deviations from normality or homoscedasticity.

**Table 4.1** Summary of models for the analysis of (a) juvenile coral abundances, (b) juvenile coral taxonomic composition, and (c) spatial turnover of damselfish territories. Models include linear mixed-effects (LME) models and a generalized linear mixed model (GLMM).

| | Model | Transformation/Distribution | Fixed effects | Random effects |
|---|---|---|---|---|
| (a) | LME | square-root transformation | Territorial grazer presence/absence | site / transect / month |
| (b) | GLMM | quasi-Poisson error distribution | Territorial grazer presence/absence | site / transect / month |
| (c) | LME | none | Turnover of damselfish territories | site / transect |

## Results

### Juvenile coral abundance and taxonomic composition

As compared to outside of damselfish territories, there were significantly (34%) fewer juvenile corals inside intensive damselfish territories and 17% fewer juvenile corals inside indeterminate damselfish territories, but this latter difference was not statistically significant (Figure 4.2; Table 4.2). In the surveys, a total of 28 coral genera were detected: 20 outside damselfish territories, 22 inside indeterminate grazer territories, and 21 inside intensive grazer territories (Table 4.3). The four most abundant groups (*Porites*, *Acropora*, *Pocillopora*, and Faviidae) made up approximately 96% of the juvenile coral community. The ten most common genera were relatively evenly distributed among all surveyed substratum types (outside damselfish territories, inside indeterminate grazer territories, and inside intensive grazer territories; Figure 4.3). The canonical correspondence analysis (Figure 4.4) suggested that there was no overall detectable effect of indeterminate or intensive damselfish territories on the juvenile coral taxonomic composition within the four most abundant groups. Consistent with this, a GLMM analysis of the community composition of juvenile corals revealed that there was no significant effect of indeterminate or intensive damselfish on the relative abundances of the four most abundant groups of juvenile corals (Table 4.4).

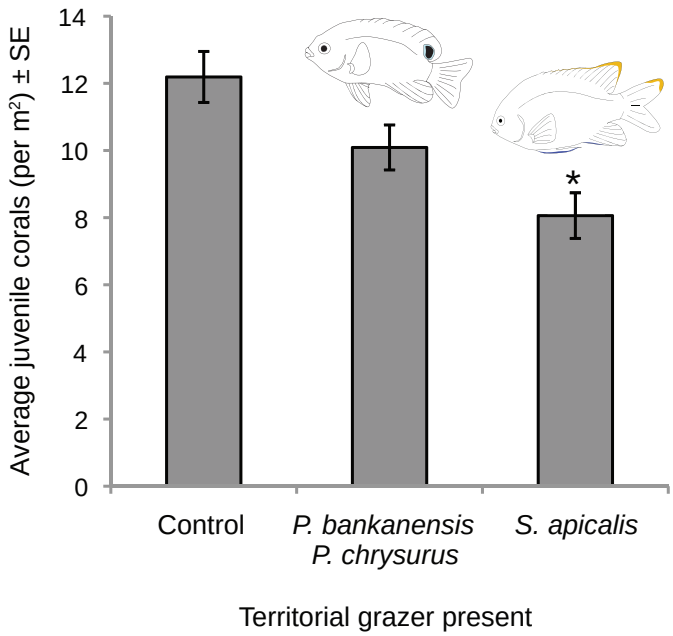



**Figure 4.2** The average number of juvenile corals in control plots (outside damselfish territories, n = 58), *Pomacentrus bankanensis* and *Pomacentrus chrysurus'* territories (indeterminate grazers, n = 55, p = 0.272), and *Stegastes apicalis'* territories (intensive grazers, n = 33, p = 0.033). The asterisk represents a significant difference from the control plots (linear-mixed effects model; $p < 0.05$; see Table 4.2).

**Table 4.2** Results (SE = standard error, df = degrees of freedom) from two linear mixed-effects (LME) models analyzing the relationship between territorial grazers and juvenile coral abundance (with the fixed effect of territorial grazer presence and the random effects of month, nested within transect, nested within site). Plots with no territorial grazer present (Control) are compared to indeterminate damselfish territories (IDTG; *Pomacentrus bankanensis*/*Pomacentrus chrysurus*) and intensive damselfish territories (ITG; *Stegastes apicalis*). Shaded cells contain statistically significant values ($p < 0.05$).

| Intercept | Treatment | Value | SE | df | T-value | p-value |
|---|---|---|---|---|---|---|
| Control | IDTG | -0.163 | 0.148 | 110 | -1.103 | 0.272 |
| | ITG | -0.379 | 0.176 | 110 | -2.154 | 0.033 |

**Table 4.3** Coral genera that occur outside damselfish territories (control), inside indeterminate damselfish territories (*Pomacentrus bankanensis*/*Pomacentrus chrysurus*), and inside intensive damselfish territories (*Stegastes apicalis*) in the surveys.

| Coral Genus | Control | *P. bankanensis* *P. chrysurus* | *S. apicalis* |
|---|---|---|---|
| *Porites* | X | X | X |
| *Acropora* | X | X | X |
| *Pocillopora* | X | X | X |
| *Goniastrea* | X | X | X |
| *Favites* | X | X | X |
| *Isopora* | X | X | X |
| *Montipora* | X | X | X |
| *Montastrea* | X | X | X |
| *Favia* | X | X | X |
| *Stylophora* | X | X | X |
| *Galaxea* | X | X | X |
| *Fungia* | X | X | X |
| *Leptoria* | X | X | X |
| *Symphyllia* | X | X | X |
| *Trachyphyllia* | | X | X |
| *Psammacora* | | X | X |
| *Platygyra* | | X | X |
| *Echinopora* | | | X |
| *Cyphastrea* | | X | X |
| *Oulophyllia* | | | X |
| *Lobophyllia* | X | | X |
| *Acanthastrea* | X | X | |
| *Moseleya* | X | X | |
| *Leptastrea* | | X | |
| *Scolymia* | | X | |
| *Turbinaria* | X | | |
| *Seriatopora* | X | | |
| *Pavona* | X | | |
| TOTAL | 20 | 22 | 21 |

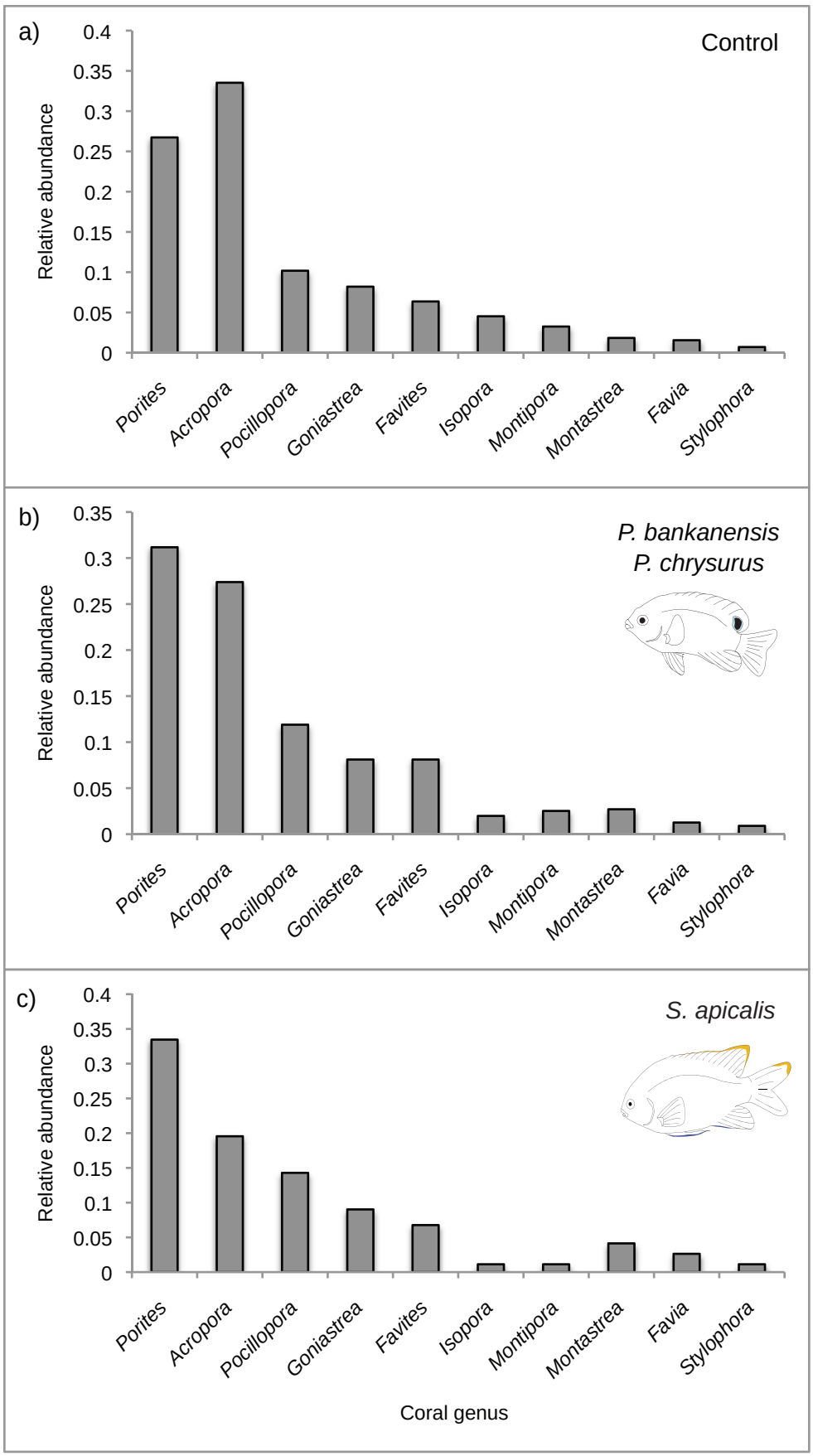

a)
Control
Relative abundance
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Porites
Acropora
Pocillopora
Goniastrea
Favites
Isopora
Montipora
Montastrea
Favia
Stylophora
b)
P. bankanensis
P. chrysurus
Relative abundance
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Porites
Acropora
Pocillopora
Goniastrea
Favites
Isopora
Montipora
Montastrea
Favia
Stylophora
c)
S. apicalis
Relative abundance
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Porites
Acropora
Pocillopora
Goniastrea
Favites
Isopora
Montipora
Montastrea
Favia
Stylophora
Coral genus

**Figure 4.3** Total relative abundances of the ten most abundant coral genera (n ≥ 5 for all groups) in (a) control plots (outside damselfish territories, n = 58), (b) *Pomacentrus bankanensis'* and *Pomacentrus chrysurus'* territories (indeterminate grazers, n = 55), and (c) *Stegastes apicalis'* territories (intensive grazers, n = 33).

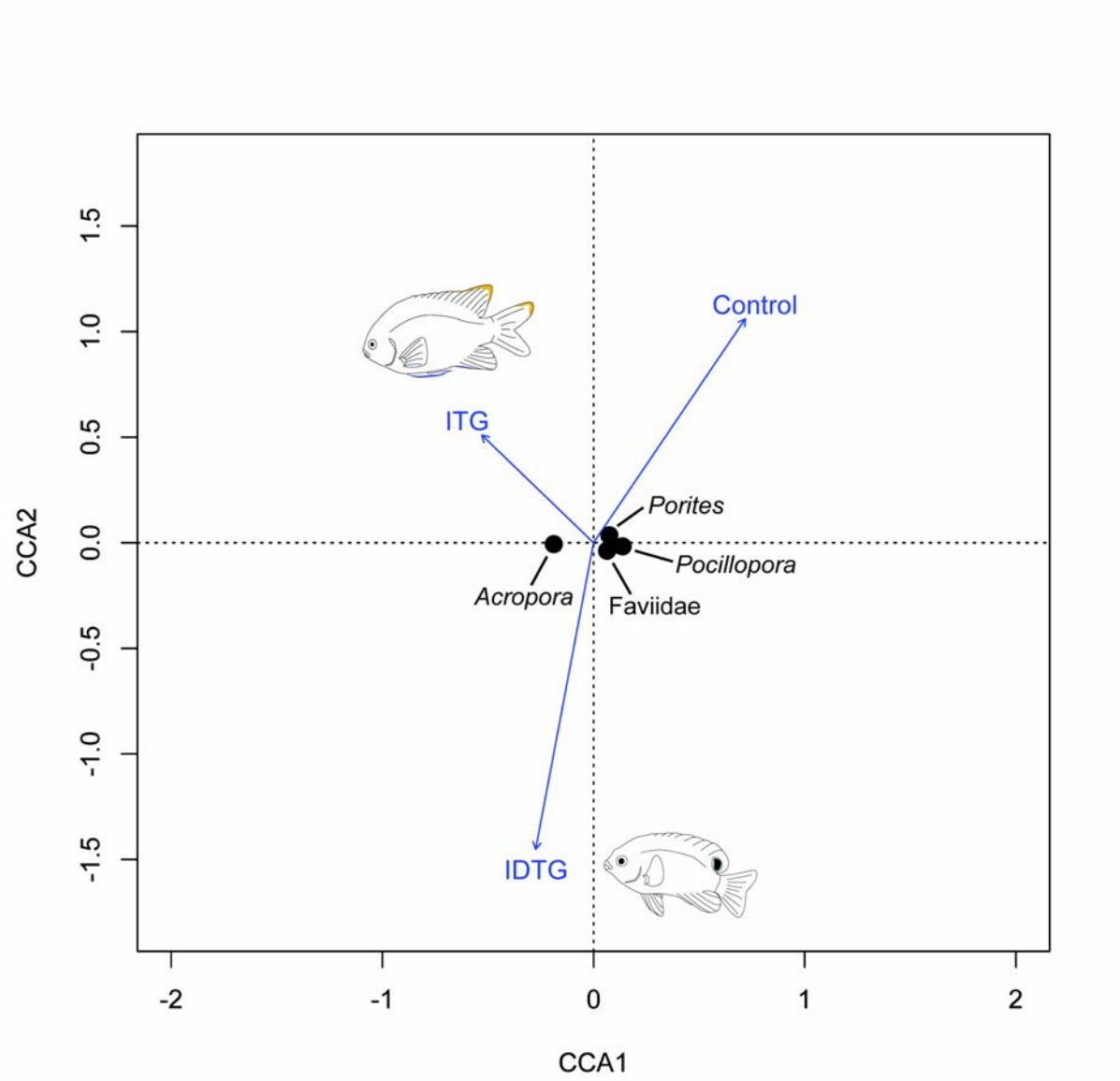



**Figure 4.4** The first two axes of a canonical correspondence analysis based on the correlation between the most abundant coral genera/family (points: *Porites*, *Acropora*, *Pocillopora*, and Faviidae) and territorial damselfish presence (vectors: control [no damselfish present], IDTG [indeterminate territorial grazer; *Pomacentrus bankanensis*/*Pomacentrus chrysurus*], and ITG [intensive territorial grazer; *Stegastes apicalis*]).

**Table 4.4** Results (SE = standard error) from four generalized linear mixed-models (GLMM) using penalized quasi-likelihood (PQL) with quasi-Poisson distribution analyzing the relationship between territorial grazers and relative juvenile coral abundance in the four most abundant coral groups (with the fixed effect of territorial grazer presence and the random effects of month, nested within transect, nested within site). Plots with no territorial grazer present (Control) are compared to indeterminate damselfish territories (IDTG; *Pomacentrus bankanensis*/*Pomacentrus chrysurus*) and intensive damselfish territories (ITG; *Stegastes apicalis*) for (a) *Porites*, (b) *Acropora*, (c) *Pocillopora*, and (d) Faviidae. Shaded cells contain statistically significant values ($p < 0.05$).

| | Coral Genus/Family | Intercept | Treatment | Value | SE | t-value | p-value |
|---|---|---|---|---|---|---|---|
| (a) | *Porites* | Control | IDTG | 0.086 | 0.116 | 0.740 | 0.461 |
| | | | ITG | 0.070 | 0.137 | 0.507 | 0.613 |
| (b) | *Acropora* | Control | IDTG | -0.078 | 0.143 | -0.544 | 0.588 |
| | | | ITG | -0.067 | 0.179 | -0.373 | 0.710 |
| (c) | *Pocillopora* | Control | IDTG | -0.069 | 0.200 | -0.344 | 0.732 |
| | | | ITG | 0.079 | 0.224 | 0.352 | 0.726 |
| (d) | Faviidae | Control | IDTG | 0.117 | 0.165 | 0.716 | 0.478 |
| | | | ITG | 0.019 | 0.195 | 0.096 | 0.924 |

**Spatial turnover**

Over the two six-month periods, there was a 39.7% mean turnover from presence to absence of territorial grazers (Table 4.5). More than half (51.5%) of control plots outside of damselfish territories became part of an indeterminate or intensive damselfish territory. Likewise, 31% of indeterminate damselfish territories experienced turnover to control plots, and 28.6% of intensive damselfish territories experienced turnover to control plots (Table 4.5). Spatial turnover from indeterminate damselfish territories to intensive damselfish territories, or *vice versa*, was minimal, with only one occurrence (Table 4.5).

Turnover from control plots to indeterminate damselfish territories resulted in a slight decrease in the abundance of juvenile corals (average loss of 24% of coral colonies); conversely, turnover from indeterminate damselfish territories to control plots resulted in a slight increase in the abundance of juvenile corals (average gain of 23.6% of coral colonies; Figure 4.5). A similar pattern emerged for the turnover of intensive damselfish territories. Turnover from control plots to intensive damselfish territories resulted in a significant decrease in the abundance of juvenile corals (average loss of 43.7% of coral colonies; LME: $p < 0.05$); conversely, turnover from intensive damselfish territories to control plots resulted in a significant increase in the abundance of juvenile corals (average gain of 47.5% of coral colonies; LME: $p < 0.05$; Table 4.6; Figure 4.5).

**Table 4.5** Sample size of plots with no territorial damselfish (control), indeterminate damselfish territories (IDTG; *Pomacentrus bankanensis*/*Pomacentrus chrysurus*), and intensive damselfish territories (ITG; *Stegastes apicalis*) over two six-month periods (n = 83). The left column indicates the initial presence or absence of a territorial grazer, and the top row indicates the presence or absence of a territorial grazer after six months. The shaded cells indicate no spatial turnover.

| | Control | ETG | ITG |
|---|---|---|---|
| Control | 16 | 14 | 3 |
| IDTG | 9 | 20 | 0 |
| ITG | 6 | 1 | 14 |

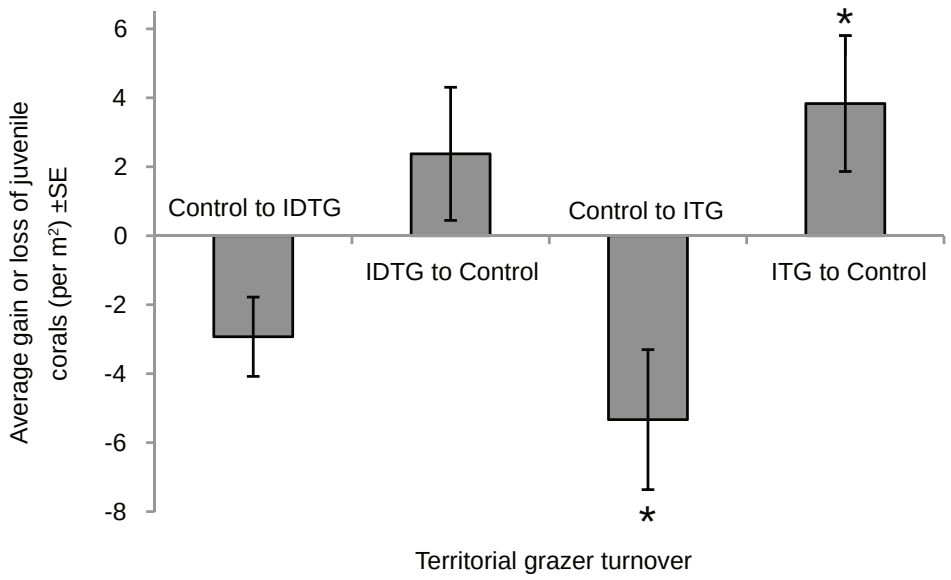



**Figure 4.5** Average gain or loss of juvenile corals over two six-month periods after turnover from a control plot to an indeterminate damselfish territory (Control to IDTG, n = 14, p = 0.097), from an indeterminate damselfish territory to a control plot (IDTG to Control, n = 8, p = 0.093), from a control plot to an intensive damselfish territory (Control to ITG, n = 3, p = 0.047), and from an intensive damselfish territory to a control plot (ITG to Control, n = 6, p = 0.011). Asterisks represent significant differences from plots that experienced no turnover (linear mixed-effects model; $p < 0.05$; see Table 4.6).

