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Effects of coral-dwelling damselfishes' abundances and diversity on host coral dynamics

Thesis submitted by
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STATEMENT OF ETHICS AND PERMITS

This research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in *the James Cook University Code for the Responsible Conduct of Research (2007)*, *James Cook University Animal Welfare and Ethics Statement (2018)*, *James Cook University Standard Practices and Guidelines (2007), James Cook University Health, Safety, and Environment Management System (2017), and Great Barrier Reef Marine Park Authority Research Guidelines (2017).*

Specifically, this project was implemented in accordance with James Cook University Animal Ethics, The Great Barrier Reef Marine Park Authority, and Queensland Government Fisheries permits.

Ethics:
- Animal Ethics A2351 (*Impacts of aggregating fish on nutrients, sediments, and lifetime reproductive output*)
- Animal Ethics A2207 (*The study of growth rates, demography and life history of reef fishes*)
- Animal Ethics A2186 (*Effects of fish on coral physiology, growth, and survival)*

for research or teaching involving animals by the Human Research Ethics Committee at James Cook University, in compliance with the Australian Code for Practice for the Care and Use of Animals for Scientific Purposes, and Queensland Animal Care and Protection Act 2001.

Great Barrier Reef Marine Park Permits:
- Great Barrier Marine Park Authority G13/35909.1
- Great Barrier Marine Park Authority G15/37657.1
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for use of and entry to zones in the Amalgamated Great Barrier Reef Marine Park section (as established by the Great Barrier Reef Marine Park Act 1975, and the Great Barrier Reef Coast Marine Park (as established by the Marine Parks Act 2004 (QLD)) in accordance with the details set out herein.

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GENERAL ABSTRACT

Interspecific interactions, particularly positive interactions, between organisms and their physical environment are important forces in shaping ecological diversity and ecosystem structure. In coral reef ecosystems, the associations between habitat-forming corals and coral reef fishes have critical implications for the structure and function of coral reef ecosystems. Coral-dwelling damselfishes rely on branching corals for shelter and confer benefits to their host corals that promote enhanced performance, growth, and colony health. However, there is variability (in strength and symmetry) in both fish-derived and coral responses to abiotic factors and partner ecology. Global environmental change is likely to considerably disrupt fish-coral interactions on reefs through reef degradation, coastal sedimentation, and severe widespread bleaching events. Prior to collapse, however, fish-coral interactions have the potential to act as stabilizing forces on reefs, promoting coexistence, and enhancing the coral holobiont during accelerated environmental change. Thus, the overall focus of this thesis was to understand the relationship between coral-dwelling damselfishes and their small branching coral colony hosts. Specifically, I investigated the prevalence of these fish-coral associations across space, the variations in the intensity of damselfish-coral interactions over time and evaluated the influence of these coral-dwelling damselfishes on the health of their host corals under two types of environmental stress.

In **Chapter 2**, I addressed one of the critical first steps to understanding the magnitude by which coral-dwelling damselfishes impact coral health by establishing the abundance and prevalence of select, fish-coral interaction pairs across different coral colonies, habitats, and seascapes. Through a series of underwater surveys at locations spanning > 1700 km of the Great Barrier Reef, I aimed to: (a) determine if suitable coral habitat governs patterns in damselfishes'

distributions and abundances, and (b) quantify variations in damselfish species-specific biomass among coral colonies species. The abundance of fish-coral associations varied with respect to exposure level and habitat with an overall average prevalence of ~30% occupancy, with biomass hotspots confined to sheltered lagoon sand patch and reef slope habitats. Further analysis of colony microstructure traits revealed that isolation from adjacent colonies, branch spacing patterns, and colony orientation governed fine-scale usage. The research presented in Chapter 2 illustrates that coral occupancy (coral-dwelling or sole habitat use) varies significantly by damselfish species, and subsequent fish-derived services are confined to specific reef habitats.

While coral-dwelling damselfishes are intimately associated with branching corals, interspecific behavioural variation can alter the nature and strength of these interactions with corals, thereby altering the dynamics of small-scale coral association networks and benefits conferred to host corals. **Chapter 3** used *in-situ* observations to explore interspecific differences in diurnal and nocturnal behaviour among five coral-dwelling damselfish species. Resident damselfishes displayed marked differences in colony interaction and usage, with *Dasycllus* species exhibiting frequent and sustained interactions with host corals. *Pomacentrus* species displayed weaker associations and behaviours consistent with commensalistic interactions. Host coral bleaching status altered damselfishes' interactions with colonies, forecasting shifting interchanges between fishes and corals under future stress conditions. Quantifying these focal fishes' behaviours through small-scale observations is relevant to interspecific interactions and coral holobiont persistence, as environmental stressors alter the prevalence of coral-damselfish interactions and the intensity of associated mutualistic services.

Global environmental change, particularly in the forms of amplified sedimentation and elevated sea-surface temperatures, could pose to significantly alter how these fish-coral interactions function in isolation and as components of the entire coral holobiont. Many species interactions, mutualistic ones in particular, arise from the ability of species to modify local conditions and diminish stress for their own benefit as well as for their partners, thereby conferring resilience. In **Chapters 4 and 5**, I evaluated the influence of coral-dwelling fishes (*Dascyllus aruanus* and *Pomacentrus moluccensis*, selected due to their abundance and behaviours exhibited in Chapters 2 and 3) on the health of their host corals (*Pocillopora damicornis*) under two types of environmental stress. When exposing the fish-coral system to daily manipulated severe sedimentation stress in **Chapter 4**, damselfishes were able to significantly reduce sediment accumulation and sediment-induced partial mortality on coral hosts, 2-10-fold more, compared with fish-vacant colonies. Colonies with *Dascyllus aruanus* exhibited up to two-fold higher chlorophyll and protein concentrations under sediment conditions compared with other treatments, reinforcing the positive nature and benefits connected with a frequent and sustained (strong) interaction with host colonies. Further linking these results to the behaviour of the damselfish species (Chapter 3), diurnal and nocturnal position of *D. aruanus* and *P. moluccensis* in aquaria, helped explain the species-specific services rendered. In Chapter 4, I demonstrated that fish mutualisms may be critical for maintaining coral health and resilience under chronic and severe sediment stress and indicated that some mutualistic or facilitative interactions may become more important for species persistence as stress levels increase.

Many studies have independently investigated the effects of increased sea-surface temperatures on fishes and coral bleaching, but little is known about the impacts of coral-dwelling damselfishes on the health of their coral hosts, during and after a thermal-bleaching event. With many services that damselfishes provide to their host colonies, especially those that mimic natural mechanisms mitigating external stress, in **Chapter 5**, I hypothesized that colonies with symbiont damselfishes would bleach less and recover more quickly during thermal bleaching events, compared to vacant corals, due to key services of enhanced water flow and nutrients. During a natural thermal anomaly, it is evident that *P. damicornis* with damselfish that are subjected to temperature stress have higher *Symbiodinium* (+25%), chlorophyll (+30%), and tissue proteins (+57%). These results were reflected in a manipulated thermal bleaching experiment in aquaria, where corals with damselfish subjected to temperature stress again had significantly more *Symbiodinium* (five-fold), chlorophyll (nine-fold), and tissue biomass (three-fold) compared with vacant colonies during the recovery period. Tissue component differences translated into considerably higher photosynthetic rates in *P. damicornis* colonies with fish, compared with non-damselfish colonies. However, from the *in-situ* results from the 2016 bleaching event, it is evident that this fish influence on colony susceptibility/resilience and recovery operates only under moderate level stressors, as severe bleaching events overwhelm the coral holobiont, rendering fish-services insufficient to maintain coral health.

This thesis reveals the importance of resident fishes as a fundamental aspect of the dynamic interface between corals and the abiotic environment. Although limited spatially across reef seascapes, and heavily dependent upon the species-specific behaviour of fish partners, these findings suggest that certain coral-dwelling damselfishes have the ability to mediate the impacts of environmental change with regards to coral colony stress susceptibility and survival.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Interactions drive ecosystem diversity and function

Complex interactions between species and their local environments structure ecological communities (Bolker et al. 2003; Bairey et al. 2016). These associations exist at the micro- and macro-scale, they range from being negative to positive in nature, and they can destabilize or help to maintain community composition and biodiversity (Bronstein 1994a, b; Bairey et al. 2016; van de Leemput et al. 2016). Positive interactions, often containing multi-level symbiotic networks of co-evolved partners, influence key processes such as resource acquisition, protection, and transfer of nutrients (Bronstein 1994a, b; Hacker and Gaines 1997; Schmitt and Holbrook 2003). Mutualistic symbioses are a type of inter-specific interaction, characterized by a tight inter-dependence between species. Such interactions are extremely common in nature; in fact, every organism on Earth is involved in at least one form of mutualism (Six 2009). However, the tight dependence between species means that the persistence of the holobiont (the entire symbiotic organism) during times of environmental change depends on the acclimatization capacity and/or environmental tolerance of each member of the symbiosis (e.g. Soto-Ortiz 2015). Understanding how symbioses operate under different environmental conditions is important for predicting how ecosystems will function in a changing world.