**Table 4.6** Results (SE = standard error, df = degrees of freedom) from a linear mixed-effect (LME) model analyzing the relationship between territorial grazer turnover and the resulting gain or loss of juvenile corals (with the fixed effect of turnover and the random effect of transect nested within site). Plots with no damselfish territory turnover (No turnover) are compared to turnover from control plots to indeterminate damselfish territories (Control to IDTG [*Pomacentrus bankanensis*/*Pomacentrus chrysurus*]), turnover from indeterminate damselfish territories to control plots (IDTG to Control), turnover from control plots to intensive damselfish territories (Control to ITG [*Stegastes apicalis*]), and turnover from intensive damselfish territories to control plots (ITG to Control). Shaded cells contain statistically significant values ($p < 0.05$).

| Turnover | Value | SE | df | T-value | p-value |
|---|---|---|---|---|---|
| No turnover (intercept) | -0.250 | 1.165 | 67 | -0.214 | 0.831 |
| Control to IDTG | -2.108 | 1.251 | 67 | -1.684 | 0.097 |
| IDTG to Control | 2.755 | 1.616 | 67 | 1.705 | 0.093 |
| Control to ITG | -5.083 | 2.513 | 67 | -2.023 | 0.047 |
| ITG to Control | 4.803 | 1.836 | 67 | 2.616 | 0.011 |

## Discussion

In comparing the impacts of indeterminate and intensive territorial grazers on juvenile corals, it was found that territorial damselfishes have unexpectedly dynamic effects on coral communities. Intensive territorial grazers harboured 34% fewer juvenile corals and indeterminate territorial grazers harboured 17% fewer juvenile corals, but the taxonomic composition of juvenile corals was very similar outside and inside of damselfish territories, as well as between territorial grazer behavioural guilds. The most unexpected finding was a high rate of turnover (39.7%) from territorial grazer presence to absence (and *vice versa*) on the benthos of the reef crest and associated changes in juvenile coral abundance. The spatial turnover results suggest that juvenile coral abundances can rapidly decline under the engineering behaviours of a territorial damselfish, or they may recover with the loss of a damselfish territory. In this study, juvenile corals were defined as corals with a minimum diameter of 1 cm and a maximum diameter of 5 cm; yet, corals with a diameter of less than 1 cm are relatively abundant on reef fronts (Roth & Knowlton 2009). Thus, after turnover from intensive damselfish territories to control plots, it is likely that these small juvenile corals, which were not reported in the surveys, played a large role in the substantial increase in the abundance of juvenile corals. These findings imply that territorial grazers have a negative effect on juvenile coral populations on the exposed reef crest, and they also highlight the unexpectedly dynamic nature of this relationship.

By considering both indeterminate and intensive territorial grazers, this study provides insights into the differential effects of territorial grazer behavioural guilds on benthic dynamics. The abundances of juvenile corals are more affected by intensive territorial grazers, such as *S. apicalis*, than by indeterminate territorial grazers, such as *P. bankanensis* and *P. chrysurus*. Likewise, spatial turnover of intensive territorial grazers has a stronger effect on juvenile coral abundance than spatial turnover of indeterminate grazers. While

intensive territorial grazers propagate turf algae, particularly *Polysiphonia* spp., to significantly higher levels than outside of damselfish territories (Brawley & Adey 1977; Sammarco 1983; Jones et al. 2006; Ceccarelli et al. 2011), indeterminate grazers cultivate mixed-species farms, with comparatively low-levels of filamentous turf algae (Emslie et al. 2012). Because grazed turf algae has been shown to have inhibitory effects on coral settlement (Birrell et al. 2001), intensive territorial grazers may inhibit coral recruitment due to space occupation by thick turf algae, thus reducing juvenile coral abundances as compared to benthic plots outside of damselfish territories (Arnold et al. 2010). This highlights the differences between intensive and indeterminate territorial grazers and demonstrates the importance of considering differences in functional niches of territorial grazers and their effect on the coral reef benthos. In the analyses, the estimated effect of indeterminate territorial grazers on juvenile coral abundances was intermediate between territories of intensive grazers and benthic plots without damselfish territories, suggesting that indeterminate territorial grazers may have an effect similar to, but smaller than, that of intensive territorial grazers. Previous work suggests that indeterminate territorial grazers have subtle effects on the benthos; for instance, Emslie et al. (2012) report minimal differences between benthic assemblages inside indeterminate damselfish territories as compared to outside of damselfish territories. While estimates demonstrate that indeterminate territorial grazers have a smaller impact on the abundance of juvenile corals than intensive territorial grazers, it is important to recognize that neither the null hypothesis of no effect, nor an alternative hypothesis that the effect is the same as that of intensive territorial grazers, can be rejected with 95% confidence.

Previous studies report that the number of genera of coral spat as well as adult coral diversity are higher inside of damselfish territories on the sheltered back reef and fringing reef slope due to their active exclusion of herbivorous and corallivorous fishes (Sammarco &

Carleton 1981; Gochfeld 2010). I did not find higher numbers of juvenile coral genera within damselfish territories (Table 2), which may be due to local scale differences associated with geographic location, habitat type (back reefs versus front reefs), or study species in each particular study. Sammarco & Carleton (1981) studied the effects of the intensive territorial grazer *Hemiglyphidodon plagiometopon* on the back reef, whereas this study examines intensive and indeterminate grazers on the reef crest. Further, there are marked behavioural differences, and thus differences in territorial structure, even within territorial grazer behavioural guilds (Casey et al. 2014). The vast majority of studies that consider the effects of territorial grazers on coral communities use *S. nigricans* (Indo-Pacific: e.g., Glynn & Colgan 1988; Done et al. 1991; Suefuji & van Woesik 2001; White & O'Donnell 2010) or *Stegastes planifrons* (Caribbean: e.g., Kaufman 1977; Sammarco & Williams 1982) as their study species on the back reef. These species are not comparable to *S. apicalis*, a less intensive grazer than *S. nigricans* and *S. planifrons*, nor are these studies on the back reef comparable to a study on the reef crest, which is a much more dynamic environment for coral recruitment and survival due to higher rates of acute and chronic disturbance (Huston 1985; Connell et al. 1997).

Although many studies take into account the effects of intensive territorial grazers, such as *Stegastes*, on corals, very little work has been done on indeterminate territorial grazers. My results indicate smaller differences in benthic plots without damselfish territories for indeterminate as compared to intensive damselfish territories. Indeterminate territorial grazers farm a very thin mixed-species filamentous turf and do not fully exclude roving grazers from their territories (Emslie et al. 2012). Regardless of territorial grazer presence, filamentous turf algae are common across coral reef substratum (Brawley & Adey 1981); however, filamentous algae outside of damselfish territories are more intensively grazed since they are the main dietary component of several abundant grazing fishes on the GBR,

such as *Acanthurus lineatus*, *Acanthurus nigricans*, *Zebrasoma scopas* and *Kyphosus cinerascens* (Choat et al. 2002). Although low-level turf algal colonization has been shown to inhibit coral recovery and settlement (Birkeland 1977; Connell et al. 1997), previous literature also suggests that corals may achieve competitive superiority over thin algal turfs (van Woesik 1998; McCook 2001; Diaz-Pulido & McCook 2002). Therefore, indeterminate territorial grazers, such as *P. bankanensis* and *P. chrysurus*, propagate turf algae to an extent that is an intermediary between benthic plots without damselfish territories and the territories of intensive grazers. Consequently, although indeterminate territorial grazers do influence coral settlement and survival to a degree that was not previously recognized, intensive territorial grazers have a much greater impact on coral communities.

By analyzing juvenile coral communities as a function of the temporal turnover of damselfish territories, I have found that damselfish-coral-algae linkages are highly dynamic in reef crest environments. As previous studies suggest, the behaviour of territorial grazers on sheltered back reefs have multifaceted impacts on coral recruitment and survival (Letourneur et al. 1997; White & O'Donnell 2010). However, these findings elucidate the role of territorial damselfishes on the reef crest, which has, to date, received much less attention. Overall, territorial pomacentrids had a negative impact on juvenile coral abundances; yet, the damselfish turnover results reveal an unexpectedly dynamic system. While juvenile coral abundances can rapidly decline under the cultivation behaviours of a territorial damselfish, I found that juvenile coral abundances may likewise rapidly recover with the loss of a damselfish territory. Thus, despite the overall negative influence of territorial damselfishes on coral communities, there is potential for coral recovery on reefs occupied by territorial pomacentrids due to these high rates of territorial turnover and subsequent rapid increases in juvenile coral abundances. Corals are sedentary species that are highly sensitive to temporal spatial shifts in biotic and abiotic regimes (Sandin & McNamara 2012). Consequently, the

overall negative impact and the dynamic nature of damselfish territories on the reef crest have important implications for benthic assemblages on the reef crest.

# Chapter 5: A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs

## Introduction

Trophic cascades occur in both terrestrial and aquatic systems (Pace et al. 1999) and result from reciprocal predator-prey interactions, which cause alternating increases and decreases in the biomass of trophic levels throughout a food web (Hairston 1960; Polis et al. 2000). For instance, in a simple three-tiered system that includes predators, herbivores, and primary producers, the loss of predators can release herbivore populations from predation-related mortality and subsequently suppress the abundance and biomass of primary producers (Pace et al. 1999). This 'linear' theory of simple stepwise effects has been challenged on the basis that it oversimplifies the complex species interactions within food webs and ignores other factors, such as omnivory, ontogenetic changes in diet, and nutrient availability, which may affect food web dynamics (Polis & Strong 1996).

Further analysis of trophic cascade patterns led to the discrimination between species-level and community-level cascades (Polis 1999; Schmitz et al. 2000). Species-level cascades are trophic cascades that occur in a subset of a community, affecting only a few primary consumers and producers. For example, the exclusion of birds from bilberry shrubs caused an increase in insect larval density followed by a decline in bilberry (Polis et al. 2000). Conversely, community-level cascades affect the biomass of an entire trophic level in the aggregate (Polis et al. 2000). Trophic cascade theory is widely used across the ecological literature to showcase the repercussions of anthropogenic disturbance to predators on the biomass of primary producers. For instance, in Yellowstone National Park, the reintroduction of wolves has limited elk foraging behaviour, which has promoted the successful

establishment of aspen in the mesic upland steppe and riparian habitats (Ripple et al. 2001). In addition, due to the overexploitation of oceanic fishes in western Alaska, killer whales have overhunted sea otters, allowing high abundances of sea urchins to flourish, which caused severe deforestation of kelp forests (Estes et al. 1998).

In marine environments, substantial declines in the abundance and biomass of predators have occurred worldwide (Pauly et al. 1998; Jackson et al. 2001; Myers & Worm 2003). The depletion of predators has been reported to cause trophic cascades in various marine ecosystems (Dulvy *et al*. 2004; Baum & Worm 2009). For example, overfishing predatory fishes in the Baltic Sea led to an increase in small-bodied predatory fish, followed by a reduction of gastropod grazers, and ultimately, this contributed to macroalgae blooms (Eriksson et al. 2009). Depletion of predators in marine systems can also indirectly cause cascading effects, for instance by modifying the behaviour of mesopredators and herbivores, thus altering lower-level ecological interactions (Byrnes et al. 2006; Madin et al. 2010; McCauley et al. 2010).

On coral reefs, trophic cascades have been hypothesized to occur when overfishing of apex predators triggers an increase in mesopredators, causing subsequent declines in herbivorous fishes via mesopredator release (Ritchie & Johnson 2009). Following declines in herbivorous fishes, macroalgae and turf algae cover increase, which can reduce the cover of coral (Rasher et al. 2013) and crustose coralline algae (CCA) abundance (O'Leary & McClanahan 2010) via competition effects. Alternatively, direct overfishing of mesopredators may result in increases in territorial damselfishes due to prey release (Ceccarelli et al. 2006). Coral reef mesopredator abundance has been negatively correlated with the presence of territorial damselfishes (Vermeij et al. 2015), and this can potentially influence benthic composition since territorial damselfishes propagate thick turf algae, which

lowers the abundance of juvenile corals (Casey et al. 2015b), and have been linked to increases in the prevalence of coral disease (Casey et al. 2014; Vermeij et al. 2015).

To date, very little unambiguous empirical evidence of trophic cascades in coral reef systems is available (Ferretti et al. 2010). Several properties of coral reef food webs may weaken or inhibit trophic cascades and explain the conflicting results of different studies. Reef species have a high degree of omnivory and trophic versatility (Thompson et al. 2007), and reefs are relatively open systems, which permit trophic interactions with the pelagic environment (Polis et al. 1997). Consequently, coral reefs may deviate from the linear trophic chains that classical trophic cascade theory assumes. While overfishing has been linked to apex predator declines, it has also resulted in a lower biomass of mesopredators and herbivores (the Hawaiian Islands; Friedlander & DeMartini 2002), the domination of planktivorous fishes and algae (the Northern Line Islands; Sandin et al. 2008), and a mesopredator release resulting in lower levels of herbivorous fishes and higher algal cover (northwest Australia; Ruppert et al. 2013). However, in these systems, predator fishing gradients co-vary with other anthropogenic effects, such as fishing for herbivorous fishes changes in water quality due to pollution and runoff. Here, we resolve these issues by investigating of the repercussions of predator removal on coral reef fishes and benthic composition across a spatially dispersed predator density gradient that is largely independent of other confounding factors (i.e. removal of other trophic levels and pollution).

The Great Barrier Reef (GBR), Australia, is one of the world's largest and best-protected reef systems (Pandolfi et al. 2003; Russ et al. 2008). The implementation of strictly enforced marine protected areas in the GBR conserves high levels of apex predators (Dulvy 2006; Robbins et al. 2006) and effectively increases mesopredator abundance and biomass (Williamson et al. 2004; McCook et al. 2010). Yet, two of the most abundant apex predators, the gray reef shark (*Carcharhinus amblyrhynchos*) and whitetip reef shark (*Triaenodon*

*obesus*) have been depleted in some areas (Robbins et al. 2006), and there are significantly higher abundances of targeted mesopredators such as coral trout (*Plectropomus* spp.) in marine protected areas (Russ et al. 2008). As a result, there are strong gradients in the density of reef sharks and targeted mesopredators across fished and protected management zones (Robbins et al. 2006; Ayling & Choat 2008; Russ et al. 2008). In contrast to reports of trophic cascades on coral reefs (e.g., a mesopredator density gradient had a significant negative correlation with the biomass of planktivorous damselfishes, Graham *et al*. 2003), there is no evidence of strong top-down effects from predatory fishes to mobile herbivorous fishes on the GBR (Rizzari et al. 2014). However, previous studies have not quantified the direct and/or indirect links between predators and benthic composition (corals *versus* algae) and have overlooked the role of small-bodied territorial damselfishes in controlling benthic composition. Unlike many other coral reef regions, fishers on the GBR target apex predators and mesopredators almost exclusively; there is virtually no fishing for herbivorous fishes (Bellwood et al. 2004), and the effects of the coral harvest fishery are negligible (Harriot 2001). Thus, gains or losses of herbivorous fishes and coral cover can be attributed to trophic interactions rather than the effects of human exploitation. Of equal importance, pollution and runoff are exceptionally low on the outer reefs of the GBR (Alongi & McKinnon 2005). In this context, the outer GBR provides an ideal system to investigate trophic cascade theory by examining predatory fish populations and associated trophic interactions across management zones.

Thus, the overall aim of this chapter is to test trophic cascade theory by determining how herbivorous fishes and benthic communities respond to a human-induced predator density gradient across management zones on the GBR. Under a traditional trophic cascade framework, a decline in apex predators in fished areas is expected to cause an increase in mesopredators, followed by a decrease in herbivorous fishes, followed by an increase in

macroalgae and turf algae and a corresponding decline in coral and CCA cover. Alternatively, a decline in targeted mesopredators in fished areas is expected to cause an increase in territorial damselfishes, followed by an increase in turf algae and a decline in coral cover. To test these hypothesized frameworks, I examined whether the observed trophic structure on the GBR fits the ecological predictions of trophic cascade theory.

## Methods

### Study sites

This study was undertaken on 15 spatially separated coral reefs on the outer GBR, Australia, at two distinct latitudes: the Ribbon Reefs at 14°S and the Swains Reefs at 21°S (Figure 5.1). Data were collected in austral summer months (between February and March in 2013 in the Ribbons and between March and April in 2014 in the Swains). I examined three management zones designated by the GBR Marine Park Authority: (1) fished zones that are open to general use and permit fishing and collecting, (2) no-take zones that permit diving and boating activities but prohibit extractive activities (i.e. fishing), and (3) no-entry zones that are strictly enforced preservation zones that are inaccessible for all human activities, including research (except under a special permit). In the Ribbon Reefs, I surveyed six reefs, two per management category: Jewell and Hicks Reefs (fished), Day and Yonge Reefs (no-take), and Carter and Hilder Reefs (no-entry). While the majority of trophic surveys on the GBR only include an examination of open fishing and no-take zones (i.e., Russ et al. 2008; Emslie et al. 2015), the inclusion of no-entry zones provides a unique opportunity to compare no-entry zones to open fishing and no-take zones. By taking into account no-entry zones, we utilize a broader, three-tiered predator-density gradient to elucidate potential top-down effects on non-targeted fishes and benthic composition across management zones in the GBR. In the Swains, I surveyed nine reefs, three per management category: Herald's Prong No. 2,

Unnamed 21-466, and Unnamed 21-500 (fished), Herald's Prong No. 3, Unnamed 21-544, and Recreation Reef (no-take), and Bell Cay, Frigate Cay and Unnamed 21-507 (no-entry). Altogether, I surveyed five reefs in each management zone. The duration of protection of the reefs in no-take and no-entry zones ranged from 11 to 27 years (Table 5.1).

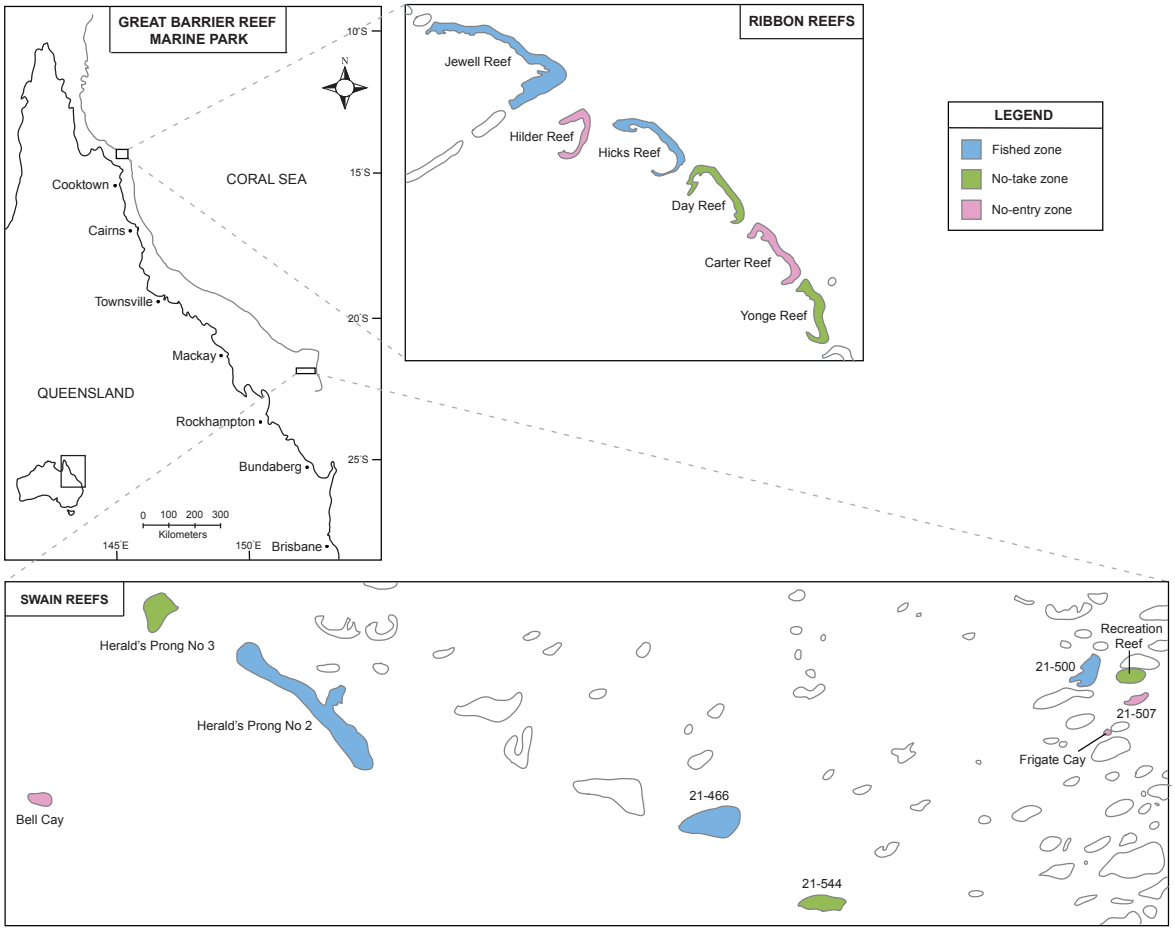



**Figure 5.1** Map of the study reefs in the Great Barrier Reef Marine Park. Six reefs were surveyed in the Ribbons Reefs (Jewell, Hicks, Day, Yonge, Carter, and Hilder Reefs), and nine reefs were surveyed in the Swain Reefs (Herald's Prong No. 2, Unnamed 21-466, Unnamed 21-500, Herald's Prong No. 3, Unnamed 21-544, Recreation, Bell Cay, Frigate Cay, and Unnamed 21-507 Reefs).

**Table 5.1** GPS coordinates (Location) and years of protection (Protection) of each reef in the Ribbon Reefs and the Swain Reefs included in this study.

| Zone | Region | Reef | Location | Protection |
|---|---|---|---|---|
| Fished | Ribbons | Jewell Reef | 14°23'S, 145°22'E | -- |
| | | Hicks Reef | 14°26'S, 145°29'E | -- |
| | Swains | Herald's Prong No.2 | 21°41'S, 151°32'E | -- |
| | | Unnamed 21-466 | 21°50'S, 151°59'E | -- |
| | | Unnamed 21-500 | 21°40'S, 152°24'E | -- |
| No-take | Ribbons | Yonge Reef | 14°34'S, 145°37'E | 11 |
| | | Day Reef | 14°29'S, 145°32'E | 11 |
| | Swains | Herald's Prong No.3 | 21°36'S, 151°22'E | 11 |
| | | Unnamed 21-544 | 21°55'S, 152°60'E | 25 |
| | | Recreation Reef | 21°40'S, 152°26'E | 25 |
| No-entry | Ribbons | Carter Reef | 14°32'S, 145°35'E | 23 |
| | | Hilder Reef | 14°26'S, 145°24'E | 23 |
| | Swains | Bell Cay Reef | 21°48'S, 151°15'E | 11 |
| | | Frigate Cay Reef | 21°44'S, 152°25'E | 27 |
| | | Unnamed 21-507 | 21°42'S, 152°27'E | 27 |

**Study species**

To quantify apex predators, mesopredators, and herbivorous fishes on the GBR, I further split these categories into several groups. Apex predators included all reef shark species, which comprise the top trophic level on coral reefs: *T. obesus*, *C. amblyrhynchos, C. melanopterus*, and *C. albimarginatus*. Mesopredators were categorized as either targeted or non-targeted mesopredators, depending on recreational and commercial fisheries (Frisch et al. 2014). Targeted mesopredators included *Plectropomus laevis*, *P. leopardus, Lethrinus miniatus*, and *Lutjanus carponotatus*. Non-targeted predators included all other members of the families Lethrinidae, Lutjanidae, Serranidae, and Haemulidae, and the labrid genera *Choerodon* and *Cheilinus*. Herbivorous fishes were split into mobile herbivores and territorial grazers. Mobile herbivores included Labridae in the tribe Scarini (parrotfishes) and the families Acanthuridae, Siganidae, and Kyphosidae. Territorial grazers were composed of *Acanthurus lineatus, A. nigrofuscus,* and territorial members of the family Pomacentridae. To survey for benthic composition, corals were identified to species, macroalgae were identified to genus, and other benthic classifications included turf algae, CCA, soft coral, sponges, rubble, and sand.

**Visual censuses**

To assess the abundance and biomass of reef fishes and benthic composition, I used underwater visual censuses. Each reef was surveyed at four different sites. The study sites were on the reef slope, at a depth of 6-10 m. For the apex predator surveys, an observer conducted two 45-minute timed swims at each site and recorded the abundance and estimated total length (TL) of apex predators identified to species (see Rizzari et al. 2014). For the targeted mesopredator, non-targeted mesopredator, mobile herbivore, territorial grazer, and benthic composition surveys, three observers laid four 50 m transects at each site, with each

transect at least 10 m apart. The first observer laid the 50 m transects and used 10 m wide belt transects to record the abundance and estimated TL of adult (individuals > 10 cm) targeted mesopredators, adult non-targeted mesopredators, and adult mobile herbivores identified to species. The second observer followed the same 50 m transects, but used 2 m wide belt transects, and recorded the abundance of adult territorial grazers identified to species. A third observer used the point intercept method (PIT), recording the benthic composition every 50 cm along the same 50 m transects. Consequently, at each reef, there was a total of eight transects (timed swims) for the apex predator surveys and sixteen transects for all other surveys (mesopredator, mobile herbivore, territorial grazer, and benthic composition). To calculate the biomass of fishes, I used published length-weight relationships (Kulbicki et al. 2005) and converted all values to kilograms per hectare.

**Data analysis**

*Fit of data to a theoretical trophic cascade*

To determine whether my dataset fits the theoretical predictions of a trophic cascade, I fit a piecewise structural equation model (SEM) to the data. Piecewise SEMs incorporate several linear models into a single causal pathway analysis using directional separation (d-separation) tests (series of independence claims that statistically identify causal relationships and missing links (i.e. pathways) in a directed acyclic graph (DAG); Shipley 2009). Unlike a traditional SEM, piecewise SEMs are capable of including nested models, random effects, non-normal distributions, and are less dependent on large sample sizes (Lefcheck & Duffy 2014). Thus, piecewise SEMs are applicable to nested ecological count data such as my dataset. I constructed the piecewise SEM based on the theoretical framework of a coral reef trophic cascade (Figure 5.2). Specifically, I predicted an effect of management zone or protection (fished [unprotected] vs. no-take and no-entry [protected]) on fished predators (apex

predators and targeted mesopredators), which I hypothesized to cascade through to herbivorous fishes (mobile herbivores and territorial grazers) and benthic composition (corals and algae). Model specifications for the SEM included six nested mixed-effects models for the abundance of apex predators, targeted mesopredators, mobile herbivores, territorial grazers, corals, and algae (see Table 5.2). I formulated these models with either the package *nlme* to fit linear mixed-effects (LME) models or the package *lme4* to fit generalized mixed-effects models (GLMM). Random effects were specified as site nested within reef. I examined model assumptions, including normality of errors and homogeneity of variances, graphically. To correct for heteroscedasticity and non-normality, square-root transformations were applied to the abundance of apex predators, targeted mesopredators, mobile herbivores, and territorial grazers, and Poisson distributions were used for counts of corals and turf algae. To check the fit of square-root transformations, I assessed residual plots, which were approximately normally distributed and did not reveal deviations from homoscedasticity. When Poisson distributions were applied, model fit was assessed using Pearson chi-squared tests. The piecewise SEM was performed with the package *piecewiseSEM* (Lefcheck & Duffy 2014). The SEM fit was examined using the null probabilities associated with each independence claim (k) from Shipley's d-separation test. To assess whether probabilities were likely to occur by chance, the sum of the null probabilities were tested against a chi-squared distribution with 2k degrees of freedom, which yielded Fisher's *C* statistic, a value that permits the acceptance or rejection of the causal model based on statistical significance. Shipley's d-Regression coefficients for each pathway were extracted from the piecewise SEM, and a Holm-Bonferroni correction was applied to the p-values to determine significant pathways. Partial effects plots were generated to assess the direction and magnitude of each pathway with the package *effects*. The software program R was used for all analyses. (R Core Team 2014).

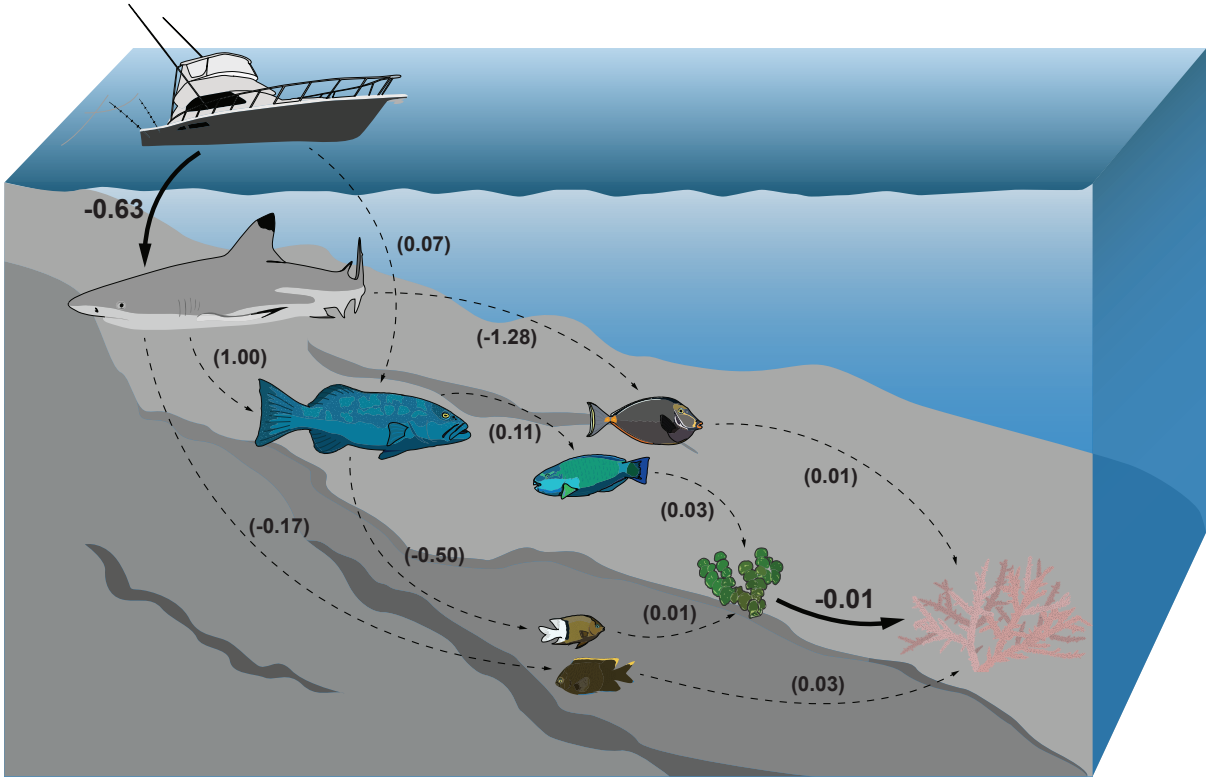



**Figure 5.2** Directed acyclic graph (DAG), describing theoretical predictions of trophic cascades from apex predators to the benthos on coral reefs. Values are the regression coefficients assigned to paths. Thick black arrows and bold values indicate significant pathways with a Holm-Bonferroni correction ($p < 0.0042$); dotted arrows and values in brackets indicate non-significant pathways.

**Table 5.2** Piecewise SEM model specifications, including transformations or distributions (Trans/Distrib) for each trophic group, fixed effects, and random effects**.** Model types include generalized linear models (GLM), linear mixed-effects (LME) models, and generalized linear mixed-models (GLMM).

| Trophic group | Model | Trans/Distrib | Fixed | Random |
|---|---|---|---|---|
| Apex predators | GLM | Square-root | Protection | -- |
| Targeted mesopredators | LME | Square-root | Protection + apex predators | Reef/Site |
| Mobile herbivores | LME | Square-root | Apex predators + targeted mesopredators | Reef/Site |
| Territorial grazers | LME | Square-root | Apex predators + targeted mesopredators | Reef/Site |
| Turf algae and macroalgae | GLMM | Poisson | Mobile herbivores + territorial grazers | Reef/Site |
| Coral | GLMM | Poisson | Mobile herbivores + territorial grazers + algae | Reef/Site |

*Effects of region and management zones on trophic groups*

To assess the effects of region (Ribbons and Swains) and management zone (fished, no-take, and no-entry) on the abundances of different trophic groups (dependent variables), I used the package *nlme* to fit linear mixed-effects (LME) models and the packages *MASS* and *glmmADMB* to fit generalized mixed-effects models (GLMM). As fixed effects, I used region, management zone, and their interaction. As random effects, I used reef, site, or site nested within reef. I examined model assumptions, including normality of errors and homogeneity of variances, graphically. To correct for heteroscedasticity and non-normality, I applied square-root transformations, a log transformation, a Poisson distribution, and negative binomial distributions. To check the fit of square-root transformations and the log transformation, I assessed residual plots, which were approximately normally distributed and did not reveal deviations from homoscedasticity. After applying the Poisson and the negative binomial distributions, model fit was assessed using Pearson chi-squared tests. The software program R was used for all analyses (R Core Team 2014).

## Results

### Fit of data to a theoretical trophic cascade

From the piecewise SEM, the d-separation tests indicated that there were no missing pathways (Table 5.3), and the SEM provided a good fit for the data ($C = 24.794$; $p = 0.131$). The piecewise SEM revealed that there were only two significant pathways: fished zones had a strong negative effect on apex predators ($p < 0.001$), and algae had a negative correlation with live coral ($p < 0.001$; Table 5.4; Figure 5.2). Partial effect plots demonstrate the direction and magnitude of each pathway, including weak, but non-significant, links (Figure 5.3). There were no cascading linkages throughout the trophic schematic: mesopredator abundance was not negatively correlated with mobile herbivore and territorial grazer

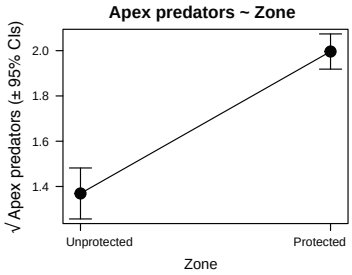
abundances, and herbivorous fish abundance was not negatively correlated with algae or positively correlated with coral abundance.

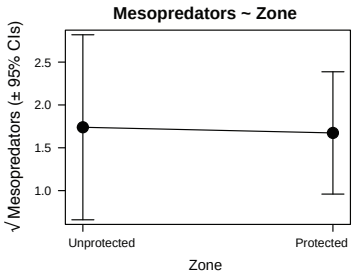
**Table 5.3** SEM independence claims from Shipley's d-separation tests, describing pathways with no linkages in the theoretical trophic cascade model, and p-values for significant missing paths. Variables are as follows: $x_1$ = protection, $x_2$ = apex predators, $x_3$ = targeted mesopredators, $x_4$ = mobile herbivores, $x_5$ = territorial grazers, $x_6$ = corals, and $x_7$ = turf algae and macroalgae. Shaded cells are statistically significant (with a Holm-Bonferroni correction; $p < 0.0042$).

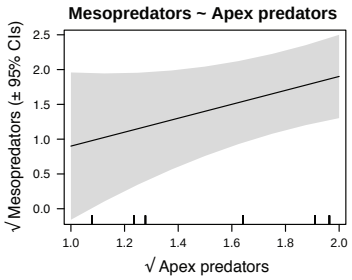
| Claim | d-separation claim | p-value |
|---|---|---|
| 1 | $(x_1, x_4) \mid \{x_2, x_3\}$ | 0.185 |
| 2 | $(x_1, x_5) \mid \{x_2, x_3\}$ | 0.226 |
| 3 | $(x_1, x_6) \mid \{x_4, x_5, x_7\}$ | 0.743 |
| 4 | $(x_1, x_7) \mid \{x_4, x_5\}$ | 0.849 |
| 5 | $(x_2, x_6) \mid \{x_1, x_4, x_5, x_7\}$ | 0.161 |
| 6 | $(x_2, x_7) \mid \{x_1, x_4, x_5\}$ | 0.563 |
| 7 | $(x_3, x_6) \mid \{x_1, x_2, x_4, x_5, x_7\}$ | 0.076 |
| 8 | $(x_3, x_7) \mid \{x_1, x_2, x_4, x_5\}$ | 0.465 |
| 9 | $(x_4, x_5) \mid \{x_2, x_3\}$ | 0.048 |

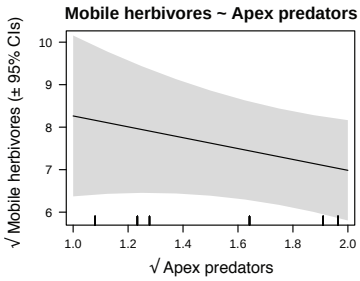
**Table 5.4** Piecewise SEM coefficients from each pathway based on a theoretical trophic cascade model on coral reefs (see Figure 2). Shaded cells are statistically significant (with a Holm-Bonferroni correction; $p < 0.0042$).

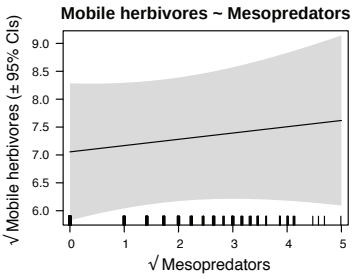
| Path | Estimate | SE | p-value |
|---|---|---|---|
| Fishing → Apex Predators | -0.627 | 0.096 | < 0.001 |
| Fishing → Targeted Predators | 0.066 | 0.708 | 0.927 |
| Apex Predators → Targeted Predators | 1.001 | 0.584 | 0.112 |
| Apex Predators → Mobile Herbivores | -1.279 | 1.000 | 0.223 |
| Targeted Predators → Mobile Herbivores | 0.113 | 0.163 | 0.490 |
| Apex Predators → Territorial Grazers | -0.174 | 0.092 | 0.060 |
| Targeted Predators → Territorial Grazers | -0.503 | 0.403 | 0.233 |
| Mobile Herbivores → Algae | 0.029 | 0.010 | 0.005 |
| Territorial Grazers → Algae | 0.006 | 0.017 | 0.747 |
| Mobile Herbivores → Coral | 0.007 | 0.008 | 0.414 |
| Territorial Grazers → Coral | 0.030 | 0.015 | 0.050 |
| Algae → Coral | -0.014 | 0.001 | < 0.001 |

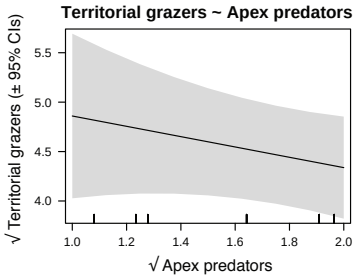

Apex predators ~ Zone
√ Apex predators (± 95% CIs)
Unprotected
Protected
Zone

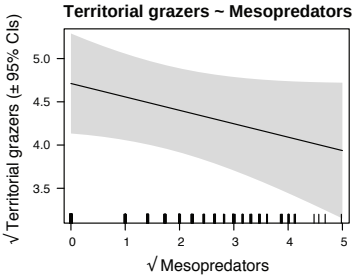

Mesopredators ~ Zone
√ Mesopredators (± 95% CIs)
Unprotected
Protected
Zone

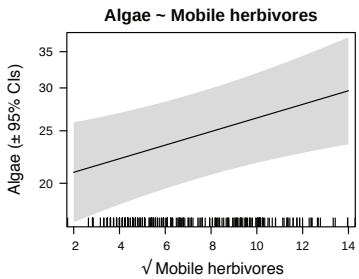

Mesopredators ~ Apex predators
√ Mesopredators (± 95% CIs)
√ Apex predators

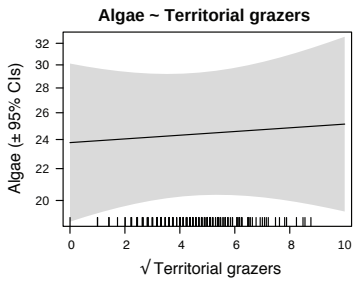

Mobile herbivores ~ Apex predators
√ Mobile herbivores (± 95% CIs)
√ Apex predators

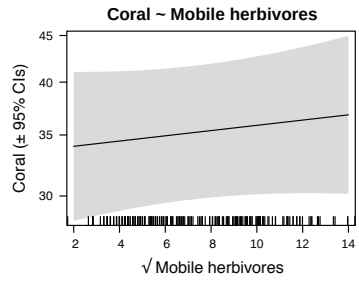

Mobile herbivores ~ Mesopredators
√ Mobile herbivores (± 95% CIs)
√ Mesopredators