Coral reefs are among the most productive and diverse ecosystems (Barlow et al. 2018), partially due to abundant positive species interactions (especially those fostering nutrient cycling, Roberts et al. 2002). Through their mutualism with dinoflagellates (*Symbiodinium* spp.), scleractinian corals act as reef framework builders, providing essential habitat structure that influences the interactions, distribution, and abundance of organisms, especially reef-associated fishes (Jackson and Winston 1982; Roberts and Ormond 1987; Alper 1998; Komyakova et al. 2018). The coral holobiont contains a suite of endosymbionts (e.g. *Symbiodinium*, fungi, and microbes) and exosymbionts (e.g. invertebrates and fishes) that interact to influence coral growth, reef nutrient cycles, and trophic dynamics (Rohwer et al. 2002; Cantrell et al. 2015; Thompson et al. 2015). The identity of the endo- and exo-symbionts can change along gradients in the physical habitat and environmental conditions, presumably in a way that maximises fitness (e.g. Silverstein et al. 2011; Morrow et al. 2015). Finally, these multi-level positive interactions are engaged in positive feedback loops with other reef organisms, leading to increased coral cover and available habitat, which in turn, increases symbiont abundance (Holbrook et al. 2011). Positive trophic interactions on reefs influence ecosystem function at the seascape scale (Mumby et al. 2009; Layman et al. 2013; Cantrell et al. 2015) and play prominent roles in shaping resilience at the coral colony and community levels under varying environmental threats (Callaway et al. 2002; He et al. 2013).

1.2 Fish-coral interactions

Coral reef fishes are some of the most prominent organisms dependent on live corals, with over 320 fish species directly interacting with 93 species of corals globally (Coker et al. 2012a, b; Coker et al. 2014). Of these fishes, 9-11% of species are obligately dependent on corals for food or shelter (Jones et al. 2004; Pratchett et al. 2008). This reliance is most evident during coral loss, which often results in widespread declines in the abundance of coral reef fishes (Jones et al. 2004; Graham et al. 2006; Pratchett et al. 2006, 2012; Coker et al. 2014), especially coral-dwelling fishes (i.e. Pomacentridae and Gobiidae). Ultimately, the composition and function of reef fish assemblages is dictated by substrate composition (i.e. coral versus algal cover, see Pratchett et al. 2008; Richardson et al. 2017a, b). Live corals not only provide complex biological structure for fishes (Caley and St John 1996), they also modulate fish competition (Munday 2002), predation, and other biological interactions, contributing to the coexistence of the high number of fish species found within reef environments (Almany 2004; Messmer et al. 2011).

Fish-coral interactions vary through time and space. The recruitment and settlement patterns of these organisms is highly dependent upon local environmental conditions that ultimately govern the survival of both corals and fish, and the saturation of corals by damselfishes (Mapstone and Fowler 1988; Schmitt and Holbrook 1996). While there are areas with consistently high numbers of fish-coral interactions (i.e. habitat hotspots, see Munday et al. 1997; Booth et al. 2000; Layman et al. 2013), most of these associations are limited spatially and temporally due to their context-dependent nature (Hopkins et al. 2016). Fishes abundance and distribution, in particular, is governed by local habitat structure, especially by the presence of branching coral species (i.e. *Acropora*, *Pocillopora*, *Stylophora*, and *Porites*). Several groups of fishes (i.e. Gobiidae, Blenniidae, Apogonidae, and Pomacentridae) live within the complex branching structure of corals (Untersteggaber et al. 2014). As a result, this interaction between branching corals and coral-dwelling fishes may be critical to the ecology, survival and co-evolution of both partners (Kiers et al. 2010; Litsios et al. 2012; Pratchett et al. 2012; Chase et al. 2014). However, the overall prevalence of fish-coral association pairs, and the abundance/density of fish on corals per each coral species, has yet to be fully documented, thus preventing full quantification of fishes' impacts on individual colonies, populations, and community level processes.

Coral colony usage and dependency varies considerably among fish species and life stages (Jones et al. 2004; Coker et al. 2014; Richardson et al. 2017a). Most fish-coral interactions are transient and temporary, such as a fish swimming under a table coral, foraging (Cole et al. 2011), or using branching corals as temporary refuge from predators (Beukers and Jones 1998; Coni et al. 2012) or from UV intensity (Kerry and Bellwood 2015). However, certain interactions are more permanent and intimate, such as specialist coral gobies (e.g., *Gobiodon azillaris*) that spend their entire lives within the branches of a single coral colony (Munday et al. 1997). The duration and intensity of the relationship between fish and corals (see Figure 1.1) determines the potential services they can provide to host corals. While it is well known that fishes gain shelter (Wilson et al. 2008), food (Cole et al. 2008), and refuge within coral colonies (Stewart and Jones 2001; Schmitt and Holbrook 2002; Caley and St John 1996), the benefits that fishes confer to corals are less apparent. Small-scale observations of the behaviour and movements of different fish species within and around coral colonies is required to understand the benefits those species provide to their coral host, and whether such benefits vary among coral species and/or among habitats.