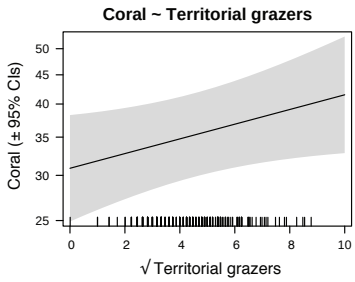

Territorial grazers ~ Apex predators
√ Territorial grazers (± 95% CIs)
√ Apex predators


Territorial grazers ~ Mesopredators
√ Territorial grazers (± 95% CIs)
√ Mesopredators


Algae ~ Mobile herbivores
Algae (± 95% CIs)
√ Mobile herbivores


Algae ~ Territorial grazers
Algae (± 95% CIs)
√ Territorial grazers


Coral ~ Mobile herbivores
Coral (± 95% CIs)
√ Mobile herbivores


Coral ~ Territorial grazers
Coral (± 95% CIs)
√ Territorial grazers

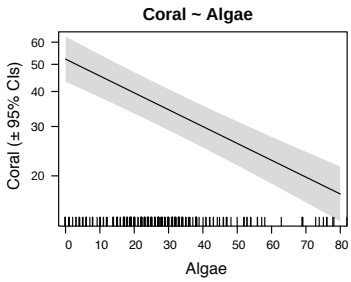

Coral ~ Algae
Coral (± 95% CIs)
Algae

**Figure 5.3** Partial effect plots for each pathway in the piecewise SEM (see Table 5.4; Figure 5.2).

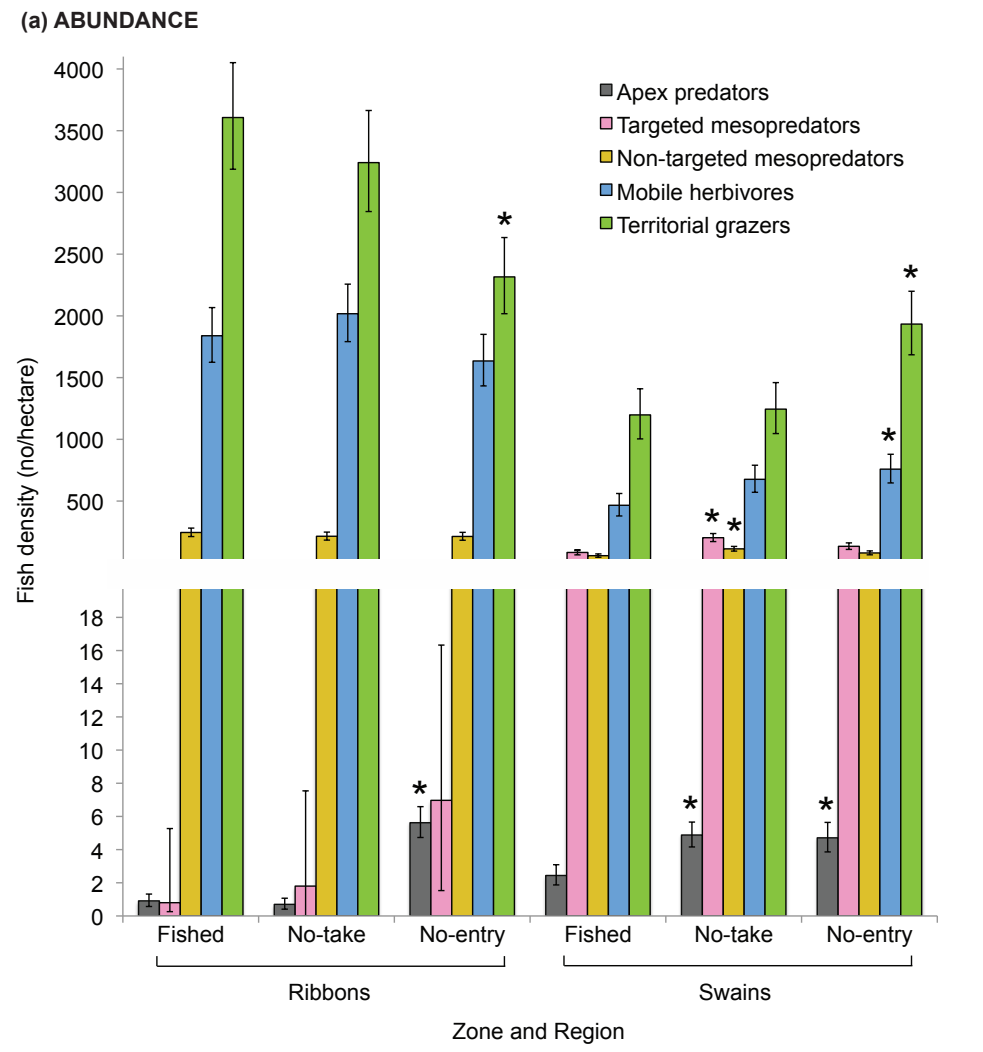
**Effects of region and management zones on trophic groups**

Models predicting spatial variation in fish abundance revealed that some groups of fishes increased in abundance in no-take and no-entry zones, but this was highly dependent on region (Figure 5.4a; Table 5.5; Table 5.6). Apex predator abundance was significantly higher in no-entry zones in both the Ribbons and the Swains. In the Ribbon Reefs, the abundance of reef sharks was six-fold higher in no-entry zones as compared to fished zones, and in the Swain Reefs, the abundance of reef sharks was two-fold higher in no-entry zones as compared to fished zones. However, targeted and non-targeted mesopredator abundance was higher in no-take zones only in the Swains, and mobile herbivore abundance was higher in only no-entry zones in the Swains. The abundance of territorial grazers exhibited an interaction between region and management zone; they were lower in no-entry zones in the Ribbons and higher in no-entry zones in the Swains. With the exception of fished and no-entry zones for apex predators, region had a significant impact on the abundance of fishes across management zones (Table 5.6). For fish abundance, strong regional effects include (on average across reefs, comparing Ribbons to Swains): a 44-fold higher abundance of targeted mesopredators in the Swains, a three-fold higher abundance of non-targeted mesopredators in the Ribbons, a three-fold higher abundance of mobile herbivores in the Ribbons, and a two-fold higher abundance of territorial grazers in the Ribbons (Table 5.5).

Likewise, fish biomass increased for some groups of fishes in no-take and no-entry zones, but this was also highly dependent on region (Figure 5.4b; Table 5.7; Table 5.6). In the Ribbons, the biomass of reef sharks was ten-fold higher in no-entry zones as compared to fished zones, but in the Swains, there was no difference in the biomass of reef sharks. Targeted mesopredator biomass was higher only in no-take zones in the Swains. Non-targeted mesopredator biomass was higher in no-take and no-entry zones in the Swains. Mobile herbivores were only higher in no-entry zones in the Swains. No significant trends

emerged for territorial grazer biomass across management zones in either region. Again, region had a significant effect across management zones for fish biomass, with the exception of fished and no-take zones for apex predators, no-take zones for non-targeted mesopredators, and no-entry zones for territorial grazers (Table 5.6). For apex predators in no-entry zones, there was an eight-fold higher biomass in the Ribbons compared to the Swains. As reported for fish abundance, similar strong regional effects prevailed for fish biomass (on average across reefs, comparing Ribbons to Swains): there was a 24-fold higher biomass of targeted mesopredators in the Swains, a two-fold higher biomass of non-targeted mesopredators in the Ribbons, a two-fold higher biomass of mobile herbivores in the Ribbons, and a two-fold higher biomass of territorial grazers in the Ribbons (Table 5.7).

Unlike the fish results, the benthic models revealed that management zones had no significant impact on benthic composition, and region had a limited effect on overall benthic composition (Figure 5.5; Table 5.8; Table 5.6). There was a significant effect of region on no-take and no-entry zones for CCA as well as for rubble and sand, with CCA having a five-fold higher abundance in the Ribbons compared to the Swains, while rubble and sand had a five-fold higher abundance in the Swains compared to the Ribbons (Table 5.8; Table 5.6).


(a) ABUNDANCE
Apex predators
Targeted mesopredators
Non-targeted mesopredators
Mobile herbivores
Territorial grazers
Fish density (no/hectare)
4000
3500
3000
2500
2000
1500
1000
500
18
16
14
12
10
8
6
4
2
0
Fished
No-take
No-entry
Fished
No-take
No-entry
Ribbons
Swains
Zone and Region

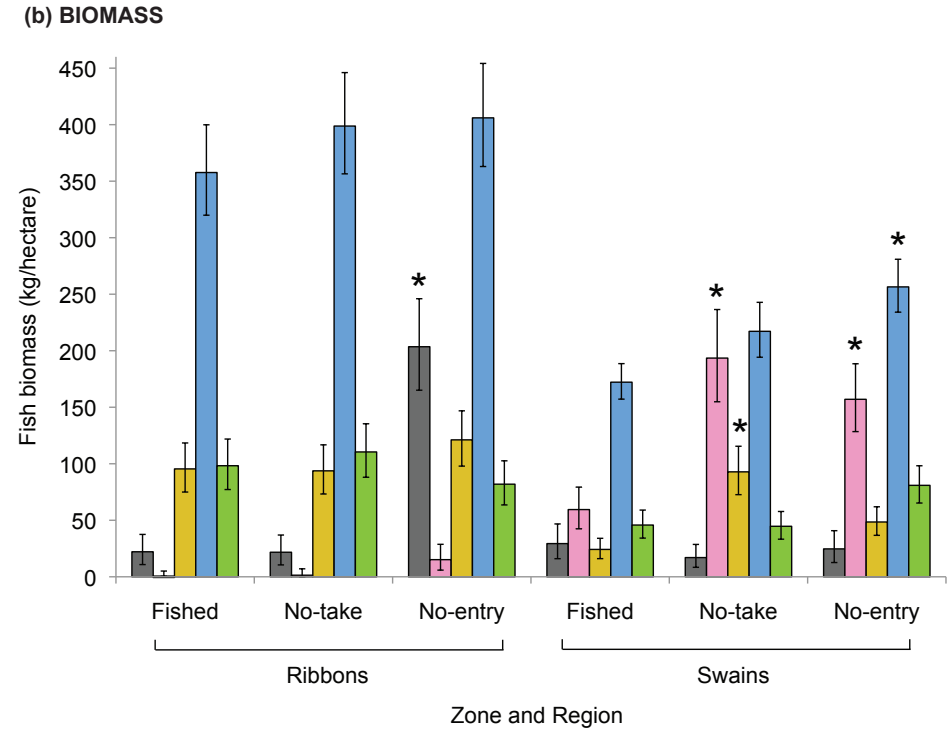

(b) BIOMASS
Fish biomass (kg/hectare)
450
400
350
300
250
200
150
100
50
0
Fished
No-take
No-entry
Fished
No-take
No-entry
Ribbons
Swains
Zone and Region

**Figure 5.4** Back transformed mean values (± SE) from LME models of fish (a) abundance (number/ha) and (b) biomass (kg/ha) for the two geographic regions (Ribbon Reefs and Swain Reefs) across fished, no-take, and no-entry management zones. Asterisks indicate significant values ($p < 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

**Table 5.5** Abundance results for fishes (number/ha): back transformed mean values (±SE), T-values, and p-values (significance) from LME models with square-root transformations (Square-root) for the two geographic regions (Ribbon Reefs and Swain Reefs) across fished, no-take, and no-entry management zones. Shaded cells are statistically significant ($p \leq 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

| Trophic group | Model | Trans/ Distrib | Region | Zone | Value | SE(+) | SE(-) | T/z value | p-value |
|---|---|---|---|---|---|---|---|---|---|
| Apex predators | LME | Square-root | Ribbons | Fished | 0.91 | 0.41 | 0.34 | 4.88 | --- |
| | | | | No-take | 0.70 | 0.37 | 0.29 | -0.44 | 0.67 |
| | | | | No-entry | 5.62 | 0.97 | 0.89 | 5.11 | <0.01 |
| | | | Swains | Fished | 2.44 | 0.65 | 0.57 | 7.99 | --- |
| | | | | No-take | 4.88 | 0.78 | 0.72 | 2.49 | 0.03 |
| | | | | No-entry | 4.71 | 0.93 | 0.85 | 2.15 | 0.05 |
| Targeted meso-predators | LME | Square-root | Ribbons | Fished | 0.80 | 4.47 | 0.55 | 0.64 | --- |
| | | | | No-take | 1.80 | 5.74 | 1.80 | 0.22 | 0.83 |
| | | | | No-entry | 6.97 | 9.36 | 5.43 | 0.88 | 0.40 |
| | | | Swains | Fished | 83.77 | 22.24 | 19.63 | 8.00 | --- |
| | | | | No-take | 203.19 | 33.91 | 31.30 | 3.15 | 0.01 |
| | | | | No-entry | 133.49 | 27.77 | 25.15 | 1.48 | 0.17 |
| Non-targeted meso-predators | LME | Square-root | Ribbons | Fished | 245.61 | 35.51 | 33.11 | 14.32 | --- |
| | | | | No-take | 215.00 | 33.66 | 31.21 | -0.65 | 0.53 |
| | | | | No-entry | 213.44 | 33.18 | 30.79 | -0.69 | 0.51 |
| | | | Swains | Fished | 57.68 | 14.37 | 12.78 | 8.50 | --- |
| | | | | No-take | 112.98 | 19.80 | 18.20 | 2.40 | 0.04 |
| | | | | No-entry | 79.74 | 16.76 | 15.16 | 1.06 | 0.32 |
| Mobile herbivores | LME | Square-root | Ribbons | Fished | 1839.09 | 228.17 | 214.83 | 16.61 | --- |
| | | | | No-take | 2017.47 | 239.55 | 226.11 | 0.56 | 0.58 |
| | | | | No-entry | 1634.79 | 215.50 | 202.16 | -0.67 | 0.50 |
| | | | Swains | Fished | 465.91 | 95.47 | 86.58 | 10.24 | --- |
| | | | | No-take | 676.19 | 114.11 | 105.22 | 1.48 | 0.14 |
| | | | | No-entry | 758.45 | 120.59 | 111.70 | 2.00 | 0.05 |
| Territorial grazers | LME | Square-root | Ribbons | Fished | 3606.59 | 444.62 | 418.78 | 16.71 | --- |
| | | | | No-take | 3241.44 | 422.18 | 396.34 | -0.61 | 0.54 |
| | | | | No-entry | 2315.80 | 318.77 | 298.22 | -2.48 | 0.02 |
| | | | Swains | Fished | 1197.94 | 211.54 | 194.35 | 11.81 | --- |
| | | | | No-take | 1244.59 | 215.02 | 197.90 | 0.16 | 0.87 |
| | | | | No-entry | 1933.55 | 265.90 | 248.77 | 2.26 | 0.03 |

**Table 5.6** The relative significance of geographic region (Ribbon Reefs or Swain Reefs) in fished, no-take, and no-entry management zones based on LME models and GLMMs (model details in Table 5.3, Table 5.4, and Table 5.5) for the (a) abundance of fishes and benthic groups (CCA is crustose coralline algae) and the (b) biomass of fishes. Shaded cells are statistically significant ($p \leq 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

| | (a) ABUNDANCE | | | (b) BIOMASS | | |
|---|---|---|---|---|---|---|
| **Trophic group** | **Fished** | **No-take** | **No-entry** | **Fished** | **No-take** | **No-entry** |
| Apex predators | 0.06 | <0.01 | 0.50 | 0.73 | 0.78 | <0.01 |
| Targeted mesopredators | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |
| Non-targeted mesopredators | <0.01 | 0.02 | <0.01 | <0.01 | 0.98 | 0.02 |
| Mobile herbivores | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |
| Territorial grazers | <0.01 | <0.01 | <0.01 | 0.05 | 0.03 | 0.97 |
| Corals | 0.22 | 0.29 | 0.77 | -- | -- | -- |
| Macroalgae | 0.3 | 0.88 | 0.47 | -- | -- | -- |
| Turf algae | 0.5 | 0.14 | 0.87 | -- | -- | -- |
| CCA | 0.08 | 0.01 | 0.05 | -- | -- | -- |
| Rubble and sand | 0.13 | 0.04 | 0.05 | -- | -- | -- |

**Table 5.7** Biomass results for fishes (kg/ha): back transformed mean values (±SE), T-values, and p-values (significance) from LME models with square-root transformations (Square-root) and a LME model with a log transformation (Log) for the two geographic regions (Ribbon Reefs and Swain Reefs) across fished, no-take, and no-entry management zones. Shaded cells are statistically significant ($p \leq 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

| Trophic group | Model | Trans | Region | Zone | Value | SE (+) | SE (-) | T value | p-value |
|---|---|---|---|---|---|---|---|---|---|
| Apex predators | LME | Square-root | Ribbons | Fished | 22.13 | 15.36 | 11.33 | 3.32 | --- |
| | | | | No-take | 21.72 | 15.23 | 11.21 | -0.02 | 0.98 |
| | | | | No-entry | 203.53 | 42.48 | 38.46 | 4.77 | <0.01 |
| | | | Swains | Fished | 29.37 | 17.39 | 13.36 | 3.82 | --- |
| | | | | No-take | 17.00 | 11.64 | 8.62 | -0.69 | 0.51 |
| | | | | No-entry | 24.68 | 16.11 | 12.08 | -0.22 | 0.83 |
| Targeted mesopredators | LME | Square-root | Ribbons | Fished | 0.62 | 4.46 | 0.16 | 0.54 | --- |
| | | | | No-take | 1.40 | 5.66 | 1.32 | 0.19 | 0.85 |
| | | | | No-entry | 15.16 | 13.57 | 9.27 | 1.50 | 0.17 |
| | | | Swains | Fished | 59.47 | 19.90 | 17.04 | 6.44 | --- |
| | | | | No-take | 193.49 | 42.96 | 38.65 | 3.27 | 0.01 |
| | | | | No-entry | 157.02 | 31.45 | 28.58 | 2.85 | 0.02 |
| Non-targeted mesopredators | LME | Square-root | Ribbons | Fished | 95.45 | 22.95 | 20.48 | 8.79 | --- |
| | | | | No-take | 93.73 | 23.01 | 20.49 | -0.06 | 0.96 |
| | | | | No-entry | 121.14 | 25.69 | 23.23 | 0.79 | 0.45 |
| | | | Swains | Fished | 24.21 | 9.83 | 8.16 | 5.38 | --- |
| | | | | No-take | 92.84 | 22.65 | 20.18 | 3.28 | 0.01 |
| | | | | No-entry | 48.48 | 13.46 | 11.81 | 1.59 | 0.15 |
| Mobile herbivores | LME | Log | Ribbons | Fished | 357.66 | 42.23 | 37.77 | 41.04 | --- |
| | | | | No-take | 398.77 | 47.30 | 42.29 | 0.69 | 0.49 |
| | | | | No-entry | 406.02 | 48.16 | 43.06 | 0.80 | 0.43 |
| | | | Swains | Fished | 172.17 | 16.42 | 14.99 | 42.23 | --- |
| | | | | No-take | 217.17 | 25.64 | 22.93 | 1.61 | 0.11 |
| | | | | No-entry | 256.47 | 24.46 | 22.33 | 3.09 | <0.01 |
| Territorial grazers | LME | Square-root | Ribbons | Fished | 98.26 | 23.61 | 21.07 | 8.80 | --- |
| | | | | No-take | 110.45 | 24.91 | 22.38 | 0.37 | 0.72 |
| | | | | No-entry | 81.93 | 20.68 | 18.36 | -0.55 | 0.59 |
| | | | Swains | Fished | 45.78 | 13.24 | 11.56 | 7.38 | --- |
| | | | | No-take | 44.68 | 13.10 | 11.42 | -0.06 | 0.95 |
| | | | | No-entry | 80.90 | 17.33 | 15.65 | 1.72 | 0.12 |

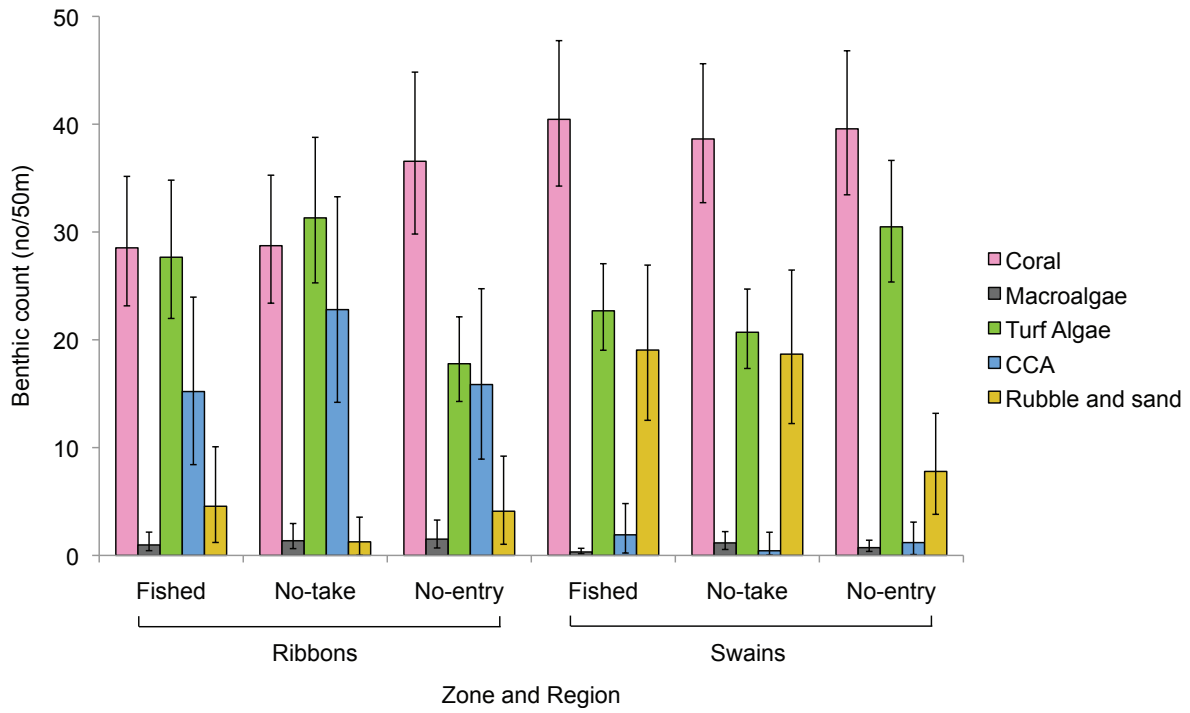



**Figure 5.5** Back transformed mean values (± SE) from LME models and GLMMs of benthic composition (number/50 m) for the two geographic regions (Ribbon Reefs and Swain Reefs) across fished, no-take, and no-entry management zones. Asterisks indicate significant values ($p < 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

**Table 5.8** Abundance results for benthic composition (number/50 m; CCA is crustose coralline algae): back transformed mean values (±SE), T-values (or z-value), and p-values (significance) from a GLMM with a poisson distribution (Poisson), GLMMs with a negative binomial distribution (Neg Binom), and LME models with square-root transformations (Square-root), for the two geographic regions (Ribbon Reefs and Swain Reefs) across fished, no-take, and no-entry management zones. Shaded cells are statistically significant ($p \leq 0.05$), which represent tests of the null hypothesis that the relevant treatment differs from fished zones from each respective region.

| Trophic group | Model | Trans/ Distrib | Region | Zone | Value | SE(+) | SE(-) | T/z value | p-value |
|---|---|---|---|---|---|---|---|---|---|
| Corals | GLMM | Poisson | Ribbons | Fished | 28.53 | 6.63 | 5.38 | 16.00 | --- |
| | | | | No-take | 28.73 | 6.54 | 5.33 | 0.02 | 0.98 |
| | | | | No-entry | 36.56 | 8.27 | 6.75 | 0.85 | 0.42 |
| | | | Swains | Fished | 40.45 | 7.30 | 6.19 | 3.70 | --- |
| | | | | No-take | 38.63 | 6.98 | 5.91 | -0.19 | 0.85 |
| | | | | No-entry | 39.57 | 7.24 | 6.12 | -0.09 | 0.93 |
| Macro-algae | GLMM | Neg binom | Ribbons | Fished | 0.97 | 1.19 | 0.53 | -0.04 | --- |
| | | | | No-take | 1.36 | 1.60 | 0.73 | 0.30 | 0.76 |
| | | | | No-entry | 1.51 | 1.77 | 0.82 | 0.40 | 0.69 |
| | | | Swains | Fished | 0.32 | 0.34 | 0.17 | -1.57 | --- |
| | | | | No-take | 1.16 | 1.05 | 0.61 | 1.33 | 0.18 |
| | | | | No-entry | 0.72 | 0.69 | 0.35 | 0.83 | 0.41 |
| Turf algae | GLMM | Neg binom | Ribbons | Fished | 27.66 | 7.15 | 5.68 | 14.43 | --- |
| | | | | No-take | 31.31 | 7.47 | 6.03 | 0.40 | 0.69 |
| | | | | No-entry | 17.78 | 4.35 | 3.50 | -1.39 | 0.16 |
| | | | Swains | Fished | 22.69 | 4.37 | 3.66 | 17.73 | --- |
| | | | | No-take | 20.70 | 4.01 | 3.36 | -0.37 | 0.71 |
| | | | | No-entry | 30.48 | 6.16 | 5.12 | 1.16 | 0.25 |
| CCA | LME | Square-root | Ribbons | Fished | 15.20 | 8.76 | 6.78 | 3.91 | --- |
| | | | | No-take | 22.80 | 10.47 | 8.60 | 0.62 | 0.55 |
| | | | | No-entry | 15.85 | 8.89 | 6.92 | 0.06 | 0.95 |
| | | | Swains | Fished | 1.91 | 2.90 | 1.69 | 1.70 | --- |
| | | | | No-take | 0.43 | 1.72 | 0.40 | -0.64 | 0.54 |
| | | | | No-entry | 1.19 | 1.90 | 1.11 | -0.25 | 0.81 |
| Rubble and sand | LME | Square-root | Ribbons | Fished | 4.56 | 5.52 | 3.36 | 2.05 | --- |
| | | | | No-take | 1.26 | 2.29 | 1.25 | -0.70 | 0.50 |
| | | | | No-entry | 4.10 | 5.11 | 3.07 | -0.08 | 0.94 |
| | | | Swains | Fished | 19.05 | 7.88 | 6.52 | 5.29 | --- |
| | | | | No-take | 18.67 | 7.80 | 6.44 | -0.04 | 0.97 |
| | | | | No-entry | 7.79 | 5.39 | 3.98 | -1.34 | 0.21 |

## Discussion

Despite a six-fold gradient in the abundance of apex predators and a 250-fold gradient in the abundance of targeted mesopredators across management zones, there was no evidence for cascading effects to lower trophic levels, including mobile herbivores, territorial grazers, and benthic composition in the world's largest coral reef system. The abundance and biomass of mesopredators and herbivorous fishes were highly dependent on region, and less so on management zone, with only apex predators and targeted mesopredators increasing in protected areas in both regions. However, we found no evidence of mesopredator release or prey release, and there was no correlation between the densities of predators and herbivorous fishes. Further, fish assemblages and management zones had no effect on benthic composition, although there were some differences in benthic assemblages between the northern and southern regions. Our results are largely consistent with recently published distributions of apex predators, targeted mesopredators, and herbivorous fishes on the GBR (Rizzari et al. 2014). Similarly, despite increased abundances and densities of targeted mesopredators in no-take zones as compared to fished zones, non-targeted members of the fish assemblage and hard coral cover did not reveal clear patterns across management zones (Emslie et al. 2015). The regional variations in fish and benthic assemblages and the inconsistency of our results with trophic cascade theory highlight the importance of considering environmental factors associated with geographic region in marine trophic interactions alongside human impacts such as fishing (Taylor 2014; Jouffray et al. 2015).

Our application of a structural equation model directly tests trophic cascade theory, decisively demonstrating that reef sharks and targeted mesopredators have minimal top-down effects across management zones. However, our findings strongly contrast with previous examples of putative human-induced trophic cascades on coral reefs. Whereas we found that the removal of predators by fishing had no cascading effects on fish or benthic assemblages,

previous work has suggested that the loss of predators is associated with cascading effects to lower trophic levels (Sandin et al. 2008; Ruppert et al. 2013). Consistent with our results, fishing-induced declines in apex predators and mesopredators in the Line Islands did not affect the overall abundance of herbivorous fishes (Sandin et al. 2008). Conversely, we found no relationship between predator abundance and territorial damselfishes or benthic composition while Sandin et al. (2008) attributed a reduction in predation to a 60-fold increase in the biomass of territorial damselfishes as well as an increase in planktivorous fish abundance and macroalgae and turf algae cover. Unlike the GBR, predator fishing in the Line Islands co-varies with other human impacts such as the extraction of herbivorous fishes, pollution, and runoff, which may account for the discrepancy between these studies. In another recent study in northwestern Australia, Ruppert et al. (2013) suggested that a three-fold higher abundance of apex predators on non-fished *versus* fished reefs resulted in a lower abundance of mesopredators and a higher abundance of herbivorous fishes due to mesopredator release, which is inconsistent with our results. This inconsistency could be due to extensive fishing pressure across many trophic levels (including the extraction of predators, herbivorous fishes, sea cucumbers (*Holothuroidea* spp.), and top snails (*Trochidae* spp.)) from northwestern Australia, which likely confounds the effects of predator removal from this system. In that study, region also confounds fishing pressure since the protected reefs and fished reefs are located at distinct latitudes; this design contrasts with our study, which includes replicate protected and fished reefs within the different regions.

Global trends of herbivorous fish abundances also reveal a contrasting pattern to our results: in a global meta-analysis of fishing effects on herbivorous fishes, significant reductions in the biomass of mobile herbivores was reported in fished areas, while territorial grazers increased in abundance and biomass under fishing pressure (Edwards et al. 2014). Again, in the majority of regions included in this meta-analysis, such as the Caribbean and

the South Pacific Islands, extensive fishing for herbivorous fishes and pollution likely co-vary with effects of predator removal on coral reefs. In contrast to previous claims of human-induced trophic cascades, our analysis of how marine protected areas affect fish and benthic communities excludes confounding factors such as the extraction of other trophic levels, pollution, and runoff, permitting a realistic assessment of trophic cascade theory on coral reefs. Our findings demonstrate the importance of distinguishing between fishing-induced trophic cascades that are solely instigated by the loss of predators rather than broader anthropogenic-induced ecosystem collapse on coral reefs, which is often due to a multitude of factors in addition to fishing pressure.

This study reveals distinct differences in fish assemblages between the two regions, with a higher abundance and biomass of targeted mesopredators in the Swains and a higher abundance and biomass of non-targeted mesopredators, mobile herbivores, and territorial grazers in the Ribbons. Regional effects may exist due to differences in the amount of fishing pressure, environmental conditions such as nutrient input and reef geomorphology across the GBR (Hutchings et al. 2008), or the heterogeneous effects of stochastic disturbance events such as cyclones and bleaching events (Jouffray et al. 2015). According to a long-term monitoring-program across the GBR, there have been no changes in coral cover attributed to specific disturbances events between 1986 and 2004 in the Ribbon Reefs; conversely, in the outer Swain Reefs, recurrent crown-of-thorns starfish (*Acanthaster planci*) outbreaks in 1991 and 2001-2004 have caused severe declines in branching coral cover, especially *Acropora* spp. (Sweatman et al. 2011). Declines in acroporid cover are associated with the loss of small-bodied coral-associated fishes, such as territorial damselfishes (Emslie et al. 2008), which may explain the lower abundance and biomass of territorial grazers in the Swains compared to the Ribbons. Although all of the reefs in the present study were on the outer GBR, each reef has a unique set of geo-physical conditions. For example, nutrient enrichment

from seabird colonies or high levels of habitat complexity may have substantial bottom-up effects on coral reef fish populations (Beukers & Jones 1998). Given the higher magnitude of regional effects in comparison to fishing effects on the GBR, this demonstrates the need to consider the effects of stochastic disturbances and regional differences in geo-physical conditions (e.g. Taylor 2014) in highly dynamic ecosystems such as coral reefs before attributing differences in fish abundance and biomass to fishing effects alone. Similar to fish communities, we found no significant cascading trophic links between the abundance of herbivorous fishes and benthic composition, but there were some regional differences in benthic composition, with CCA on average five times as abundant in the Ribbons, and rubble and sand on average nearly five times as abundant in the Swains. This regional difference could be due to a variety of environmental and geo-physical conditions that were not directly considered (e.g. the positioning of the reefs on the shelf), which indicates that environmental factors play a larger role in shaping benthic trophic structure than the direct effects of fishing.

Omnivory and trophic versatility are common among species that live on coral reefs, which can violate the assumptions that underpin trophic cascade theory (Thompson et al. 2007). Omnivory is highly prevalent in tropical fish communities (Choat et al. 2004; Teixeira-de Mello et al. 2009), and it may dampen the effects of consumer influence and prevent the progression of linear trophic cascades (Strong 1992). This is further enhanced by trophic versatility, which allows a species to opportunistically feed across several trophic levels, resulting in diffuse predation effects that obscures any prey-release when predators are removed (Bellwood et al. 2006). For example, *P. leopardus* is a frequently targeted mesopredator that is nearly absent from unprotected reefs in the Ribbons but abundant on protected reefs in the Swains. This species is reported to show high variation in consumed prey items, preying on up to forty different taxa, including pelagic and reef fishes, mollusks, and crustaceans from a single location (Kingsford 1992). In contrast, large predatory labrids

such as *Cheilinus undulatus* are protected from fishing and thus equally common on protected and unprotected reefs across the GBR. Similar to *P. leopardus*, they have been reported to consume a wide-range of piscine and invertebrate prey (Randall et al. 1978). This dilution of interaction strength in predator-prey relationships in both targeted and non-targeted mesopredators provides a possible explanation as to why I was unable to detect a cascading effect across a gradient of targeted predators. In addition, coral reef food webs are open to pelagic environments due to their spatial discontinuity and extensive exchange with pelagic systems. Spatial heterogeneity of coral reefs enhances nutrient and prey subsidies, which may augment predator populations and further intensify the complexity of trophic interactions (Polis et al. 1997). Thus, trophic versatility, omnivory, and open food webs are all factors that considerably obfuscate linear processes such as trophic cascades, and this may explain their rarity on coral reefs.

I provide empirical evidence that a trophic cascade is not detectable on the outer GBR despite significant declines of predators in fished management zones (Robbins et al. 2006; Russ et al. 2008; Emslie et al. 2015). There was no evident impact of predatory fishes on herbivorous fishes or of herbivorous fishes on benthic composition. Our results highlight the need to consider regional effects and stochastic disturbances (i.e. *A. planci* outbreaks in the Swains) in complex marine systems such as coral reefs since indirect effects may play a substantial role in shaping coral reef ecosystems. Our findings also call for a reassessment of trophic interactions on coral reefs given the limited top-down impact of apex predators on fish and benthic communities, which would allow us to better gauge the impact of human-mediated disturbances in the marine environment (Hussey et al. 2014). Trophic interactions on coral reefs are inherently opportunistic, with high degrees of omnivory and trophic versatility, which may undermine linear processes such as trophic cascades. Understanding

complex trophic interactions in an ecosystem is essential in order to pinpoint weaknesses that may underlie ecological theory, such as the predictions embedded in trophic cascade models.

# Chapter 6: General Discussion

## Summary of Key Findings

In this thesis, I have analyzed the role of territorial grazers in trophic dynamics, incorporating potential trophic links from predators to territorial damselfishes to microbial assemblages on the Great Barrier Reef (GBR). The findings from this thesis yield new insights into the role of territorial grazers in microbial benthic dynamics, spatial distributions of juvenile corals, and large-scale trophic interactions. In Chapter 2 and Chapter 3, I assessed the impact of territorial grazer behaviour and community structure on benthic algal and coral microbial communities. Chapter 2 revealed that territorial damselfishes increase the abundance of potential coral disease pathogens as well as the prevalence of coral disease. Chapter 3 indicated that although territorial grazers do not differentially affect coral microbial assemblages, coral transplantation may increase susceptibility to coral disease. In Chapter 4, I determined the role of territorial damselfishes on the abundance and distribution of juvenile corals on the reef crest over time. A surprisingly high rate of territorial turnover revealed the dynamic nature of damselfish-coral-algal linkages and the high potential for territorial grazers to alter coral assemblages over time. Lastly, in Chapter 5, I surveyed large-scale trophic structure to test for evidence of trophic cascade effects on territorial damselfishes across the outer GBR. Despite higher predator density in protected areas, there was no evidence of cascading effects to territorial grazers or other lower trophic levels. This demonstrates that top-down effects on abundances of coral reef fishes are weak. This thesis provides a comprehensive examination of the role of territorial grazers in trophic interactions from benthic dynamics to large-scale spatial trends across the outer GBR.

Due to the high abundance of damselfishes across shallow coral reefs (Klumpp et al. 1987; Meekan 1995), the findings from this thesis have broad implications for the

conservation and management of coral reefs. Knowledge of the rates of spread and modes of transmission of coral disease pathogens is limited, and identifying reservoirs for marine disease is a major priority within ocean disease research (Harvell et al. 1999; Harvell et al. 2004; Bourne et al. 2009). By revealing the first link among fish behaviour, reservoirs of potential coral disease pathogens, and the prevalence of coral disease, the findings of Chapter 2 represent a notable advancement for marine disease research. In addition, a recent global meta-analysis reports that declines of mesopredators and mobile herbivorous fishes due to overfishing are causing higher abundances of damselfishes worldwide (Edwards et al. 2014). Since increases in damselfish populations may also translate to increases in reservoirs of opportunistic pathogens linked to coral disease, there is a further need to elucidate the linkages between damselfishes, fishing pressure, and coral disease to facilitate informed decisions for the management of coral reefs.

Chapter 3 represents the first analysis of the effects of transplantation on coral bacterial assemblages. Although there was not a direct impact of territorial grazers on coral microbial communities, the increase in potential coral disease pathogens after coral transplantation suggests that transplanted corals may be more susceptible to coral disease under stressful conditions. Since coral transplantation is often utilized for coral reef restoration (Harriott & Fisk 1988b; Jaap 2000; Thornton et al. 2000; Soong & Chen 2003; Rinkevich 2005; Muko & Iwasa 2011), the negative impact of transplantation on coral microbial communities indicates a potential problem with this conservation method. Given the large role that microbial communities play a in the health and resilience of coral reefs (Knowlton & Rohwer 2003; Teplitski & Ritchie 2009; Garren & Azam 2012), these results emphasize the importance of examining coral restoration management strategies beyond macro-organismal trends.

Aside from providing new insights into microbial communities, the findings in this thesis also contextualize large-scale trophic interactions involving territorial grazers. Territorial grazers have differential effects on benthic dynamics according to behavioural guild: the abundances of juvenile corals were more affected by intensive territorial grazers than by indeterminate territorial grazers. While intensive territorial grazers propagate turf algae, particularly *Polysiphonia* spp., to significantly higher levels than outside of damselfish territories (Brawley & Adey 1977; Sammarco 1983; Jones et al. 2006; Ceccarelli et al. 2011), indeterminate grazers cultivate mixed-species farms, with comparatively low-levels of filamentous turf algae (Emslie et al. 2012). Intensive territorial grazers may inhibit coral recruitment due to space occupation by thick turf algae, which have inhibitory effects on coral settlement (Birrell et al. 2001). Territorial grazers also had a surprisingly high rate of temporal turnover. While juvenile corals can rapidly decline under the cultivation behaviours of a territorial damselfish, they can likewise rapidly recover with the loss of a damselfish territory. Thus, due to high rate of territorial turnover, there is potential for coral recovery on reefs occupied by territorial damselfishes. Since corals are sedentary organisms and highly sensitive to spatial and temporal shifts (Sandin & McNamara 2012), the dynamic patterns of damselfish territories may play a large role in shaping coral and algae assemblages on the reef crest over time.