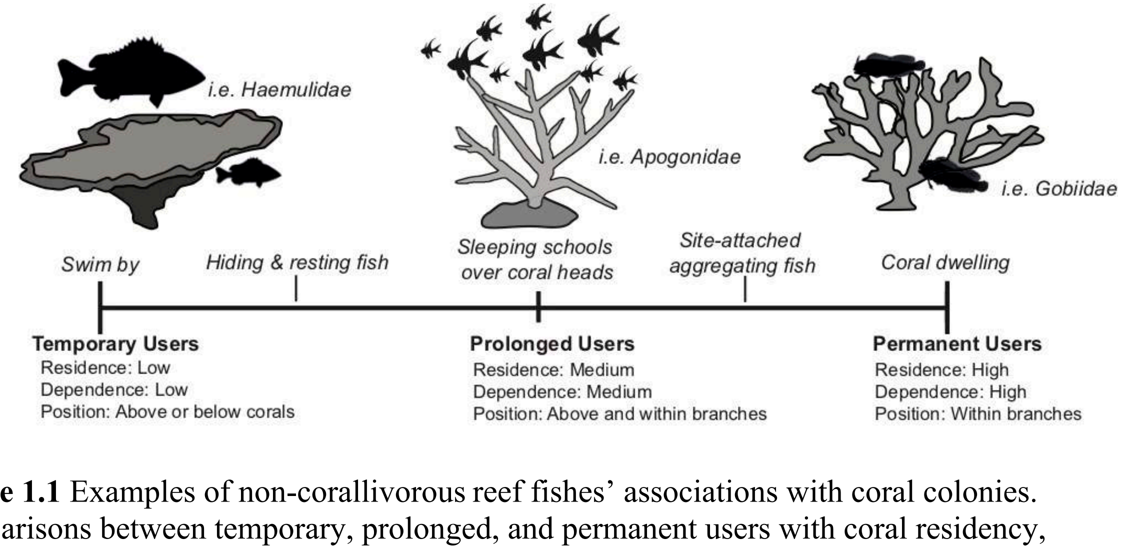


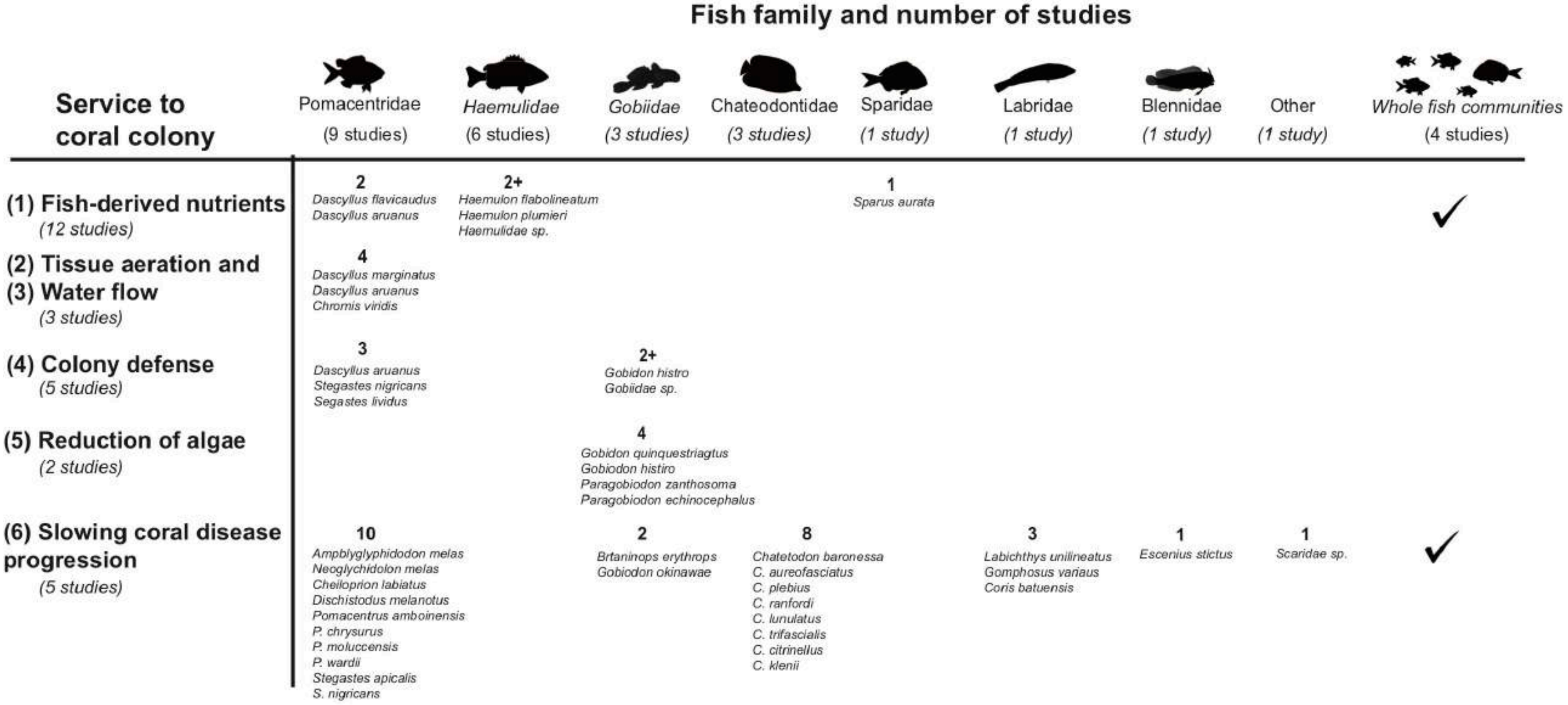
Figure 1.1 Examples of non-corallivorous reef fishes' associations with coral colonies. Comparisons between temporary, prolonged, and permanent users with coral residency, dependency, and positional use detailed.

1.3 How fishes help corals

Several of the services fishes provide to corals are potentially important for the structure and function of reef ecosystems, as they govern the fluxes of nutrients and mass among individuals and species (Dell et al. 2014). These services can happen directly for individual coral colonies, or indirectly through interaction networks (Wootton 2002; Cantrell et al. 2015) with the benefits ranging from an individual fish, to groups of fish, to entire fish communities (Burkepile et al. 2013; Allgeier et al. 2014). Directly, the chief mechanisms by which fishes provide positive impacts to coral colonies are through (1) nutrient provision (i.e. bio-recycling and nutrient provision, see Holbrook et al. 2008; Shantz et al. 2015), with secondary mechanisms of (2) enhanced water flow and aeration of tissues (Goldshmid et al. 2004; Berenshtein et al. 2015), (3) colony defence (Gochfeld 2010; Chase et al. 2014), (4) algae reduction (Dixson and Hay 2012), and a tertiary mechanism of (5) slowing the progression of coral disease (Chong-Seng et al. 2011, Figure 1.2). These services produce quantifiable benefits at the coral colony level such as increased *Symbiodinium* densities, higher chlorophyll levels, and increased nitrogen, phosphorous (Holbrook et al. 2008), and proteins (Woods 2015) within coral tissues. These changes can in turn, lead to increases in rates of calcification (Shantz and Burkepile 2014), photosynthesis (Garcia-Herrera et al. 2017), and overall coral growth (Meyer et al. 1983; Liberman et al. 1995; Holbrook et al. 2008).

Previous research has identified 39 fish species from 7 families that provide direct positive contributions to coral health at the colony level (Table 1.1). Of these, the family Pomacentridae, exhibits the highest number of species involved (14 species), and provides at least four of the above-mentioned services to host coral colonies, primarily from the coral genera *Acropora*, *Pocillopora*, and *Seriatopora*.

Table 1.1 List of fish species by family with explicitly documented beneficial services to corals. The number for each service is the total number of fish species recorded. A '✓' in the 'whole fish communities' column indicates that fish communities have been documented to provide the listed service to corals.



Fish family and number of studies

Service to coral colony	Pomacentridae (9 studies)	*Haemulidae* (6 studies)	*Gobiidae* *(3 studies)*	Chateodontidae *(3 studies)*	Sparidae *(1 study)*	Labridae *(1 study)*	Blennidae *(1 study)*	Other *(1 study)*	*Whole fish communities* (4 studies)
(1) Fish-derived nutrients *(12 studies)*	**2** *Dascyllus flavicaudus* *Dascyllus aruanus*	**2+** *Haemulon flabolineatum* *Haemulon plumieri* *Haemulidae sp.*			**1** *Sparus aurata*				✓
(2) Tissue aeration and (3) Water flow *(3 studies)*	**4** *Dascyllus marginatus* *Dascyllus aruanus* *Chromis viridis*								
(4) Colony defense *(5 studies)*	**3** *Dascyllus aruanus* *Stegastes nigricans* *Segastes lividus*		**2+** *Gobidon histro* *Gobiidae sp.*						
(5) Reduction of algae *(2 studies)*			**4** *Gobidon quinquestriagtus* *Gobiodon histiro* *Paragobiodon zanthosoma* *Paragobiodon echinocephalus*						
(6) Slowing coral disease progression *(5 studies)*	**10** *Ampblyglyphidodon melas* *Neoglychidolon melas* *Cheilopríon labiatus* *Dischistodus melanotus* *Pomacentrus amboinensis* *P. chrysurus* *P. moluccensis* *P. wardii* *Stegastes apicalis* *S. nigricans*		**2** *Brtaninops erythrops* *Gobiodon okinawae*	**8** *Chatetodon baronessa* *C. aureofasciatus* *C. plebius* *C. ranfordi* *C. lunulatus* *C. trifascialis* *C. citrinellus* *C. klenii*		**3** *Labichthys unilineatus* *Gomphosus variaus* *Coris batuensis*	**1** *Escenius stictus*	**1** *Scaridae sp.*	✓

References: Weber and Woodhead 1970; Lassig 1981; Meyer et al. 1983; Meyer and Shultz 1985a, b; Liberman et al. 1995; Bonigorni et al. 2003; Goldshmid et al. 2004; Holbrook et al. 2008; Cole et al. 2009; Gochfeld 2010; Chong-Seng et al. 2011; Zikova et al. 2011; Dixson and Hay 2012; Dirnwoeber and Herler 2013; Shantz and Burkepile 2014; Allgeier et al. 2014; Berenshtein et al. 2015; Chase et al. 2014; Shantz et al. 2015; Garcia-Herrera et al. 2017; Huntington et al. 2017

The ecological importance of aggregating, coral-dwelling damselfishes, other than as a food source for higher trophic-level fish, may be best represented in their services to small branching colonies, such as augmenting tissue composition and overall coral health (Figure 1.2). The magnitude of the services that fish provide to coral colonies will depend on colony-use behaviour of different fish species and, potentially, on the interactions among fish species living within multi-species aggregations on individual coral heads. Current research, however, is lacking quantification of the specific colony-use behaviour of different fish species, especially for damselfishes, the most abundant fishes on coral reefs (Allen et al. 2003; Coker et al. 2014).

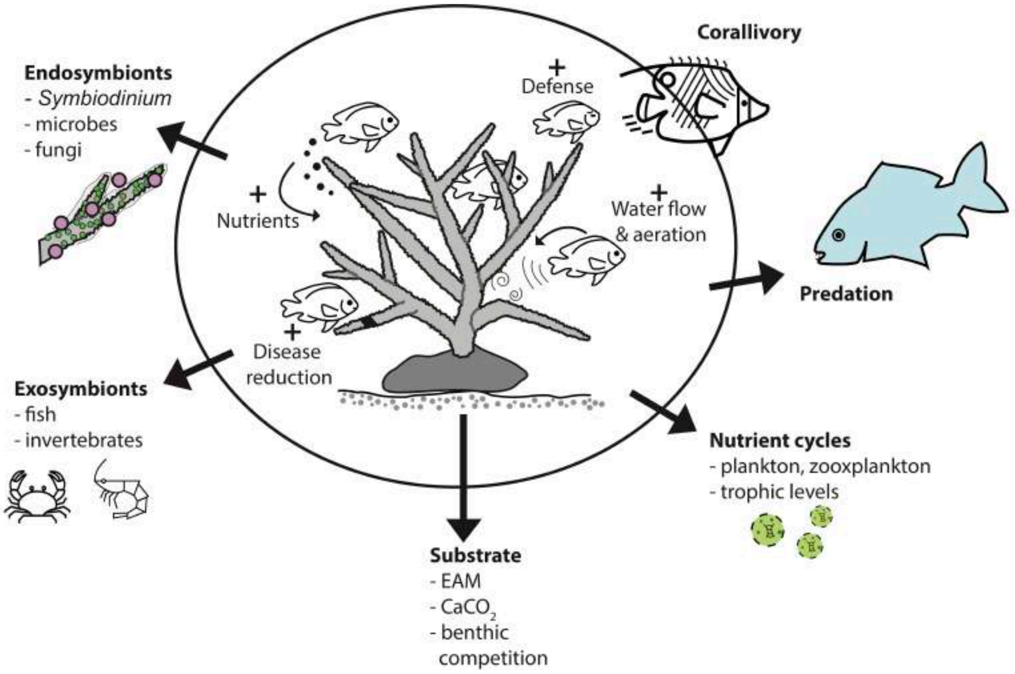


Figure 1.2 Visualization of direct positive fish-derived services for coral health (inside the circle) and connection of the coral holobiont with reef functions and processes (outside the circle).

Indirectly, herbivorous fishes can reduce algae present on reefs (Green and Bellwood 2009), facilitating coral settlement (Bonaldo and Bellwood 2011) and growth by adult colonies. Detritivores can remove sediments trapped within the endolithic algal matrix (Goatley and

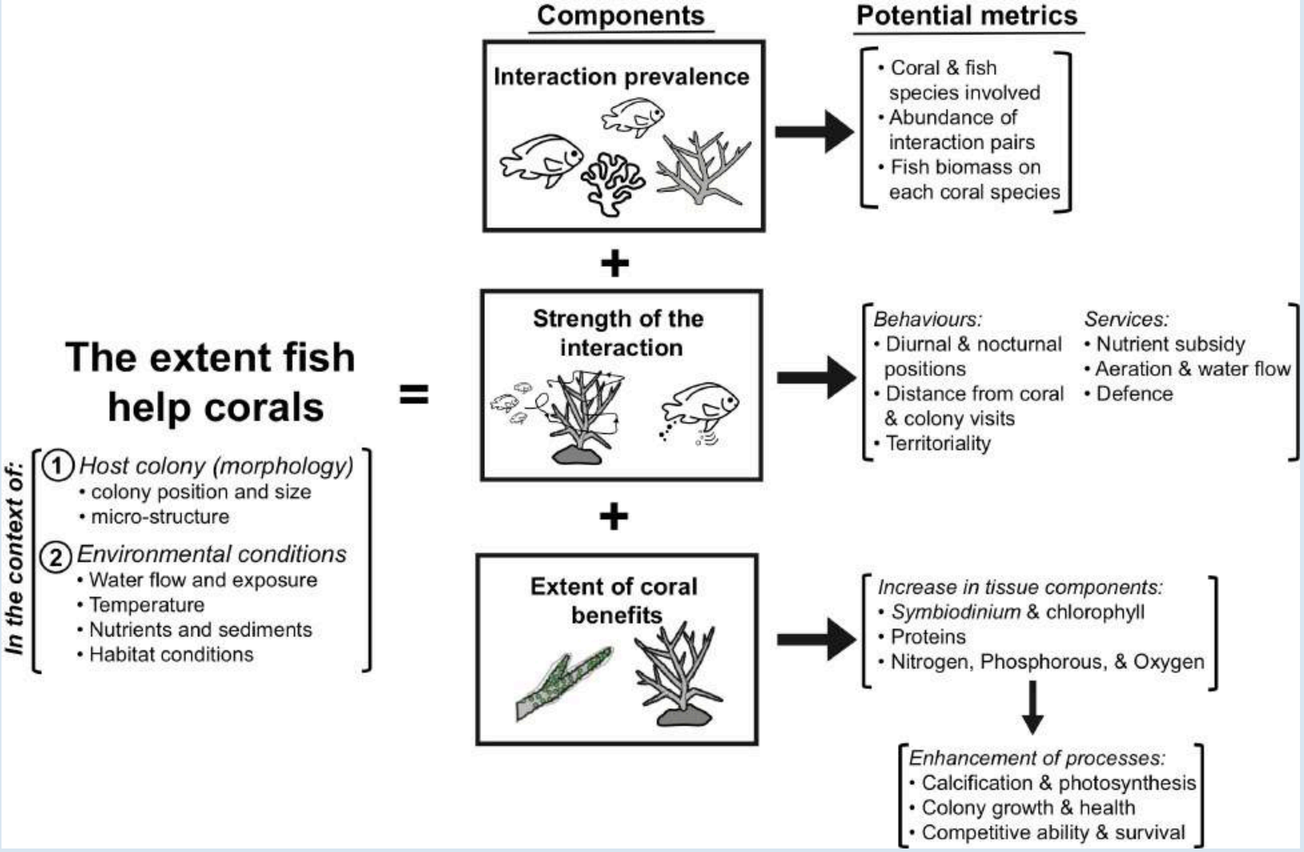
Bellwood 2010), diminishing the impacts of bottom-up processes that negatively impact corals through smothering, reducing energy reserves, and lowering coral immunity (Rogers 1990; Pollock et al. 2014; Sweet and Brown 2016). Lowering algae and sediments on reefs is linked with coral cover in a positive feedback loop, thus promoting ecosystem resilience (Pratchett et al. 2011) by maintaining high coral cover and preventing phase shifts to algae- and sediment-dominated states (Bellwood et al. 2006; Mumby et al. 2009).

1.4 Determining the extent fishes help corals

Under varying environmental conditions, positive interactions among species can shift in strength or importance, potentially leading to a different cost-benefit ratio for interacting species (Holland et al. 2002; Sachs and Simms 2006; Kiers 2010). One of the critical first steps to understanding the overall net effect of fishes on coral populations is to determine: (a) the interaction prevalence, (b) the strength of the interaction, and (c) the translation of these services to increases in coral fitness (Box 1.1). Moreover, each of these factors must be understood in the context of: (1) the host colony identity and (2) the environmental conditions, both of which mediate the overall association (Wong and Candolin 2015).

Box 1.1 A simplified calculation for the extent fishes help corals

The extent to which fishes enhance the fitness of coral population depends upon the prevalence of fish-coral interaction pairs, the specific services that fish provide to coral colonies, and the fish biomass present on coral heads. The total biomass of fishes on coral hosts is linked with certain density-dependent services, such as nutrient provision (Meyer and Schultz 1985a, b; Layman et al. 2013; Shantz et al. 2015). The species-specific behaviours of fishes determine which services are provided to corals, and the magnitude of the services depend on fish biomass. Finally, fish-derived services enhance coral health by multiple different components like the number of *Symbiodinium* or nitrogen or phosphorous within the coral tissue, and how these enhance the processes of photosynthesis, calcification, and overall coral growth. The framework for the magnitude of direct positive fish impacts on corals is situated within the context of (1) the host colony and (2) environmental conditions which will mediate the overall association.



1.5 How local and global environmental stressors will impact coral-fish interactions

Coral reefs are increasingly vulnerable to degradation via anthropogenic stressors associated with climate change impacts and coastal development (Hughes 1993; Sweet and Brown 2016; Hughes et al. 2017a, 2018a). In particular, sedimentation and climate change are recognized as major threats to reef persistence; they in turn, lead to a cascade of other negative impacts including sea surface temperature rise, ocean acidification, storm events, and turbidity (including associated feedback loops, see Solomon et al. 2007; Prezeslawski et al. 2008). Increased sedimentation and decreased water quality (i.e. turbidity, see Furnas 2003; Brodie et al. 2012; GBRMPA 2014) disrupts coral growth and recruitment, herbivory, and processes associated with reef photosynthesis, productivity and resilience (Fabricius 2005; Goatley et al. 2016). Global warming (e.g. increased sea-surface temperatures, Hoegh-Guldberg 1999), is a major threat to reef ecological integrity and function through bleaching (e.g. 2016 and 2017 global bleaching events, Hughes et al. 2017a; 2018a), coral mortality (Hughes et al. 2018b), loss of fishes (Pratchett et al. 2012), and phase shifts (Bellwood et al. 2006). The multiple stressors will concurrently impact corals and fish both acutely and chronically, leading to community level regime shifts (Tebbett et al. 2018).