While the effects of damselfishes on coral, algae, and microbial assemblages are readily apparent, the factors that influence the distribution and abundance of territorial grazers across the outer GBR are less clear. Despite finding higher abundances of predators in marine protected areas, there was no evidence of cascading top-down effects to herbivorous fishes and benthic communities. Previous examples of putative human-induced trophic cascades on coral reefs strongly contrast with these findings. Others report that declines of predators resulted in cascading effects to lower trophic levels, resulting in a lower

biomass of mesopredators and herbivores (the Hawaiian Islands; Friedlander & DeMartini 2002), the domination of planktivorous fishes and algae (the Northern Line Islands; Sandin *et al*. 2008), and a mesopredator release resulting in lower levels of herbivorous fishes and higher algal cover (northwest Australia; Ruppert *et al*. 2013). However, in these systems, predator fishing gradients co-vary with other anthropogenic effects, such as fishing for herbivorous fishes, pollution, and runoff. In contrast, this analysis of how marine protected areas affect fish and benthic communities was conducted across a spatially dispersed predator density gradient on the outer GBR, permitting a more targeted assessment of trophic cascades on coral reefs. In addition to considering the influence of human impact on fish and benthic communities, recent studies have emphasized the importance of ephemeral environmental events such as cyclones and bleaching events (Jouffray et al. 2015). For instance, in the Swain Reefs, recurrent crown-of-thorns starfish (*Acanthaster planci*) outbreaks in 1991 and 2001-2004 corresponded with severe declines in branching coral cover, especially *Acropora* spp. (Sweatman *et al*. 2011), which provide habitat for territorial damselfishes and may explain the lower abundance and biomass of territorial grazers in the Swains compared to the Ribbons (Emslie *et al*. 2008). Further, biogeographic factors, such as reef configuration, habitat complexity, and wave exposure, have been shown to obscure potential fishing effects on coral reef fishes (Taylor 2014). The most notable trend in fish and benthic assemblages on the outer GBR was the difference between the two regions, which demonstrates the need to consider the impact of stochastic disturbances and biogeographic features before attributing differences in fish abundance and biomass to fishing effects alone. The findings of Chapter 5 highlight the need to reassess the intricacies of trophic interactions on coral reefs to better quantify the impact of human-mediated disturbances alongside indirect regional effects.

Although the exact factors that drive damselfish populations across the GBR remain uncertain, the overall conclusions from this thesis illustrate the key role of territorial grazers

in coral-algae-microbial dynamics. These findings also emphasize the importance of microbial communities for ecological dynamics of the macro-benthos and the necessity of controlling for confounding human impacts when assessing trophic interactions in highly dynamic, complex environments such as coral reefs.

## Future Directions

New ecological and microbiological questions have emerged from a range of unexpected and noteworthy results from this thesis. Given the higher abundance of potential coral disease pathogens in the EAM inside *Stegastes*' territories as well as the actual higher prevalence of coral disease (Chapter 2; Casey et al. 2014), I expected to find corresponding higher abundances of potential coral disease pathogens in transplanted corals inside *Stegastes*' territories (Chapter 3; Casey et al. 2015a). However, I found a high abundance of potential pathogens linked to BBD both inside and outside *Stegastes*' territories. It is likely that the initial stress of transplantation masked any effects of territorial damselfishes on coral microbial communities. To extend on this chapter, it would be worthwhile to investigate how the initial establishment of damselfish territories impact coral microbial communities over time. Further, although Chapter 3 yields important insights for coral restoration efforts, this was not the original aim of the project, so a slightly different experimental design (i.e., considering the survival rates of different sized fragments) would have been preferred from a restoration perspective.

Although cyanobacterial patches often precede the onset of BBD lesions (Sato et al. 2010) and cyanobacteria are seasonally abundant inside damselfish territories (Casey et al. 2014), the fine-scale processes that drive coral disease dynamics in damselfish territories remain unknown. To build upon previous findings, it would be beneficial to analyse the seasonality of bacterial communites, especially the microbes linked to BBD, in the EAM

inside *Stegastes*' territories. Further, a direct experimental manipulation (i.e. removal of damselfish) would indicate how turf algal and microbial communities develop inside compared to outside *Stegastes*' territories after territorial establishment. Lastly, an investigation of the similarity between microbial communities in corals exposed to turf algae and corals with BBD inside *Stegastes*' territories would elucidate whether turf algae exposure increases susceptibility to BBD. By isolating bacterial assemblages in turf algae-exposed corals and BBD-affected corals inside *Stegastes*' territories, this would indicate which species or communities of bacteria cause BBD in damselfish territories. Using techniques such as histopathology (hemotoxylin and eosin staining), fluorescence in situ hybridization (FISH), and 16S rDNA sequencing could reveal whether turf algae cultivation is likely to precede the contraction of BBD, and it may also provide new insights into the intricacies of BBD propagation. Ultimately, analyzing the fine-scale microbial dynamics that underlie coral disease in damselfish territories would enable scientists and managers to understand and predict large-scale patterns of coral disease that threaten coral reef ecosystems.

The absence of significant pathways between trophic groups on the outer GBR was also an unexpected finding. Despite a six-fold gradient in the abundance of apex predators and a 250-fold gradient in the abundance of mesopredators across management zones on the GBR, there were no detectable top-down effects to lower trophic levels. Although territorial grazers have a negative impact on juvenile coral abundance on the reef crest (Chapter 4; Casey et al. 2015b), there was no significant relationship between territorial grazers and coral or turf algae cover on the outer reef (Chapter 5). While this appears to be a contradicting result, a number of factors may explain these findings. Aside from the presence of territorial grazers, many other organisms and geomorphological conditions shape benthic composition on coral reefs (Hutchings et al. 2008). For instance, high abundances of mobile grazing herbivores, poor conditions for the establishment of corals, or macroalgae blooms after a

disturbance event may veil the effects of territorial grazers on coral and algae assemblages (McCook et al. 2001; Hughes 2007b). To deduce the specific factors that drive large-scale patterns of territorial damselfishes and benthic composition across coral reefs, a quantification of the indirect factors (i.e. wave exposure, nutrient availability, reef configuration, and the composition of benthic substratum) needs to be undertaken in concert with large-scale fish and benthic surveys. Large-scale spatial imagery would allow for the analysis of reef configuration, which often drives biotic communities on coral reefs (Taylor 2014) and may have bottom-up effects on the distribution of territorial damselfishes. Further, in consideration of the high rates of turnover of damselfish territories on the reef crest (Casey et al. 2015b), corals may be given the opportunity to recover after the loss of a damselfish territory, and adult corals are less likely to be negatively impacted by territorial grazers due to size escape, which may explain the absence of a strong relationship between territorial grazers and coral cover. Due to the overall dynamic nature of coral reef systems on the reef crest (Casey et al. 2015b), especially in the context of historic disturbance events (Jouffray et al. 2015), there is a need for long-term monitoring across the outer GBR to garner a holistic understanding of the patterns and processes that influence the distribution of territorial grazers. In conclusion, by integrating fine-scale microbial analyses with large-scale investigations of trophic interactions, we can begin to discern the complexities embedded within trophic dynamics on coral reefs.

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# Appendix A: Table A1 and References (Chapter 2)

**Table A1** Assignments of bacterial genera into metabolic categories (autotrophs, heterotrophs, and potential pathogens). "R" denotes reference for metabolic grouping.

| Autotrophs | R | Heterotrophs | R | Potential pathogens | R |
|---|---|---|---|---|---|
| *Anabaena* | S1 | *Afifella* | S19 | *Bartonella* | S37 |
| *Aphanizomenon* | S1 | *Candidatus* Microthrix | S20 | *Cardiobacterium* | S38 |
| *Arthrospira* | S2 | *Chondromyces* | S21 | *Inquilinus* | S39 |
| *Chamaesiphon* | S3 | *Congregibacter* | S22 | *Leptolyngbya** | S40 |
| *Cylindrospermopsis* | S4 | *Flammeovirga* | S23 | *Oscillatoria** | S40 |
| *Gloeobacter* | S5 | *Kordia* | S24 | | |
| *Microcoleus* | S6 | *Lewinella* | S25 | | |
| *Nitrospira* | S7 | *Magnetococcus* | S26 | | |
| *Paracoccus* | S8 | *Magnetospirillum* | S27 | | |
| *Planktothricoides* | S9 | *Methylobacterium* | S28 | | |
| *Prochlorococcus* | S10 | *Nisaea* | S29 | | |
| *Prochlorothrix* | S9, S11 | *Oceanicola* | S30 | | |
| *Rhodovibrio* | S12 | *Opitutus* | S31 | | |
| *Spirulina* | S13 | *Phaeobacter* | S32 | | |
| *Synechococcus* | S14 | *Pirellula* | S33 | | |
| *Thermosynechococcus* | S15 | *Rhodopirellula* | S34 | | |
| *Thioalkalivibrio* | S16 | *Ruegeria* | S32 | | |
| *Thiorhodovibrio* | S17 | *Shinella* | S35 | | |
| *Trichodesmium* | S18 | *Wolbachia* | S36 | | |

***Leptolyngbya* and *Oscillatoria* are coral-specific potential pathogens associated with black band disease.

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# Appendix B: Table B1 and References (Chapter 2)

**Table B1** Summary of cyanobacterial potential coral pathogens (that were assigned to *Leptolyngbya*; comprised of 168 OTUs) matched to bacteria with the highest sequence similarity in BLAST, including the OTU number, percent abundance (of our OTUs), identity (percent similarity), definition (grouping of top match), environmental source, accession number and reference. Asterisks indicate additional high BLAST matches that are associated with corals, coral disease and marine environments.

| OTU | Percent | Identity | Definition | Source | Accession | Ref |
|---|---|---|---|---|---|---|
| OTU_3 | 19.928 | 98 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_344 | 13.814 | 98 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_1560 | 7.951 | 92 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_12 | 5.567 | 98 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_3458 | 3.653 | 95 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_5 | 3.161 | 94 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_60 | 2.855 | 99 | Uncultured bacterium clone | Necrosed coral tissue | AY529887 | S47 |
| OTU_30 | 2.264 | 98 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_38 | 2.089 | 94 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 96 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_2408 | 2.089 | 91 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_40 | 2.056 | 99 | Uncultured bacterium clone | Oolitic sand | JX504463 | S45 |
| | | 98 | Uncultured bacterium clone | Associated with *Porites* sp. | EU636615 | S78* |
| OTU_45 | 2.012 | 96 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_287 | 1.947 | 99 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_35 | 1.848 | 97 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_63 | 1.695 | 99 | Uncultured marine bacterium clone | CaCO3 deposition, metallic artificial reef | FJ594839 | S48 |
| | | 98 | Uncultured cyanobacterium clone | Black band diseased coral tissue | EF123578 | S101* |
| OTU_57 | 1.367 | 92 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |
| OTU_76 | 1.006 | 96 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_263 | 0.973 | 99 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_90 | 0.908 | 97 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 97 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_114 | 0.908 | 96 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_1582 | 0.886 | 97 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_122 | 0.809 | 98 | Uncultured bacterium clone | *Porites astreoides* | GU118939 | S49 |

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|---|---|---|---|---|---|---|
| OTU_123 | 0.689 | 99 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_229 | 0.667 | 96 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_1729 | 0.623 | 96 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_153 | 0.591 | 95 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_171 | 0.525 | 96 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 97 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_189 | 0.481 | 98 | Uncultured cyanobacterium | Marine sediment | AM177431 | S50 |
| OTU_1659 | 0.470 | 97 | Uncultured bacterium clone | Diseased tissue | JQ516288 | S69 |
| OTU_55 | 0.470 | 98 | Uncultured *Rivularia* sp. | Rock surface of calcareous river | EU009142 | S91 |
| | | 98 | Uncultured bacterium clone | Biofilm, glass | JF262020 | S102* |
| OTU_87 | 0.470 | 94 | Uncultured Oscillatoriales cyanobacterium clone | Quartz, Tibet desert | FJ790628 | S92 |
| OTU_238 | 0.470 | 96 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_266 | 0.459 | 99 | Uncultured bacterium clone | *Montipora* tissue | FJ809378 | S52 |
| OTU_199 | 0.448 | 94 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 93 | Uncultured bacterium clone | Coral-associated | AF365814 | S42* |
| OTU_2230 | 0.448 | 92 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203574 | S46 |
| OTU_1397 | 0.427 | 98 | *Aphanocapsa* sp. | Bahamian marine stromatolite | EU249123 | S66 |
| OTU_1049 | 0.416 | 99 | Uncultured bacterium clone | Biofilm, glass | JQ727046 | S61 |
| OTU_1891 | 0.416 | 96 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_1142 | 0.416 | 97 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_225 | 0.405 | 96 | Uncultured bacterium clone | Sandy carbonate sediment | EF208676 | S51 |
| | | 96 | *Aphanocapsa* sp. | Bahamian marine stromatolite | EU249123 | S66* |
| OTU_2136 | 0.383 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - diseased tissue | FJ203286 | S46 |
| OTU_1301 | 0.328 | 97 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_353 | 0.306 | 97 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_342 | 0.295 | 99 | Uncultured bacterium clone | Oolitic sand | JX504282 | S45 |
| OTU_350 | 0.284 | 99 | Uncultured bacterium clone | *Diploria strigosa* | GU118301 | S49 |
| OTU_764 | 0.284 | 94 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_147 | 0.273 | 98 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203523 | S46 |
| OTU_523 | 0.262 | 95 | Uncultured cyanobacterium clone | White syndrome, *Turbinaria mesenterina* | EU780386 | S55 |
| OTU_3487 | 0.262 | 95 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_375 | 0.252 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_441 | 0.241 | 97 | Uncultured cyanobacterium clone | Intertidal thrombolites | GQ484027 | S54 |
| OTU_425 | 0.219 | 99 | Uncultured bacterium clone | *Crassostrea gigas* | JF827522 | S53 |
| OTU_189 | 0.219 | 96 | Cyanobacterium | Black band diseased *S. siderea* | EF372582 | S93 |
| OTU_792 | 0.186 | 97 | *Calothrix* sp. | Rock surface, littoral zone, Baltic Sea | AM230670 | S73 |
| | | 96 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43* |
| OTU_2732 | 0.175 | 94 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_432 | 0.175 | 98 | Uncultured cyanobacterium | Microbial mat | DQ181693 | S95 |

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|---|---|---|---|---|---|---|
| | | | clone | | | |
| OTU_1172 | 0.164 | 96 | Uncultured cyanobacterium clone | Permeable shelf sediment | DQ289927 | S64 |
| OTU_1609 | 0.164 | 92 | Oscillatoriales cyanobacterium | Oscillatoriales cyanobacterium | KC463193 | S68 |
| OTU_298 | 0.164 | 96 | Uncultured cyanobacterium | Sponge cortex | AM259864 | S44 |
| OTU_2653 | 0.153 | 95 | Uncultured bacterium clone | Associated with *Porites* sp. coral | EU636510 | S78 |
| OTU_3096 | 0.153 | 96 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_2047 | 0.142 | 96 | Uncultured bacterium clone | Particle-attached bacteria fraction | EU636510 | S78* |
| OTU_744 | 0.131 | 94 | Uncultured bacterium clone | Endolith | JX258078 | S56 |
| OTU_763 | 0.131 | 96 | Uncultured cyanobacterium | Sponge cortex | AM259864 | S44 |
| OTU_783 | 0.131 | 95 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |
| OTU_2099 | 0.131 | 95 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_473 | 0.131 | 92 | Uncultured Oscillatoriales cyanobacterium clone | Quartz, Tibet desert | FJ790628 | S92 |
| OTU_648 | 0.120 | 92 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_859 | 0.109 | 97 | Uncultured bacterium clone | Coral-associated | AF365850 | S42 |
| OTU_978 | 0.109 | 99 | Uncultured cyanobacterium | *Xestospongia muta* sponge | GU590841 | S58* |
| OTU_1021 | 0.109 | 96 | *Chroococcidiopsis* sp. | *Chroococcidiopsis* sp. | JF810076 | S60 |
| OTU_1024 | 0.109 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203615 | S46 |
| OTU_75 | 0.109 | 95 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |
| OTU_787 | 0.098 | 97 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_931 | 0.098 | 99 | Uncultured bacterium clone | Coral mucus | FJ152382 | S57 |
| OTU_951 | 0.098 | 94 | Uncultured cyanobacterium clone | Intertidal thrombolites | GQ484055 | S54 |
| OTU_1093 | 0.098 | 97 | Uncultured bacterium clone | Seawater | KC294803 | S62 |
| OTU_1135 | 0.098 | 96 | *Leptolyngbya* sp. | Red Sea | JX470180 | S63 |
| OTU_1476 | 0.098 | 95 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_2679 | 0.098 | 91 | *Rivularia* sp. | Intertidal zone | KC989702 | S80 |
| OTU_1010 | 0.098 | 93 | Uncultured cyanobacterium | Seawater | AM259746 | S44 |
| | | 93 | Uncultured cyanobacterium clone | Black band disease mat | JX463422 | S96* |
| OTU_91 | 0.098 | 96 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 97 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_421 | 0.098 | 97 | *Aphanocapsa* sp. | Bahamian marine stromatolite | EU249123 | S66 |
| OTU_1860 | 0.098 | 96 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203604 | S46 |
| OTU_1002 | 0.087 | 96 | Uncultured bacterium | Highly saline rhizospheric soil | HG938349 | S59 |
| OTU_1003 | 0.087 | 96 | Uncultured bacterium clone | Necrosed coral tissue | AY529887 | S47 |
| OTU_1630 | 0.087 | 97 | Uncultured bacterium | Highly saline rhizospheric soil | HG938349 | S59 |
| OTU_1111 | 0.077 | 95 | Uncultured bacterium clone | *Porites astreoides* | GU118939 | S49 |
| OTU_1313 | 0.077 | 96 | Uncultured organism clone | *Acropora palmata* | GU119575 | S49 |
| OTU_1372 | 0.077 | 95 | *Cyanothece* sp. | *Cyanothece* sp. | AY620238 | S65 |
| OTU_2686 | 0.077 | 97 | Uncultured bacterium clone | *Diploria strigosa* | GU118152 | S49 |

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|---|---|---|---|---|---|---|
| OTU_2890 | 0.077 | 91 | *Calothrix* sp. | Rock surface, littoral zone, Baltic Sea | AM230670 | S73 |
| OTU_590 | 0.077 | 98 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96 |
| OTU_1462 | 0.066 | 94 | Uncultured cyanobacterium | Marine sediment | AM168001 | S67 |
| OTU_1655 | 0.066 | 99 | Uncultured bacterium clone | Oolitic sand | JX504288 | S45 |
| OTU_1666 | 0.066 | 95 | Uncultured bacterium clone | Oolitic sand | JX504329 | S45 |
| OTU_3573 | 0.066 | 96 | Uncultured bacterium clone | *Diploria strigosa* | GU118152 | S49 |
| OTU_425 | 0.066 | 98 | Cyanobacterium endosymbiont | *Rhopalodia gibba* | AB546730 | S94 |
| OTU_560 | 0.066 | 98 | *Cyanothece* sp. | *Cyanothece* sp. | CP000806 | S82 |
| OTU_1709 | 0.055 | 87 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203376 | S46 |
| OTU_1832 | 0.055 | 92 | Uncultured bacterium clone | Sandy carbonate sediment | EF208676 | S51 |
| OTU_2116 | 0.055 | 94 | Uncultured bacterium clone | Necrosed coral tissue | AY529887 | S47 |
| OTU_2160 | 0.055 | 93 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_3125 | 0.055 | 94 | Uncultured organism clone | *Acropora palmata* | GU119563 | S49 |
| OTU_3185 | 0.055 | 98 | Uncultured bacterium | Sediment of Lake Jusan | AB779889 | S87 |
| OTU_3388 | 0.055 | 92 | Uncultured bacterium clone | *Montastraea faveolata* - diseased tissue | FJ203286 | S46 |
| OTU_3557 | 0.055 | 97 | *Cyanothece* sp. | *Cyanothece* sp. | CP001701 | S90 |
| OTU_3657 | 0.055 | 96 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 96 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_340 | 0.055 | 97 | *Aphanocapsa* sp. | Bahamian marine stromatolite | EU249123 | S66 |
| OTU_816 | 0.055 | 99 | Uncultured bacterium clone | *Diploria strigosa* | GU118301 | S49 |
| OTU_1014 | 0.055 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_1714 | 0.044 | 97 | Uncultured *Halomicronema* sp. clone | Hamelin pool seawater | EF150805 | S70 |
| OTU_2080 | 0.044 | 98 | *Porphyridium purpureum* chloroplast | *Porphyridium purpureum* | AP012987 | S71 |
| OTU_2098 | 0.044 | 90 | Uncultured organism clone | *Acropora palmata* | GU119563 | S49 |
| OTU_2125 | 0.044 | 96 | Uncultured bacterium clone | Sea | JF514264 | S72 |
| | | 96 | Uncultured bacterium clone | Particle-attached bacteria | EU628072 | S78* |
| OTU_2151 | 0.044 | 92 | *Calothrix* sp. | Rock surface, littoral zone, Baltic Sea | AM230670 | S73 |
| | | 94 | Uncultured cyanobacterium clone | microbial mat of black band disease | JX022546 | S103* |
| OTU_2181 | 0.044 | 94 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_2194 | 0.044 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_2252 | 0.044 | 99 | Uncultured marine bacterium clone | CaCO3 deposition, metallic artificial reef | FJ594844 | S48 |
| | | 97 | *Leptolyngbya* sp. | *Leptolyngbya* sp. | AY493584 | S104* |
| OTU_2261 | 0.044 | 95 | Uncultured cyanobacterium clone | Sediments, polluted with crude oil | JQ580215 | S74 |
| OTU_2353 | 0.044 | 97 | Uncultured cyanobacterium clone | *Montastrea faveolata* | FJ425596 | S75 |
| OTU_2541 | 0.044 | 96 | Uncultured bacterium clone | Biofilm on artificial substrates | KC299299 | S76 |
| OTU_2553 | 0.044 | 95 | Uncultured marine microorganism clone | coastal tropical surface seawater | KC425580 | S77* |

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|---|---|---|---|---|---|---|
| OTU_2613 | 0.044 | 96 | Uncultured bacterium clone | *Montastraea franksi* | GU118716 | S49 |
| OTU_2635 | 0.044 | 96 | Uncultured bacterium clone | *Montastraea faveolata*, aquarium 23 days | FJ202607 | S46 |
| OTU_2758 | 0.044 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203581 | S46 |
| OTU_2824 | 0.044 | 96 | *Cyanothece* sp. | *Cyanothece* sp. | CP000806 | S82 |
| OTU_2899 | 0.044 | 97 | Uncultured bacterium clone | BBD affected corals | GU471944 | S41 |
| OTU_3186 | 0.044 | 95 | Uncultured bacterium clone | Sediment collected from Merri Creek | EU284458 | S88 |
| OTU_172 | 0.044 | 96 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415796 | S43 |
| OTU_614 | 0.044 | 93 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |
| OTU_1083 | 0.044 | 93 | Uncultured cyanobacterium clone | Microbial mat | DQ181685 | S95 |
| OTU_1129 | 0.044 | 91 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203574 | S46 |
| OTU_1159 | 0.044 | 94 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203524 | S46* |
| OTU_1318 | 0.044 | 91 | Uncultured cyanobacterium clone | Intertidal thrombolites | GQ483866 | S54 |
| OTU_1346 | 0.044 | 94 | Uncultured cyanobacterium clone | White syndrome, *Turbinaria mesenterina* | EU780364 | S55* |
| OTU_1510 | 0.044 | 95 | Uncultured bacterium clone | Seawater next to dolphin | JQ197040 | S97 |
| | | 95 | Uncultured bacterium clone | Marine bulk water | JX016995 | S105* |
| OTU_1540 | 0.044 | 98 | Uncultured cyanobacterium clone | White syndrome, *Turbinaria mesenterina* | EU780386 | S55 |
| OTU_2657 | 0.033 | 98 | Uncultured bacterium clone | *Acropora eurystoma* exposed to pH 7.3 | GU319302 | S79 |
| OTU_2741 | 0.033 | 97 | *Gloeothece* sp. | *Gloeothece* sp. | AB067580 | S81 |
| OTU_2775 | 0.033 | 96 | *Leptolyngbya* sp. | Red Sea | JX470180 | S63 |
| OTU_2779 | 0.033 | 97 | Uncultured bacterium clone | Oolitic sand | JX504499 | S45 |
| OTU_2857 | 0.033 | 94 | Uncultured bacterium clone | Antarctic soil, glacier forefield | JX172450 | S83 |
| | | 94 | Uncultured cyanobacterium clone | Beach sediment | JX041703 | S84* |
| OTU_2956 | 0.033 | 96 | Uncultured cyanobacterium clone | Beach sediment | JX041703 | S84 |
| OTU_3022 | 0.033 | 91 | Uncultured cyanobacterium clone | Intertidal thrombolites | GQ484055 | S54 |
| OTU_3038 | 0.033 | 93 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_3043 | 0.033 | 93 | Uncultured organism clone | Guerrero Negro hypersaline mat | JN513686 | S85 |
| OTU_3063 | 0.033 | 97 | Cyanobacterium sp. | Soil | KC695862 | S86 |
| OTU_3140 | 0.033 | 91 | Uncultured bacterium clone | *Montastraea faveolata*, aquarium 23 days | FJ202541 | S46 |
| OTU_3471 | 0.033 | 96 | Uncultured bacterium clone | BBD affected corals | GU471954 | S41 |
| OTU_3494 | 0.033 | 97 | Uncultured cyanobacterium | Microbial mat from stromatolite head | AB602500 | S89 |
| OTU_3548 | 0.033 | 93 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_68 | 0.033 | 92 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |
| OTU_214 | 0.033 | 97 | Uncultured cyanobacterium | Seawater | AM259754 | S44 |
| | | 97 | Uncultured cyanobacterium clone | Black band disease mat | JX463398 | S96* |
| OTU_532 | 0.033 | 97 | *Cyanothece* sp. | *Cyanothece* sp. | AB067581 | S81 |

| | | | | | | |
|---|---|---|---|---|---|---|
| OTU_840 | 0.033 | 98 | Uncultured bacterium clone | Necrosed coral tissue | AY529887 | S47 |
| OTU_1221 | 0.033 | 99 | Uncultured Nostocales cyanobacterium clone | Intertidal button thrombolitic mat | HQ415797 | S43 |
| OTU_1687 | 0.033 | 96 | Uncultured bacterium clone | *Porites astreoides* | GU118939 | S49 |

| | | | | | | |
|---|---|---|---|---|---|---|
| OTU_1729 | 0.033 | 92 | Uncultured marine bacterium clone | CaCO3 deposition, metallic artificial reef | FJ594843 | S48 |
| | | 92 | *Leptolyngbya* sp. | Red Sea | JX481735 | S63* |
| OTU_1799 | 0.033 | 93 | Uncultured cyanobacterium | Coastal water | AB691165 | S98 |
| | | 93 | Uncultured bacterium clone | Coral-associated | AF365467 | S42* |
| OTU_1878 | 0.033 | 96 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203524 | S46 |
| OTU_2252 | 0.033 | 91 | Uncultured bacterium isolate | Mesophilic terrestrial mat | EF126282 | S99 |
| OTU_1754 | 0.022 | 92 | Filamentous thermophilic cyanobacterium | Filamentous cyanobacterium | DQ471445 | S100 |
| OTU_1755 | 0.022 | 91 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203574 | S46 |
| OTU_72 | 0.011 | 95 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_308 | 0.011 | 96 | Uncultured bacterium clone | BBD affected corals | GU471955 | S41 |
| OTU_466 | 0.011 | 96 | Uncultured bacterium clone | Coral-associated | AF365814 | S42 |
| OTU_1047 | 0.011 | 97 | Uncultured bacterium clone | *Montastraea faveolata* - healthy tissue | FJ203453 | S46 |

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# Appendix C: Table C1 and References (Chapter 3)

**Table C1** Assignments of bacterial genera into metabolic categories (autotrophs, heterotrophs, and potential pathogens). "R" denotes reference for metabolic grouping.

| Autotrophs | R | Heterotrophs | R | Potential pathogens | R |
|---|---|---|---|---|---|
| *Anabaena* | S1 | *Afifella* | S25 | *Acinetobacter* | S65 |
| *Arthrospira* | S2 | *Alicyclobacillus* | S26 | *Aeromonas* | S66 |
| *Calothrix* | S3 | *Anderseniella* | S27 | *Balneatrix* | S67 |
| *Chamaesiphon* | S4 | *Candidatus* Microthrix | S28 | *Bartonella* | S68 |
| *Chrococcidiopsis* | S5 | *Comamonadaceae* | S29 | *Burkholderia* | S69 |
| *Coleochaete* | S6 | *Congregibacter* | S30 | *Candidatus* Amoebophilus | S70 |
| *Crenothrix* | S7 | *Cystobacterineae* | S31 | *Chryseobacterium* | S71 |
| *Gloeobacter* | S8 | *Endozoicomonas* | S32 | *Corynebacterium* | S72 |
| *Leptospirillum* | S9 | *Enhydrobacter* | S33 | *Escherichia* | S73 |
| *Microcrocoleus* | S10 | *Epulopiscium* | S34 | *Geitlerinema** | S74 |
| *Nitrosococcus* | S11 | *Geobacter* | S35 | *Gordonia* | S75 |
| *Pedinomonas* | S12 | *Haliea* | S36 | *Halomonas* | S76 |
| *Pellia* | S13 | *Kangiella* | S37 | *Leptolyngbya** | S74 |
| *Pleurocapsa* | S14 | *Labrenzia* | S38 | *Micrococcus* | S77 |
| *Prochlorococcus* | S15 | *Lactobacillus* | S39 | *Mycoplasma* | S78 |
| *Prochlorothrix* | S16, S17 | *Leucothrix* | S40 | *Oscillatoria** | S74 |
| *Pseudanabaena* | S18 | *Magnetospirillum* | S41 | *Propionibacterium* | S79 |
| *Rhodovibrio* | S19 | *Marinobacter* | S42 | *Pseudomonas* | S80 |
| *Rivularia* | S20 | *Massilia* | S43 | *Ralstonia* | S81 |
| *Scherffelia* | S21 | *Mesorhizobium* | S44 | *Sphingomonas** | S82 |
| *Spirulina* | S22 | *Methylobacterium* | S45 | *Staphylococcus* | S83 |
| *Synechococcus* | S23 | *Microbulbifer* | S38 | | |
| *Trichodesmium* | S24 | *Muricauda* | S46 | | |
| | | *Nannocystineae* | S31 | | |
| | | *Neptunomonas* | S47 | | |
| | | *Nitratireductor* | S48 | | |
| | | *Oceanospirillum* | S49 | | |
| | | *Pelagibius* | S50 | | |
| | | *Pelobacter* | S51 | | |
| | | *Phyllobacteriaceae* | S52 | | |
| | | *Pseudovibrio* | S38 | | |
| | | *Rheinheimera* | S53 | | |
| | | *Rhodobacteraceae* | S54 | | |
| | | *Rhodobium* | S55 | | |
| | | *Rhodopirellula* | S56 | | |
| | | *Rhodospirillaceae* | S57 | | |
| | | *Rhodovulum* | S58 | | |
| | | *Rubrobacter* | S59 | | |
| | | *Ruegeria* | S60 | | |
| | | *Salinicoccus* | S61 | | |
| | | *Thalassospira* | S62 | | |
| | | *Wenxinia* | S63 | | |
| | | *Wolbachia* | S64 | | |

***Geitlerinema*, *Leptolyngbya*, *Oscillatoria,* and *Sphingomonas* are coral-specific potential pathogens. The first three genera are associated with black band disease.

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# Appendix D: Tables D1-D9 (Chapter 3)

**Table D1** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each baseline coral sample from control plots.

| Taxa | Coral Sample | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Enhydrobacter* | 7.06 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Pseudomonas* | 27.82 | 1.57 | 2.97 | 0.11 | 0.39 | 0.79 | 0.13 | 0.00 |
| *Candidatus* Amoebophilus | 0.00 | 0.00 | 0.00 | 0.00 | 4.69 | 16.79 | 0.13 | 53.63 |
| *Microbulbifer* | 0.00 | 0.23 | 0.12 | 4.63 | 0.00 | 0.73 | 0.39 | 0.00 |
| *Neptunomonas* | 2.82 | 49.71 | 54.44 | 5.99 | 35.09 | 36.62 | 19.34 | 1.34 |
| *Gloeotrichia* | 0.00 | 0.00 | 0.00 | 0.00 | 4.20 | 2.49 | 2.50 | 4.39 |
| *Marinobacter* | 0.42 | 16.29 | 13.54 | 0.32 | 6.74 | 5.54 | 3.68 | 0.76 |
| *Staphylococcus* | 3.25 | 0.02 | 0.02 | 0.00 | 0.00 | 1.09 | 0.79 | 0.00 |
| *Rubrobacter* | 0.00 | 0.00 | 0.00 | 0.00 | 2.15 | 0.00 | 0.00 | 0.00 |
| *Sphingomonas* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 10.50 |
| *Propionibacterium* | 5.79 | 0.00 | 0.02 | 0.00 | 3.13 | 0.00 | 0.26 | 1.72 |
| *Geitlerinema* | 0.00 | 0.17 | 0.21 | 0.21 | 0.29 | 0.30 | 1.05 | 8.59 |
| *Congregibacter* | 0.00 | 0.90 | 0.06 | 13.04 | 0.00 | 2.68 | 0.00 | 0.00 |
| *Methylobacterium* | 18.36 | 0.00 | 0.00 | 0.11 | 9.87 | 0.00 | 0.39 | 0.00 |
| *Pelobacter* | 0.00 | 0.00 | 0.08 | 0.00 | 2.93 | 0.00 | 0.00 | 0.00 |
| *Corynebacterium* | 5.65 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Oceanospirillum* | 0.56 | 8.68 | 13.36 | 69.40 | 8.80 | 23.60 | 23.55 | 1.91 |
| *Lactobacillus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.76 | 0.00 |
| *Rheinheimera* | 24.72 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Halomonas* | 0.56 | 21.27 | 13.21 | 1.05 | 8.99 | 5.29 | 3.42 | 0.00 |
| *Alicyclobacillus* | 2.54 | 0.13 | 0.02 | 0.95 | 8.70 | 0.61 | 26.58 | 14.69 |
| *Thalassospira* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 3.29 | 0.00 |
| *Aeromonas* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.11 | 0.00 |

**Table D2** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each baseline coral sample from *S. apicalis*' territories.

| Taxa | Coral Sample | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Rhodovibrio* | 0.00 | 0.00 | 0.00 | 0.00 | 3.28 | 0.00 | 0.00 |
| *Pseudomonas* | 0.40 | 10.64 | 0.73 | 1.48 | 1.50 | 2.19 | 1.61 |
| *Candidatus* Amoebophilus | 0.10 | 0.00 | 3.85 | 0.00 | 5.87 | 0.00 | 4.44 |
| *Neptunomonas* | 33.30 | 2.23 | 41.28 | 13.05 | 12.57 | 28.69 | 48.06 |
| *Gloeotrichia* | 9.43 | 8.42 | 1.47 | 0.25 | 6.01 | 0.00 | 1.14 |
| *Chryseobacterium* | 0.00 | 2.48 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Marinobacter* | 1.50 | 0.00 | 1.28 | 6.16 | 3.83 | 6.57 | 11.22 |
| *Bartonella* | 0.00 | 0.25 | 0.00 | 20.69 | 0.41 | 0.00 | 0.00 |
| *Gordonia* | 0.00 | 7.43 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Propionibacterium* | 0.50 | 0.00 | 4.40 | 8.37 | 0.00 | 2.99 | 0.38 |
| *Ruegeria* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.99 | 0.00 |
| *Prochlorococcus* | 6.22 | 0.00 | 5.69 | 3.45 | 2.05 | 0.20 | 0.00 |
| *Pelobacter* | 0.00 | 0.00 | 0.00 | 3.69 | 0.41 | 1.99 | 0.03 |
| *Corynebacterium* | 0.00 | 9.65 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 |
| *Salinicoccus* | 0.00 | 2.48 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Oceanospirillum* | 36.51 | 25.74 | 15.96 | 18.47 | 55.60 | 38.25 | 10.87 |
| *Epulopiscium* | 0.00 | 0.00 | 2.20 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Halomonas* | 1.40 | 0.00 | 0.55 | 5.91 | 2.05 | 4.78 | 18.36 |
| *Alicyclobacillus* | 1.60 | 0.00 | 18.72 | 8.87 | 2.32 | 1.39 | 1.17 |
| *Leucothrix* | 0.00 | 26.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

**Table D3** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each baseline coral sample from *S. nigricans*' territories.

| Taxa | Coral Sample | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Ralstonia* | 2.31 | 0.00 | 0.84 | 2.02 | 0.06 | 0.24 | 1.28 | 0.47 | 3.42 |
| *Marinobacter* | 2.57 | 17.12 | 6.90 | 3.95 | 15.15 | 15.26 | 13.76 | 13.22 | 6.12 |
| *Pelobacter* | 0.13 | 0.19 | 3.23 | 3.34 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Oceanospirillum* | 8.35 | 5.07 | 21.74 | 12.26 | 6.56 | 1.36 | 2.68 | 4.75 | 7.68 |
| *Congregibacter* | 3.98 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Magnetospirillum* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 23.59 |
| *Neptunomonas* | 20.74 | 60.37 | 46.42 | 40.20 | 62.99 | 59.86 | 54.19 | 46.58 | 25.15 |
| *Acinetobacter* | 47.64 | 8.91 | 11.63 | 32.29 | 7.23 | 17.64 | 20.97 | 21.22 | 27.27 |
| *Candidatus* Amoebophilus | 9.21 | 0.00 | 5.85 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Halomonas* | 0.60 | 5.74 | 1.99 | 1.27 | 6.67 | 3.40 | 5.50 | 4.43 | 1.89 |
| *Gloeotrichia* | 0.39 | 0.00 | 0.47 | 0.04 | 0.00 | 0.00 | 0.00 | 6.88 | 0.00 |

**Table D4** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after six months of transplantation from control plots.

| Taxa | Coral Sample | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Trichodesmium* | 0.00 | 0.19 | 9.99 | 0.00 | 1.43 | 0.00 | 0.12 |
| *Synechococcus* | 0.34 | 0.14 | 3.28 | 0.00 | 0.71 | 0.58 | 2.55 |
| *Marinobacter* | 12.55 | 18.07 | 0.08 | 0.28 | 0.89 | 0.07 | 0.54 |
| *Pelobacter* | 1.27 | 2.13 | 0.00 | 2.15 | 0.00 | 0.00 | 0.22 |
| *Spirulina* | 0.07 | 0.00 | 1.20 | 0.00 | 2.32 | 0.66 | 0.52 |
| *Anabaena* | 0.48 | 0.19 | 2.96 | 0.00 | 2.14 | 12.35 | 8.49 |
| *Geitlerinema* | 0.11 | 0.05 | 0.40 | 0.00 | 1.07 | 2.34 | 3.15 |
| *Oceanospirillum* | 1.45 | 2.13 | 0.00 | 14.26 | 0.00 | 0.00 | 0.00 |
| *Ruegeria* | 0.41 | 0.00 | 2.32 | 0.00 | 1.60 | 0.58 | 1.00 |
| *Afifella* | 0.04 | 0.00 | 0.00 | 0.00 | 0.89 | 4.09 | 0.86 |
| *Neptunomonas* | 32.48 | 58.86 | 0.00 | 3.18 | 0.00 | 0.07 | 0.02 |
| *Acinetobacter* | 14.00 | 9.66 | 0.48 | 50.59 | 0.00 | 0.00 | 0.06 |
| *Oscillatoria* | 1.90 | 0.00 | 27.98 | 0.00 | 24.24 | 37.72 | 17.63 |
| *Bartonella* | 17.39 | 0.00 | 0.08 | 0.00 | 0.89 | 0.07 | 1.55 |
| *Leptolyngbya* | 0.15 | 0.07 | 20.86 | 0.00 | 16.40 | 7.09 | 10.70 |
| *Rhodopirellula* | 0.00 | 0.00 | 0.24 | 0.14 | 2.32 | 1.24 | 1.22 |
| *Mesorhizobium* | 0.60 | 0.00 | 0.16 | 0.00 | 2.67 | 1.17 | 0.80 |
| *Candidatus* Amoebophilus | 4.54 | 0.00 | 0.40 | 0.21 | 0.36 | 0.37 | 0.30 |
| *Pseudanabaena* | 0.00 | 0.00 | 0.00 | 0.00 | 5.70 | 1.17 | 0.12 |
| *Halomonas* | 3.28 | 5.53 | 0.00 | 0.00 | 0.18 | 0.00 | 0.10 |
| *Labrenzia* | 0.71 | 0.00 | 0.56 | 0.00 | 1.43 | 1.39 | 2.47 |
| *Kangiella* | 0.00 | 0.00 | 0.16 | 9.41 | 0.00 | 0.00 | 0.02 |
| *Escherichia* | 0.00 | 0.00 | 0.00 | 14.67 | 0.00 | 0.07 | 0.00 |
| *Rhodovibrio* | 0.15 | 0.00 | 0.56 | 0.00 | 0.00 | 0.66 | 2.03 |
| *Gloeotrichia* | 2.38 | 0.00 | 0.72 | 0.00 | 3.92 | 0.58 | 4.32 |
| *Prochlorothrix* | 0.07 | 0.00 | 1.28 | 0.00 | 0.71 | 0.95 | 2.17 |

**Table D5** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after six months of transplantation from *S. apicalis*' territories.