The complex species interactions present on coral reefs are contingent upon local environmental conditions (e.g. Kiers et al. 2010; Chase et al. 2014; Wong and Candolin 2015); and, therefore, environmental perturbations are likely to have a profound influence on coral reef biotic interactions and feedbacks (Six 2009). Therefore, a major challenge is not only determining the extent of coral-fish interactions and fish-derived benefits, but also understanding whether and how these positive interactions will operate under global environmental change (i.e. increased water temperatures, sediment deposition, pollution, and habitat degradation, Kiers et al. 2010). Profound effects of global environmental change on both the coral holobiont and reef fishes have been revealed in isolation from each other (Hoegh-Guldberg 2011; Pratchett et al. 2015; Nagelkerken and Munday 2016; Hughes et al. 2017a; 2018b). With decreased coral health and growth rates, and disruption of fishes' predator-prey interactions, foraging, and settlement patterns (e.g. turbidity, see Wenger et al. 2012; Wegner & McCormick 2013), it is uncertain whether the services that fish provide to corals are decreased, maintained or increased under different environmental conditions.

There is potential for positive species interactions (i.e. fish-coral interactions) to provide a buffer against these threats, facilitating the persistence of the coral holobiont in the face of the detrimental impacts of specific anthropogenic and natural disturbances (Kiers et al. 2010; Marquis et al. 2014). Furthermore, under these rapidly changing conditions, novel species configurations and associations are emerging (Alexander et al. 2015), thus, influencing coral holobiont dynamics and persistence. Understanding how coral reef feedbacks interact with context-specific conditions is essential to determining ecosystem resilience, disturbance threshold levels, and developing subsequent effective management strategies (Bronstein 1994a; Boada et al. 2017).

1.6 Thesis aims and objectives

The purpose of this thesis is to understand the extent to which fishes benefit coral colonies, whether such benefits are specific to certain coral and fish species and/or certain habitats, and how the effects of fishes' impact colony physiology and health (i.e.

enhancement of coral tissue and colony survival) differ under environmental stressors. By examining the relationship between aggregating, coral-dwelling fish and their host colonies, this thesis reveals where these fish-coral interactions are established, whether and how fish and coral species identity affects the nature of their interaction, and how the services that fish provide to corals change with environmental factors (i.e. sediment and temperature). Furthermore, this thesis goes beyond previous research by investigating the abiotic and biotic interactions of the fish-coral association, in order to fully determine the interaction extent from the coral perspective, and comprehensively understand the impacts of environmental stressors, on coral health and resilience. Specifically, I have the following objectives:

I. Determine the prevalence of fish-coral interactions and the occupancy of damselfishes on coral hosts across space.

Coral and fish species interactions on coral reefs have critical implications for biodiversity and ecosystem functioning. However, for an interaction between two species with dispersing larvae to occur and persist over time, the local environment must be conducive to the settlement and post-settlement survival of both species. Consequently, the occurrence of fish-coral interactions is likely to be heterogeneous among reef habitats and regions. In **Chapter 2**, I analysed the presence and abundance of damselfish-coral interaction pairs across reef regions and habitats to quantify the overall prevalence of fish-coral associations. Determining the spatial prevalence is crucial to contextualizing the extent of fish-derived services beyond a single coral colony, and to indicate whether or not fishes can impact coral populations. As a result, this interaction between branching corals and coral-dwelling fishes may be critical to the ecology, survival and co-evolution of both partners (Kiers et al. 2010; Litsios et al. 2012; Pratchett et al. 2012; Chase et al. 2014). These small-bodied damselfishes, often associated with the most vulnerable coral genera, are among the most impacted by climate change and habitat degradation (Pratchett et al. 2012); incorporation of how abiotic factors impact fish behaviour in synergy, is essential to understanding how individual corals are impacted across a range of conditions.

II. Quantify the variation in the intensity of interactions between damselfishes and their coral hosts over temporal scales to determine the strength of fish-coral associations.

The nature and intensity of associations between damselfishes and their host corals will determine the services that fish provide, thereby affecting coral colony health and potentially altering the dynamics of larger species networks (Bolnick et al. 2011). In **Chapter 3**, *in-situ* diurnal and nocturnal behavioural observations of natural aggregating fish groups on small branching coral colonies were completed to determine the nature and strength of the damselfish-coral interactions. Investigation of how fish utilize coral colonies provided an estimation of the species-specific services present, identification of which damselfish-coral pairs manifest certain services, and when they occur.

III. Evaluate the influence of coral-dwelling fishes on the health of their host corals under environmental stress.

Increasing sea surface temperature and declining water quality due to sediment run-off are two of the major threats to coral reefs. Both of these factors have negative effects on coral colonies (Hoegh-Guldberg 2011; Hughes et al. 2017a; 2018b) and on fishes (Munday et al. 2008; Pratchett et al. 2015; Nagelkerken and Munday 2016), but whether and how the interactions between fish and corals vary under warming and sedimentation remains unknown. In **Chapter 4**, I explicitly test whether coral-dwelling damselfishes can moderate the deleterious effects of sediment stress on their host coral colonies and enhance colony health through a controlled aquaria sediment experiment. The ability of aggregating damselfishes to remove sediment from host corals, while continuing to enhance coral physiology, is proposed as a novel fish-service provided to host colonies, thus helping refine predictions of how corals with and without resident damselfishes will fare under global environmental conditions.

Chapter 5 analyses the impacts of small aggregating damselfish on the health of their coral hosts (physiology, recovery, and survival) before, during and after thermal-bleaching event, *in-situ* and *ex-situ*. Part of this study was conducted in the field during the 2016 GBR bleaching event, leading to invaluable natural bleaching conditions and relevance to my experimental results. By mediating how external abiotic stressors influence coral colony health, damselfish can affect the functional responses of these interspecific interactions in a warming ocean.

IV. Synthesis: Potential for symbioses to buffer environmental change.

Coral reefs are complex systems with countless small-scale biotic interactions that impact ecosystem health and resilience. Using field surveys, manipulative field experiments, and controlled laboratory experiments, this research highlights the importance of investigating ecological relationships across the entire range of environmental conditions under which the relationships occur in nature, and within the context of environmental stressors. Furthermore, the work presented in this thesis contributes to the broader field of symbiosis research, where the conceptualization of symbioses, and the concept of the "metaorganism" (Bosch and McFall-Ngai 2011; Bang et al. 2019), is changing as we learn more about the intricacies of inter-specific interactions, and the manner in which such interactions transform, depending upon the partners involved and the physical conditions of the environment.

1.7 Thesis structure

This thesis is presented in a series of research chapters formatted for journal publication. Because the chapters have been written for submission as independent journal articles, there is inevitable repetition among some chapters. Supplementary figures and tables relevant for each chapter are provided as appendices. The four objectives listed in the Thesis aims and objectives section (above) are addressed in Chapters 2-5.

CHAPTER 2: Differential occupation of seemingly suitable coral hosts by coral-dwelling damselfishes (Pomacentridae) on Australia's Great Barrier Reef

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The content of this chapter has been submitted as:

***Chase TJ**, Hoogenboom MO **(in press)** Differential occupation of available coral hosts by coral-dwelling damselfishes (Pomacentridae) on Australia's Great Barrier Reef. Diversity*

2.1 Synopsis

Associations between habitat-forming corals and coral reef fishes have critical implications for the function and trophic dynamics of coral reef ecosystems. This study quantifies how different characteristics of reef habitat and of coral morphology, determine whether fish occupy a coral colony. *In-situ* surveys of the most prominent aggregative damselfish-coral associations at 51 different sites on 22 reefs spread along >1700 km of the Great Barrier Reef, were used to quantify interaction frequency over a large spatial scale. The prevalence of fish-coral associations between five damselfishes (*Chromis viridis*, *Dascyllus aruanus*, *Dascyllus reticulatus*, *Pomacentrus amboinensis and Pomacentrus moluccensis)* and five coral species (*Acropora intermedia*, *Acropora spathulata, Pocillopora damicornis, Seriatopora hystrix, and Stylophora pistillata*) averaged ~30% across all sites, but ranged from < 1% to 93% depending on reef exposure levels and habitat. Surprisingly, coral cover was not correlated with coral occupancy, or total biomass of damselfishes. Instead, the biomass of damselfishes was two-fold greater on sheltered sites compared with exposed sites. Reef habitat stype strongly governed these interactions with reef slope/base (25%) and shallow sand patch habitats (38%) hosting a majority of all aggregative damselfish-branching coral associations compared to reef flat (10%), crest (16%) and wall habitats (11%). Among the focal branching colonies, *Seriatopora hystrix* hosted the highest fish biomass (12.45 g occupied colony^{-1}) and *Acropora intermedia* the least (6.87 g occupied colony^{-1}). Analyses of local coral colony traits indicated multiple factors governed colony usage including spacing between colonies on the benthos, colony position, and colony branching patterns. Nevertheless, the morphological and habitat characteristics that determine whether or not a colony is occupied by fish varied among coral species. These findings suggest quantifying symbiotic fish-coral interaction prevalence across multi-dimensional reef features provides context for one of the most important and abundant reef fish families in terms of understanding the establishment, nature, realized niche, and resilience of these associations in coral population and community level processes.

2.2 Introduction

Scleractinian corals are the predominant habitat-forming organisms within coral reef ecosystems, contributing to the i) overall structure of reef habitats (Graham and Nash 2013), ii) co-existence and biodiversity of reef associated species (Bell and Gazlin 1984; Roberts and Ormond 1987; Friedlander and Parrish 1998), and iii) providing specific and critical microhabitats used by specialist species (Sale 1971; Munday et al. 1997). Consequently, the abundance of coral-dwelling and reef-associated species (e.g. invertebrate crustacea, sponges, bryozoans, and fishes) is influenced by the abundance of habitat-forming corals (Bell and Gazlin 1984; Koyakova et al. 2013), as well as by the structural complexity provided by coral-rich habitats (Graham et al. 2006; Wilson et al. 2006), and the diversity of corals (Messmer et al. 2011). Importantly, high coral cover and habitat complexity moderate predation (Beukers-Stewart and Jones 1998) and competition (Almany 2004) among reef fish species. Meanwhile, fishes that have an intimate and obligate reliance on live corals for shelter (e.g., coral Gobiidae spp.; Munday et al. 1997, coral-dwelling Pomacentridae spp.; Wilson et al. 2008) or food (e.g., coral-feeding Chaetodontidae spp.; Cole et al. 2008), often have specific preferences for select coral species which, themselves, might occur only in certain habitats. Ultimately, corals might be a limiting resource that regulates the distribution and abundance of many reef fishes (Munday et al. 1997; Jones et al. 2004), depending on their specificity to particular coral species and their reliance on live coral habitats. Understanding this process requires intensive and broad-scale quantification of fish-coral interactions to distinguish effects of habitat types from effects of coral cover.

The abundance of suitable coral, that enable fauna long-term usage or residency of associated fauna across various life stages, is one of the most importance factors dictating fish presence (Booth and Wellington 1998; Holbrook et al. 2000), evident by the fact that fishes and motile invertebrates' abundances decline sharply following coral mortality (Jones et al. 2004; Pratchett et al. 2012). Despite a strong dependence on corals by several fish families, not all coral colonies are occupied by fishes due to physical and behavioural limitations (Holbrook et al. 2000; Wilson et al. 2008). For example, at the coral colony scale, many damselfish species exhibit negative density-dependence in aggregation behaviour (i.e. fish spread out among colonies as local fish density increases), likely due to social constraints on group size (Coker et al. 2013; Chase et al. 2014). At a larger spatial scale, local availability of specific types of habitat determine spatial distribution patterns in habitat-specialized fish, (i.e., *Gobiodon spp.*, see Munday

2002). However, to fully determine the extent to which the availability of specific coral habitats constrain the abundance of reef fishes, direct measurement of the abundance of fishes on individual coral colonies is required. Previous studies have linked variation in damselfishes' abundance and diversity with habitat-related variation in the percentage of cover or functional diversity of corals (Darling et al. 2017; Emslie et al. 2019), but have not assessed whether and how features of coral colonies within habitats also influence fish abundance (Holbrook et al. 2008; Chase et al. 2018b). Assessment of fish-coral interactions at the colony level is important because this is the scale at which impacts of damselfishes on coral are the most prevalent (Holbrook et la. 2008; Chase et al. 2018b). Services that fish provide to corals are often often density-dependent (such as nutrient provision) and are heavily dependent on fish biomass (Meyer et al. 1983; Holbrook et al. 2008). Furthermore, understanding the spatial variation in coral-dwelling fish provides context for understanding how these fish influence coral populations and communities, and how these mutualisms are likely to change during external disturbances and degradation.

Habitat type and colony morphology influence the suitability of coral hosts for nearly all types of coral-associated fauna, especially fishes, as observed for both Scleractinian and Alcyonacean corals (Bay et al. 2001; Kane et al. 2009; Nash et al. 2013; Epstein and Kingsford 2019). This colony-scale association correlates with fish size (Sale 1998), with how fish utilize the coral, and with fish diet preferences, and social and spatial niches (Bay et al. 2001; Kane et al. 2009; Frédérich et al. 2009; Gajdzik et al. 2018). Indeed, seascape and colony features strongly influence feeding behaviour, expecially for zooplankton feeding damselfishes for which among-species partitioning of planktonic prey dictates how different fish species are distributed among reef zones (Wyatt et al. 2012; Gajdzik et al. 2016; McMahon et al. 2016). Moreover, for other fish taxa, including Pomacentridae, Gobiidae, and Blennidae, fine-scale (1 to 10 cm^2) differences in the suitability of coral hosts depends on much more than just the coral taxonomic identity. For example, *Dascyllus marginatus* and other aggregating damselfishes are more likely to inhabit colonies with fine branches, compared with lobed branching morphologies (Holbrook et al. 2000; Nadler et al. 2014). Furthermore, seascape features such as distance from the reef's edge and water flow velocities govern species-specific patterns and biomass due to fishes swimming ability, plankton/prey availability, and colony arrangement requirements (Fulton and Bellwood 2005; Fulton et al. 2005; Johansen et al. 2015; Sambrook et al. 2016). However, the specific reef habitat characteristics, and both within- and among-species variation in coral colony structures, that promote occupancy and residency by aggregative damselfish has yet to be fully understood, with most of this work to date focusing on Blennidae spp. and Gobiidae spp. that usually inhabit corals as individuals or pairs rather than in large aggregations (Munday 2002). Aggregative species are likely to utilize different resources, and bestow greater benefits to corals, compared with large transient and/or small solitary species.

This chapter explores variations in occupancy rates and biomass of coral-dwelling damselfishes among predominant habitat-forming coral species, as well as exploring specific habitat and colony-habitat features that influence whether or not individual coral colonies are used by coral-dwelling, planktivorous damselfishes. The prevalence (fish occupation and biomass) of fish-coral interactions is examined for five damselfish species on five coral species: multiple coral colony traits were measured *in situ* as hypotheses correlate with patterns of fish occupation and biomass. This study increases the number of studies that have quantified broad scale abundance of damselfishes associated with different colony morphologies. I investigate the distribution of these coexisting damselfishes within reef zones and fine-scale microhabitat use (to coral species level) to (a) determine if suitable coral habitat governs patterns in damselfishes' distribution and abundance (large-range dataset of surveys across the GBR, based on variation in coral cover among reefs), and (b) quantify variations in fish biomass within and among coral colony species (small-scale dataset based on observations of individual coral colonies). Investigating the multiscale spatial variation of fish-coral interactions provides insight into fishes' effects on coral health, and for predicting the functioning of interspecific and symbiotic associations within the context of global environmental change.

2.3. Materials and Methods

2.3.1 Study sites and surveys

This study was conducted in March-November 2016, in the northern Great Barrier Reef (GBR), Australia. Surveys were conducted at 51 study sites spread among 22 different reefs (Figure 2.1) including the far northern sector (n = 11 sites), the northern sector (n = 24) including Lizard Island sites (n = 16 sites), the central sector (n = 13 sites) and the southern sector near One Tree Island (n = 3 sites).

Along latitudes spanning > 10°, sites on the GBR with different aspects (sheltered = more westward facing with generally less wave energy, and exposed = more eastward facing, with higher water currents) were compared with 1-3 transects. Transects were located within different habitat zones (lagoon sand patches, flat, crest, wall (distinguished from slope by approximately vertical relief of the substratum), and slope/base (gentle gradient or approximately flat)), at different distances from shore (mid-shelf and off-shore reefs), and at varying depths (0 – 14 m, standardized to Lowest Astronomical Tide (LAT)) to quantify occupancy and resident damselfishes' biomass. Herein, occupancy is described as a colony being used as the sole site of shelter/habitat (residency) within a damselfish territory or home range (Holbrook et al. 2000; Ménard et al. 2012; Pratchett et al. 2012). Surveys focused on five species of damselfishes (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis and P. moluccensis*) and five species of branching corals (*Acropora intermedia*, *Acropora spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*). The host corals were selected for their abundance on the GBR, while also displaying differences in morphology, and particularly, branch spacing patterns due to the hypothesized role of branch spacing in determining colony occupancy (Veron 2000; Komyakova et al. 2018). All five coral species are frequently occupied by coral-dwelling damselfishes (Sale 1971; Holbrook et al. 2000; Wilson et al. 2008; Coker et al. 2013; 2014; Chase et al. 2014). Previous research demonstrates that these select coral and fish species account for >80% of non-cryptic fish-coral interactions within the GBR (Holbrook et al. 2000; Chase et al. 2014). Each of the Pomacentrid sp. have been documented to be 'coral-dwelling' with a home range of a single coral or similar < 2 m structure (Randall et al. 1990; Chase et al. 2014; Nadler et al. 2014; Emslie et al. 2019). Finally, the focal fish species represent important prey for meso- and top predators (Emslie et al. 2019) and are therefore important in reef trophic dynamics.