| Taxa | Coral Sample | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| *Trichodesmium* | 0.00 | 0.06 | 0.17 | 0.00 | 0.31 | 2.63 | 0.30 | 1.75 |
| *Ralstonia* | 11.02 | 0.04 | 0.91 | 1.78 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Synechococcus* | 0.25 | 0.08 | 0.02 | 0.00 | 2.08 | 3.57 | 1.69 | 2.21 |
| *Marinobacter* | 0.33 | 18.94 | 21.10 | 8.08 | 0.23 | 0.66 | 0.70 | 0.93 |
| *Pelobacter* | 0.00 | 0.61 | 0.47 | 5.37 | 0.62 | 0.00 | 0.30 | 1.05 |
| *Geobacter* | 3.14 | 0.00 | 0.09 | 0.42 | 0.00 | 0.00 | 0.60 | 0.00 |
| *Gloeobacter* | 0.00 | 0.00 | 0.00 | 0.00 | 0.54 | 0.00 | 0.20 | 8.16 |
| *Spirulina* | 0.00 | 0.00 | 0.00 | 0.00 | 6.01 | 2.73 | 2.49 | 4.55 |
| *Anabaena* | 0.00 | 0.55 | 0.00 | 0.00 | 8.64 | 5.93 | 12.62 | 8.04 |
| *Geitlerinema* | 0.00 | 0.00 | 0.00 | 0.00 | 1.93 | 1.03 | 2.19 | 1.63 |
| *Oceanospirillum* | 1.61 | 3.52 | 2.70 | 10.41 | 0.15 | 0.00 | 0.00 | 0.00 |
| *Ruegeria* | 0.77 | 0.06 | 0.00 | 0.06 | 2.78 | 1.41 | 0.70 | 1.75 |
| *Wolbachia* | 0.00 | 0.00 | 0.00 | 0.16 | 2.54 | 1.41 | 0.50 | 0.00 |
| *Neptunomonas* | 0.54 | 63.77 | 51.38 | 39.20 | 0.00 | 0.38 | 0.00 | 0.12 |
| *Acinetobacter* | 73.11 | 5.47 | 14.16 | 21.36 | 0.15 | 0.00 | 0.10 | 0.00 |
| *Candidatus* Microthrix | 0.00 | 0.00 | 0.00 | 0.06 | 2.39 | 0.56 | 0.00 | 1.05 |
| *Oscillatoria* | 0.02 | 0.55 | 0.02 | 0.00 | 14.80 | 16.65 | 20.97 | 14.34 |
| *Prochlorococcus* | 0.08 | 0.00 | 0.00 | 0.00 | 2.00 | 0.09 | 0.00 | 3.73 |
| *Leptolyngbya* | 0.08 | 0.19 | 0.00 | 0.03 | 14.34 | 7.24 | 22.07 | 7.23 |
| *Halomonas* | 0.00 | 3.77 | 5.96 | 2.94 | 0.00 | 0.00 | 0.10 | 0.00 |
| *Labrenzia* | 0.13 | 0.15 | 0.11 | 0.00 | 0.46 | 2.16 | 2.09 | 0.93 |
| *Rhodovibrio* | 0.00 | 0.00 | 0.02 | 0.00 | 0.23 | 0.94 | 0.50 | 3.15 |
| *Chamaesiphon* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.19 | 2.58 | 1.86 |
| *Gloeotrichia* | 0.00 | 0.00 | 0.00 | 1.07 | 1.00 | 2.26 | 0.99 | 1.63 |

**Table D6** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after six months of transplantation from *S. nigricans*' territories.

| Taxa | Coral Sample | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Balneatrix* | 2.16 | 0.79 | 2.12 | 2.12 | 1.66 | 4.47 | 0.14 | 0.03 | 1.95 |
| Rhodobacteraceae | 2.65 | 4.86 | 7.41 | 8.73 | 4.62 | 6.50 | 0.56 | 0.39 | 7.00 |
| *Rhodobium* | 1.94 | 0.12 | 1.15 | 1.92 | 2.70 | 1.72 | 0.14 | 0.03 | 2.28 |
| *Anderseniella* | 0.35 | 2.32 | 1.02 | 0.56 | 0.50 | 0.23 | 0.00 | 0.08 | 0.39 |
| *Pedinomonas* | 0.00 | 0.46 | 0.13 | 0.70 | 0.68 | 0.13 | 8.11 | 0.49 | 1.44 |
| *Crenothrix* | 0.77 | 2.28 | 2.81 | 5.05 | 3.56 | 3.70 | 0.35 | 0.00 | 3.00 |
| *Prochlorothrix* | 0.35 | 0.58 | 2.12 | 1.19 | 0.27 | 0.08 | 0.35 | 0.00 | 0.30 |
| *Pleurocapsa* | 1.23 | 0.66 | 6.16 | 2.26 | 2.43 | 2.93 | 0.35 | 0.03 | 1.23 |
| *Nitratireductor* | 0.09 | 0.00 | 0.33 | 0.31 | 0.15 | 0.10 | 6.01 | 0.00 | 0.21 |
| *Leptolyngbya* | 3.81 | 0.62 | 5.80 | 5.69 | 3.53 | 5.09 | 2.52 | 0.03 | 5.83 |
| *Endozoicomonas* | 0.07 | 50.73 | 0.26 | 0.07 | 0.86 | 0.05 | 45.98 | 88.78 | 0.00 |
| *Prochlorococcus* | 0.04 | 1.37 | 1.41 | 0.45 | 2.40 | 0.10 | 1.12 | 0.33 | 0.45 |
| Nannocystineae | 3.11 | 0.75 | 1.23 | 1.90 | 1.96 | 2.26 | 0.42 | 0.05 | 2.22 |
| *Arthrospira* | 0.57 | 0.12 | 2.40 | 0.22 | 1.01 | 0.82 | 0.70 | 0.00 | 0.45 |
| Cystobacterineae | 0.62 | 4.86 | 1.99 | 0.47 | 0.50 | 0.10 | 1.40 | 0.13 | 0.36 |
| Comamonadaceae | 0.90 | 0.58 | 0.72 | 1.10 | 1.22 | 2.36 | 0.84 | 0.08 | 5.68 |
| Phyllobacteriaceae | 2.78 | 0.95 | 0.64 | 1.22 | 1.24 | 0.82 | 0.07 | 0.03 | 0.93 |
| *Chroococcidiopsis* | 0.75 | 0.29 | 2.15 | 2.69 | 1.72 | 4.96 | 0.21 | 0.00 | 2.55 |
| *Wenxinia* | 0.82 | 2.20 | 1.92 | 1.19 | 1.27 | 0.54 | 0.77 | 0.08 | 0.84 |
| *Micrococcus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.80 | 0.00 | 0.00 |
| *Oscillatoria* | 5.31 | 0.71 | 1.33 | 2.89 | 1.60 | 11.74 | 0.63 | 0.00 | 0.87 |
| Rhodospirillaceae | 8.38 | 0.62 | 4.91 | 6.20 | 7.47 | 5.70 | 0.28 | 0.15 | 6.73 |
| *Rivularia* | 4.39 | 3.57 | 9.20 | 11.24 | 8.45 | 3.06 | 0.98 | 0.05 | 3.06 |
| *Leptospirillum* | 2.05 | 0.04 | 1.28 | 0.57 | 1.84 | 1.49 | 0.00 | 0.00 | 2.16 |

**Table D7** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after one year of transplantation from control plots.

| Taxa | Coral Sample | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Haliea* | 1.21 | 0.13 | 0.00 | 0.17 | 0.99 | 0.19 | 0.36 | 0.39 | 2.03 |
| *Balneatrix* | 4.38 | 0.28 | 0.00 | 0.04 | 2.13 | 2.35 | 1.97 | 0.42 | 3.32 |
| *Muricauda* | 1.11 | 0.04 | 0.00 | 0.00 | 2.57 | 1.20 | 0.87 | 1.00 | 0.65 |
| Rhodobacteraceae | 6.26 | 0.61 | 0.00 | 1.86 | 7.22 | 9.39 | 4.30 | 3.80 | 4.50 |
| *Pedinomonas* | 0.25 | 0.43 | 0.06 | 0.72 | 1.03 | 3.73 | 2.02 | 1.58 | 1.74 |
| *Crenothrix* | 3.82 | 0.09 | 0.00 | 0.13 | 0.94 | 8.49 | 14.67 | 1.62 | 1.10 |
| *Pleurocapsa* | 2.44 | 0.04 | 0.00 | 0.21 | 1.19 | 1.61 | 0.79 | 0.70 | 1.27 |
| *Ruegeria* | 1.16 | 0.17 | 0.34 | 0.30 | 0.92 | 0.57 | 0.74 | 0.93 | 2.34 |
| *Leptolyngbya* | 9.44 | 0.19 | 0.00 | 0.38 | 2.59 | 3.43 | 2.42 | 2.06 | 3.83 |
| *Burkholderia* | 0.03 | 0.19 | 0.26 | 2.53 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 |
| *Endozoicomonas* | 0.06 | 86.58 | 94.78 | 7.34 | 0.10 | 0.03 | 0.02 | 0.22 | 0.23 |
| *Microcoleus* | 0.08 | 0.09 | 0.00 | 0.00 | 0.21 | 0.03 | 0.07 | 0.65 | 5.40 |
| *Geitlerinema* | 0.83 | 0.00 | 0.00 | 0.00 | 1.38 | 1.56 | 2.07 | 0.62 | 0.39 |
| *Anabaena* | 0.76 | 0.04 | 0.00 | 0.04 | 2.91 | 0.73 | 2.06 | 1.58 | 0.76 |
| *Calothrix* | 9.47 | 0.06 | 0.00 | 0.00 | 1.05 | 0.13 | 0.63 | 0.02 | 0.25 |
| *Prochlorococcus* | 2.29 | 0.30 | 0.09 | 0.51 | 0.59 | 1.40 | 0.86 | 0.49 | 0.37 |
| *Scherffelia* | 0.67 | 0.43 | 0.40 | 17.30 | 0.64 | 1.47 | 2.64 | 2.78 | 2.22 |
| Nannocystineae | 3.30 | 0.09 | 0.00 | 0.08 | 1.62 | 0.79 | 0.70 | 0.57 | 3.52 |
| *Trichodesmium* | 0.17 | 0.00 | 0.00 | 0.00 | 2.36 | 0.14 | 0.05 | 0.00 | 0.08 |
| *Arthrospira* | 0.33 | 0.00 | 0.00 | 2.95 | 0.23 | 0.84 | 0.10 | 0.00 | 0.00 |
| Cystobacterineae | 1.07 | 0.32 | 2.38 | 2.49 | 1.19 | 0.90 | 0.51 | 0.39 | 0.51 |
| *Pseudovibrio* | 0.00 | 0.00 | 0.00 | 0.00 | 6.40 | 0.00 | 0.21 | 0.06 | 0.00 |
| *Acinetobacter* | 0.02 | 0.04 | 0.09 | 34.56 | 0.00 | 0.02 | 0.10 | 0.12 | 0.03 |
| *Rhodovulum* | 0.07 | 0.00 | 0.00 | 0.00 | 0.06 | 0.06 | 0.05 | 3.21 | 0.11 |
| Comamonadaceae | 1.84 | 0.06 | 0.00 | 0.00 | 0.92 | 1.28 | 0.43 | 0.51 | 2.05 |
| *Chroococcidiopsis* | 1.88 | 1.06 | 0.00 | 13.59 | 1.40 | 3.80 | 5.95 | 4.20 | 1.77 |
| *Wenxinia* | 1.62 | 0.17 | 0.00 | 0.00 | 1.50 | 0.98 | 1.08 | 3.72 | 1.21 |
| *Pelagibius* | 0.15 | 0.09 | 0.00 | 0.00 | 0.39 | 0.55 | 0.60 | 3.74 | 0.14 |
| *Oscillatoria* | 1.70 | 0.26 | 0.00 | 0.34 | 1.42 | 12.15 | 9.32 | 19.34 | 1.32 |
| Rhodospirillaceae | 1.63 | 1.00 | 0.09 | 0.08 | 5.62 | 4.91 | 6.61 | 3.40 | 3.88 |
| *Rivularia* | 6.97 | 0.11 | 0.00 | 0.34 | 9.60 | 10.31 | 2.40 | 2.09 | 5.21 |

**Table D8** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after one year of transplantation from *S. apicalis*' territories.

| Taxa | Coral Sample | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| *Balneatrix* | 1.09 | 0.97 | 3.33 | 0.10 | 0.00 | 5.66 | 1.55 | 0.00 | 0.38 |
| *Muricauda* | 0.08 | 0.47 | 0.00 | 0.03 | 0.19 | 0.80 | 0.39 | 2.66 | 0.28 |
| Rhodobacteraceae | 3.71 | 1.75 | 3.66 | 0.00 | 2.52 | 9.04 | 3.79 | 3.25 | 3.18 |
| *Rhodobium* | 2.18 | 0.90 | 0.29 | 0.00 | 0.23 | 1.02 | 0.52 | 0.42 | 1.62 |
| *Crenothrix* | 1.51 | 0.00 | 19.84 | 0.00 | 1.21 | 12.76 | 1.65 | 0.67 | 1.65 |
| *Pleurocapsa* | 1.68 | 1.98 | 0.33 | 0.00 | 0.14 | 3.04 | 2.30 | 0.25 | 2.68 |
| *Ruegeria* | 0.72 | 2.05 | 0.14 | 0.23 | 0.14 | 1.05 | 2.78 | 1.58 | 1.08 |
| *Massilia* | 0.00 | 3.92 | 0.00 | 0.00 | 0.05 | 0.02 | 0.00 | 0.58 | 0.00 |
| *Bartonella* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 15.34 |
| *Leptolyngbya* | 1.80 | 0.50 | 0.14 | 0.00 | 0.14 | 4.83 | 3.50 | 0.58 | 3.36 |
| *Burkholderia* | 0.00 | 0.45 | 3.19 | 0.30 | 0.05 | 0.00 | 0.13 | 6.99 | 0.00 |
| *Endozoicomonas* | 0.47 | 42.92 | 58.33 | 92.70 | 83.52 | 0.07 | 45.21 | 14.65 | 0.47 |
| *Nitrosococcus* | 2.56 | 0.22 | 0.67 | 0.03 | 0.23 | 0.67 | 0.16 | 0.58 | 1.06 |
| *Anabaena* | 2.00 | 0.09 | 0.00 | 0.00 | 0.00 | 0.50 | 0.19 | 0.00 | 5.39 |
| *Calothrix* | 0.06 | 0.30 | 1.38 | 0.00 | 0.70 | 5.78 | 0.13 | 0.00 | 0.24 |
| *Scherffelia* | 1.97 | 0.67 | 0.00 | 0.07 | 0.00 | 0.20 | 0.94 | 15.15 | 1.06 |
| Cystobacterineae | 0.28 | 0.00 | 0.00 | 1.58 | 0.51 | 0.12 | 0.55 | 2.83 | 0.59 |
| *Acinetobacter* | 0.04 | 9.07 | 0.00 | 0.03 | 1.03 | 0.00 | 0.00 | 0.00 | 0.02 |
| Phyllobacteriaceae | 0.72 | 1.23 | 0.33 | 0.00 | 0.00 | 0.87 | 1.23 | 0.92 | 2.92 |
| *Chroococcidiopsis* | 3.63 | 0.24 | 0.05 | 0.00 | 0.00 | 2.52 | 3.85 | 15.40 | 3.20 |
| *Wenxinia* | 0.09 | 0.86 | 0.05 | 0.00 | 0.56 | 2.14 | 1.88 | 1.08 | 0.64 |
| *Oscillatoria* | 16.20 | 0.00 | 0.10 | 0.00 | 1.68 | 2.59 | 0.19 | 0.58 | 5.72 |
| Rhodospirillaceae | 9.60 | 1.85 | 0.00 | 0.00 | 0.05 | 1.54 | 0.71 | 0.00 | 9.22 |
| *Ralstonia* | 0.00 | 0.13 | 0.10 | 0.23 | 0.00 | 0.00 | 0.03 | 6.16 | 0.05 |
| *Rivularia* | 0.38 | 12.81 | 0.38 | 0.00 | 1.40 | 8.30 | 1.29 | 0.17 | 1.25 |

**Table D9** Assignments of OTUs with at least a two percent relative abundance to genus or next lowest taxonomical unit and their respective relative abundance in each coral sample after one year of transplantation from *S. nigricans*' territories.

| Taxa | Coral Sample | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| *Rivularia* | 4.41 | 0.15 | 0.30 | 0.29 | 0.90 | 0.27 | 0.50 | 0.00 | 0.85 | 1.53 |
| Rhodobacteraceae | 10.62 | 12.50 | 3.62 | 8.85 | 7.60 | 3.43 | 4.54 | 0.03 | 5.41 | 14.83 |
| *Mycoplasma* | 3.49 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 |
| *Microcoleus* | 0.49 | 2.34 | 0.00 | 1.89 | 0.31 | 0.44 | 0.79 | 0.03 | 0.07 | 0.10 |
| *Chroococcidiopsis* | 3.10 | 3.50 | 1.15 | 4.89 | 2.69 | 2.62 | 4.68 | 0.17 | 3.21 | 3.92 |
| *Anabaena* | 1.58 | 0.83 | 2.93 | 2.68 | 0.55 | 1.62 | 1.76 | 0.07 | 0.68 | 3.56 |
| *Pellia* | 0.22 | 0.00 | 0.00 | 1.51 | 0.23 | 0.10 | 6.38 | 0.14 | 0.00 | 0.00 |
| *Pseudovibrio* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.06 | 7.62 | 0.00 |
| *Ruegeria* | 1.58 | 0.56 | 12.20 | 0.84 | 2.22 | 0.34 | 0.76 | 0.00 | 4.31 | 0.80 |
| *Crenothrix* | 8.55 | 12.60 | 0.36 | 5.13 | 13.84 | 3.06 | 1.08 | 0.03 | 1.71 | 15.23 |
| *Rhodobium* | 0.71 | 0.95 | 0.16 | 1.28 | 0.31 | 0.56 | 1.05 | 0.00 | 2.28 | 0.40 |
| Nannocystineae | 5.50 | 7.20 | 3.06 | 4.89 | 4.33 | 2.16 | 2.55 | 0.03 | 4.27 | 5.19 |
| *Pleurocapsa* | 1.74 | 3.41 | 0.92 | 2.42 | 0.94 | 0.93 | 1.87 | 0.01 | 2.56 | 0.93 |
| *Calothrix* | 11.55 | 2.07 | 18.45 | 2.13 | 1.52 | 0.07 | 0.94 | 0.04 | 2.85 | 14.83 |
| *Oscillatoria* | 5.34 | 19.68 | 0.13 | 17.68 | 1.72 | 8.06 | 2.43 | 0.04 | 0.71 | 6.05 |
| Phyllobacteriaceae | 2.56 | 1.31 | 1.28 | 0.84 | 1.72 | 1.18 | 1.00 | 0.07 | 1.89 | 0.70 |
| *Scherffelia* | 3.59 | 0.34 | 2.43 | 4.25 | 4.60 | 2.28 | 14.81 | 0.11 | 3.03 | 1.63 |
| *Leptolyngbya* | 1.53 | 1.36 | 1.84 | 2.74 | 1.01 | 0.88 | 1.73 | 0.01 | 1.07 | 1.03 |
| *Balneatrix* | 7.24 | 3.09 | 2.93 | 3.20 | 2.81 | 1.59 | 1.70 | 0.01 | 7.51 | 2.86 |
| *Endozoicomonas* | 0.00 | 0.51 | 23.72 | 0.17 | 1.48 | 0.00 | 0.00 | 96.25 | 17.09 | 0.00 |
| *Nitratireductor* | 0.00 | 0.00 | 1.28 | 0.03 | 0.04 | 0.00 | 0.09 | 0.00 | 6.02 | 0.00 |
| *Pedinomonas* | 1.20 | 0.02 | 1.45 | 2.13 | 20.47 | 29.54 | 3.83 | 0.00 | 3.60 | 2.26 |
| *Coleochaete* | 0.71 | 0.00 | 0.07 | 5.10 | 13.96 | 24.74 | 23.62 | 0.10 | 0.00 | 0.33 |
| Rhodospirillaceae | 1.63 | 4.84 | 0.69 | 3.26 | 1.72 | 1.27 | 3.92 | 0.06 | 1.89 | 1.99 |
| Comamonadaceae | 1.91 | 3.21 | 0.82 | 3.12 | 0.70 | 1.25 | 0.82 | 0.01 | 0.57 | 1.10 |