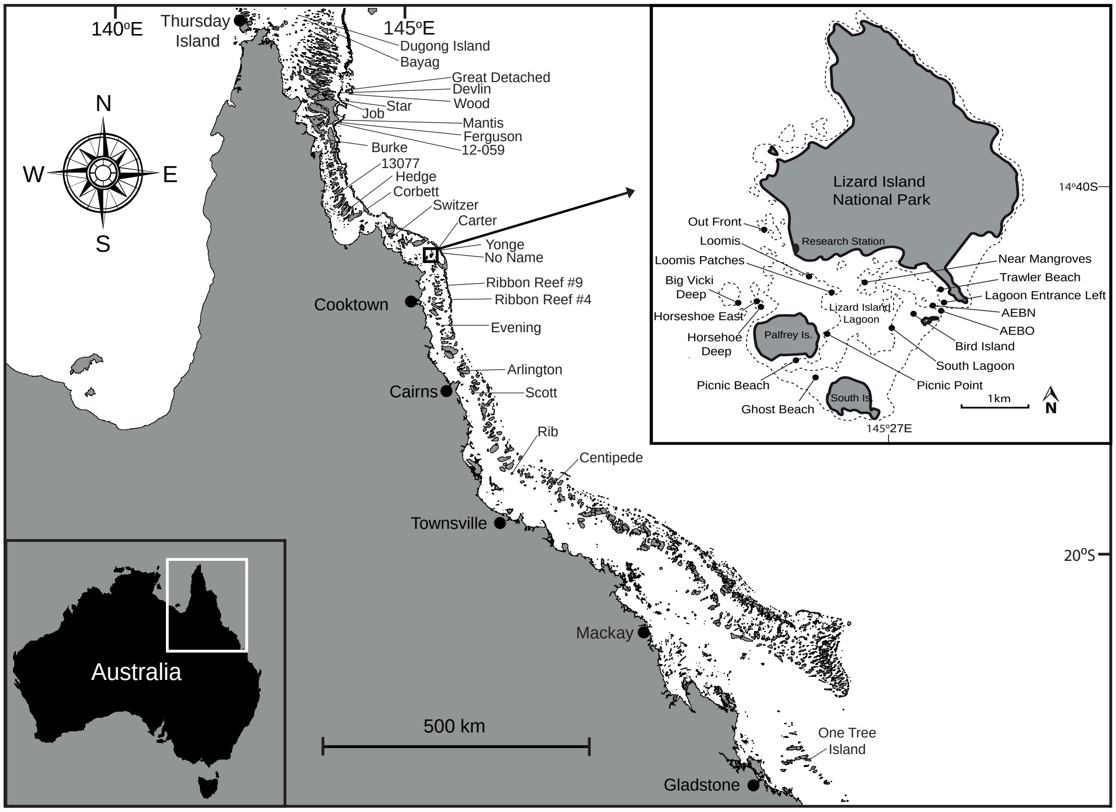


Figure 2.1 Location of study sites along the Great Barrier Reef (51 sites spread among 22 different reefs), spanning > 1700 km, with Lizard Island subset including 16 sites, surveyed between February and November 2016. At each location, the presence and abundance of five species of damselfish (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis*, *and P. moluccensis*) on five species of coral (*A. spathulata*, *A. intermedia, P. damicornis, S. pistillata*, and *S. hystrix)* were observed. Map template is provided by Geoscience Australia under a Creative Commons Attribution 4.0 International License.

At each site, the abundance and occupation (15-100 cm in diameter) of each study species (*A. intermedia*, *A. spathulata*, *P. damicornis*, *S. hystrix*, and *S. pistillata*) were recorded along a 50 m × 5 m belt transect (total area of 250 m^2) by SCUBA diving. I recorded the size and abundance of focal fish species (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis and P. moluccensis*) within each colony through a visual census on SCUBA. Along each transect, each colony was slowly approached and observed for at least 30 seconds to determine damselfish species presence and abundance for biomass estimates. For consistency, all coral and fish observations were performed by the same observer during daylight hours (between 8:00 and 18:00 h). In addition, four replicate 10 m line intercept transects were completed at each site to measure total coral cover (of all corals not just the five focal species, see Hill and Wilkinson 2004; Hughes et al. 2017a).

To assess whether and how small-scale habitat and colony morphology factors influenced fish-coral partnerships, a subset of colonies (n = 226) at 15 different sites, were assessed for local habitat and colony structure traits. These colonies were located on 11 exposed and sheltered reefs, spanning habitats at a depth range of 0-14 m, positioned in the Far North, North, Central, and Southern GBR regions as described above. Colony orientation was categorized as within a crevice, on an overhang, open, or on sand, following Hoogenboom et al. (2017). Colony structure traits measured included: colony size (colony diameter, planar area, and colony height), distance from nearby corals (isolation), and branch dimensions (i.e. inter-branch spacing and average branch width, see Chase et al. 2014; Wehrberger and Herler 2014, see Table 2.1 and Figure S2.1 in Appendix S2). Branch spacing and branch width were averaged for five measurements around each colony, with all branch measurements taken at ~15 mm from the branch tip, while colony isolation being measured as the distance to the closest habitat providing coral (i.e. branching or other complex morphology colonies). For colonies with resident fishes (n = 142), the numbers of all fishes on each focal colony were recorded and used to estimate overall biomass. Each fish was estimated by eye as they were swimming around each focal colony, and placed into general standard-length size classes of small, medium, and large, for each species respectively. Size classes data were subsequently converted to biomass estimates based on known published damselfishes' length/weight relationships generated from damselfishes captured for aquaria experiments (Chase et al. 2014; Chase et al. 2018b, Chapter 4), where damselfishes were collected using hand-nets and clove oil. Biomass estimations were supplemented from FishBase (Froese and Pauly 2019). Surveys focused on ecologically important damselfish occupancy and biomass patterns rather than fish numbers, as biomass has been directly linked to fish-derived services and benefits for corals (Holbrook et al. 2008; Burkepile et al. 2014). For the purposes of these surveys, fish biomass summarizes both fish numbers and size and the analysis did not delineate which of these components contribute more to biomass levels. For additional information regarding the details of reef seascape transects and sites and colony specifics, see Table 2.1, Appendix S2, Tables S2.2 and S2.3).

Table 2.1 Dataset summaries detailing of the (a) observed site features quantified for 51 sites, and the individual coral (b) colony orientation/position, and (c) colony structure for 226 individual colonies with and without resident damselfishes (occupancy and biomass as independent variables) on mid-shelf and offshore GBR reefs. Coral-fish interactions were focused on five focal fish species (*Chromis viridis*, *Dascyllus aruanus*, *Dascyllus reticulatus*, *Pomacentrus amboinensis*, and *Pomacentrus moluccensis*) occupying five common branching morphologies (*Acropora intermedia*, *Acropora spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata).*

(a) Reef seascape survey dataset:	**Description of data**
Sampling: 50 × 5 m belt transects n =3097 colonies on 51 sites on 22 reef, 26nfluencing sheltered (n = 28 sites) and exposed (n = 23 sites) sites, and *sand patches (n = 11 sites), reef flat (n = 5 sites), reef crest (n = 12 sites), reef wall (n = 5 sites), and reef slope (n =18 sites) habitats.*	
Latitude	Sites grouped by latitude: Far north (12.3°S to 10.5°S), North (12.3°S), Central (14.7°S to 18.9°S) and South (One Tree Island, 23.5°S)
Aspect	Exposed locations (high water flow, mainly eastern side of GBR reefs) vs sheltered locations (low water flow, mainly western side of GBR reefs)
Habitat zone	Lagoon sand patch, reef flat, reef crest, reef wall, and reef slope/base
Benthic cover(1)	Percentage cover measured on four 10 m line intercept transects at each site using the following categories: *Isopora*, *Monitpora*, tabular *Acropora*, staghorn *Acropora*, other *Acropora*, *Pocillopora damicornis*, *Seriatopora*, *Stylophora*, other pocilloporids, Mussidae, Faviidae, Poritidae, other scleractinians, soft corals, and other sessile fauna
Coral species	*Acropora intermedia*, *Acropora spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*

(b) Colony orientation/position: *Sampling: Digital photos of n = 226 colonies on 15 sites on 11 exposed and sheltered reefs (colony level dataset)*	
Colony orientation(2) (position of coral on substratum)	**Crevice** - colony grew within a crack in the reef matrix; **Open** - colony is on flat reef benthos without any obvious shading by competitors; **Sand** - colony grew above a sand patch; **Underhang** - colony was shaded by reef matrix or other colonies

(c) Colony structure: *Sampling: Digital photos of n = 226 colonies on 15 sites on 11 exposed and sheltered reefs (colony level dataset)*	
Colony diameter	Average of the longest colony diameter dimension and the diameter perpendicular to that dimension
Planar area	Digitally traced along colony perimeter
Colony height	Distance from top of coral colony to substrate
Branch width	Average width of branches (n = 5 branches colony^{-1}) located throughout the colony
Branch spacing	Average distance between branches (n = 5 branches colony^{-1}) located throughout the colony
Isolation	Distance to nearest branching, columnar, tabular, or foliaceous colony

References: (1) Hughes et al. 2017a; (2) Hoogenboom et al. 2017

2.3.2 Data Analysis

<u>Reef seascape prevalence of fish-coral interactions</u>

At the reef seascape level, the proportion of colonies occupied by fish (damselfishes and coral species pooled, as the independent variable) was analysed using a full additive beta regression model with site latitude, aspect (exposure level), habitat (generally correlated with depth), and coral cover as fixed dependent factors, and reef as a random factor. Beta regression was deemed appropriate, as it includes a logit transformation which is necessary for proportional data (Cribari-Neto and Zeileis 2010; Warton and Hui 2011). Conformity of the data with model assumptions was assessed by analyzing residual plots (QQ plots for normality and residual plots for homogeneity of variance and linearity), as well as calculations of dispersion. Additive models (latitude + aspect + habitat + coral cover) were used due to the non-factorial nature of the dataset wherein not all habitats and aspects could be sampled at each latitude.

A linear mixed-effect model (LME) was used to analyze effects of latitude, aspect, habitat, and coral cover, with total biomass (grams per 250 m^2), log +1 transformed, again at the reef seascape level. The fish biomass LME was fitted using maximum likelihood (Affleck 2015). Damselfishes' biomass data were converted to biomass per 250 m^2 of reef, using published length-weight relationships (i.e. following Chase et al. 2014). Model selection, based on Akaike Information Criteria (AICc) values, was implemented to determine the importance of latitude, aspect, habitat, and coral cover as predictors of fish biomass (see below), and assumptions for model validity were checked through QQ plots and residual plots, as well as calculations of dispersion.

In addition, the multi-model interference R package *MuMIn*, was used to perform model selection on prevalence and biomass models, based on model weights derived from AICc. *MuMIn* allows for an estimate of the variance explained by all factors included in the model (*R package MuMIn*, Bartoń 2013; Burnham and Anderson 2002). A ranking of the possible models to identify the contribution/importance of each variable as well as the number of models in which each variable was completed (function "dredge" in *R package MuMIn*).

To further compare differences among occupancy among each of the five coral species (utilizing the reef seascape proportional and biomass data, mentioned above), binomial generalized linear models (GLMs) with Tukey's HSD *post-hocs* were used to quantify differences in occupancy (all colonies, n = 3,034) and total damselfishes' biomass (only using data for occupied colonies, n = 898). Separate Kruskal-Wallis rank sum tests were performed for each damselfish species to analyze whether coral species identity (independent variable) affected the biomass of different species of resident damselfishes (dependent variable) on these 898 occupied colonies. Kruskal-Wallis tests were deemed appropriate as fish biomass data did not meet assumptions of homogeneity of variance (scatter plots of residuals vs fitted for linearity) and normality (QQ-normal plot), despite transformation. Dunn tests were used for multiple *post-hoc* comparisons between species due to unequal sample sizes, and p-values were adjusted with the Benjamini-Hochberg method to decrease type I error (Benjamini and Hochberg 1995).

Effects of colony orientation and structure on damselfishes' occupancy

To compare how colony position and structure impacted occupancy and biomass for a subset of colonies, principle component analyses (PCAs) were used to evaluate overall differences in colony morphology between corals with (n = 142) and without fish (n = 84), both with data pooled over all corals, and separately for each coral species (using the colony level dataset). These different analyses were conducted to assess whether there were particular colony structure features that influenced fish presence overall, and whether such traits were consistent among coral species. PCAs were deemed appropriate due to the multivariate nature of the data with variables (e.g., branch width and branch spacing) that were likely to be correlated with each other. The PCA ordinated colonies were based on the standardized correlation matrix between colony attributes using the R function princomp (see Mardia et al. 1979; Venables and Ripley 2002). Subsequently, the principle component (PC) 1 and 2 scores of each colony were used to represent the overall variation in colony morphology in subsequent linear models (LM) of fish occupation (presence/absence). To further differentiate occupancy patterns between the colony orientations, a binomial GLM was used with a Tukey's HSD *post-hoc* to assess between factor level differences. A lognormal linear model was used to quantify total damselfishes' biomass (only occupied colonies) with regards to colony orientation, again with a Tukey's HSD *post-hoc* comparisons.

Similarity percentage analysis (SIMPER see Clarke 1993; Warton et al. 2012) was used to determine which coral structure traits (colony diameter, planar area, colony height, branch spacing, branch width, and isolation) contributed the most to the differences among corals with and without fish. This analysis compared the importance of these structural traits for all coral species pooled and pooled across the different species of fish occupying these corals. The SIMPER analysis was performed on the PCA standardized data to assess which structure traits were driving the differences (by individual coral species and species pooled) and ranked in order according to their contribution (% or importance ranking). This similarity percentage is based on the decomposition of Bray-Curtis dissimilarity index, giving the overall contribution of individual structure traits.

Effects of colony orientation and structure on damselfishes' biomass

Total biomass of damselfishes on colonies located in different reef microhabitats (Table 2.1) were analysed with lognormal linear models. Model fit was assessed using residual plots, all of which were satisfactory (normal and homogenous). As damselfishes' biomass is a continuous variable, a series of linear models per individual coral species and for all colonies pooled were completed to determine if total damselfishes' biomass (dependent variable) varied with the two most important structure traits (independent variables) from the SIMPER of colony structure occupancy. Separate linear models for each structure trait were deemed appropriate to assess each of the structure traits in isolation (similar to Nadler et al. 2014).

All data analyses were performed in the statistical software R (R Development Core Team, 2018) using the *betareg* (Cribari-Neto and Zeileis 2010), *multcomp* (Hothorn et al. 2008), *lsmeans* (Lenth 2016), *simper* function in *vegan* (Clark 1993; Warton et al. 2012), and *MuMIn* (Burnham and Anderson 2002; Bartoń 2013) packages.

2.4 Results

2.4.1. Range of damselfishes' occupation across the GBR

During this study, a total of 5,154 damselfishes of the five species (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis and P. moluccensis*) were counted on 3,034 coral colonies across five coral species (*A. intermedia*, *A. spathulata*, *P. damicornis*, *S. hystrix*, and *S. pistillata*) on 51 transects (with combined sample area of 12,750 m^2). Overall 30% of colonies were occupied by one or more of the focal damselfish species (898 out of 3,034, all transects pooled), though mean levels of occupancy ranged from 0% at exposed, flat and crest habitat zones, up to 93% at sheltered lagoon sand patch habitats. In the full model, habitat (1) and aspect (2) were the most important variables in predicting fish occupancy (Table 2.2).

Table 2.2 Relative importance of environmental variables influencing fish-coral interactions, based on *MuMIn* model selection and model averaging, with AICc weighting schemes. Full beta regression models and linear mixed effects models (LME) for each fish metric included: latitude (Far North GBR, North GBR, Central GBR, and South GBR), aspect category (sheltered and exposed), habitat (sand patches, flat, crest, wall, slope/base), and coral cover (% hard scleractinian cover). Bolded numbers indicate the highest importance ranking (out of 100%) variable for each fish metric.

Fish metric	Model	Importance	Latitude	Exposure	Habitat	Coral cover
Fish presence	Beta regression with logit transformation	Importance	0.29	0.82	**0.93**	0.2
		N containing models	3	5	**6**	4
Total Fish biomass	Linear mixed-effects model (LME) with log+1 transformation and maximum likelihood estimation	Importance	0.06	**0.97**	0.31	0.28
		N containing models	1	**5**	3	2

In general, occupancy levels were higher in eastern aspect, sheltered sites, than western aspect, exposed sites (betareg(logit), aspect, $p = 0.002$), and highest numbers were observed in lagoon sand patches and slope habitats (betareg(logit): habitat, $p = 0.016$, Figure 2.2a, b). Latitude (betareg(logit) $p = 0.051$), and coral cover (betareg(logit) $p = 0.735$) were not significant predictors of the proportion of colonies occupied (Figure 2.2a, b).

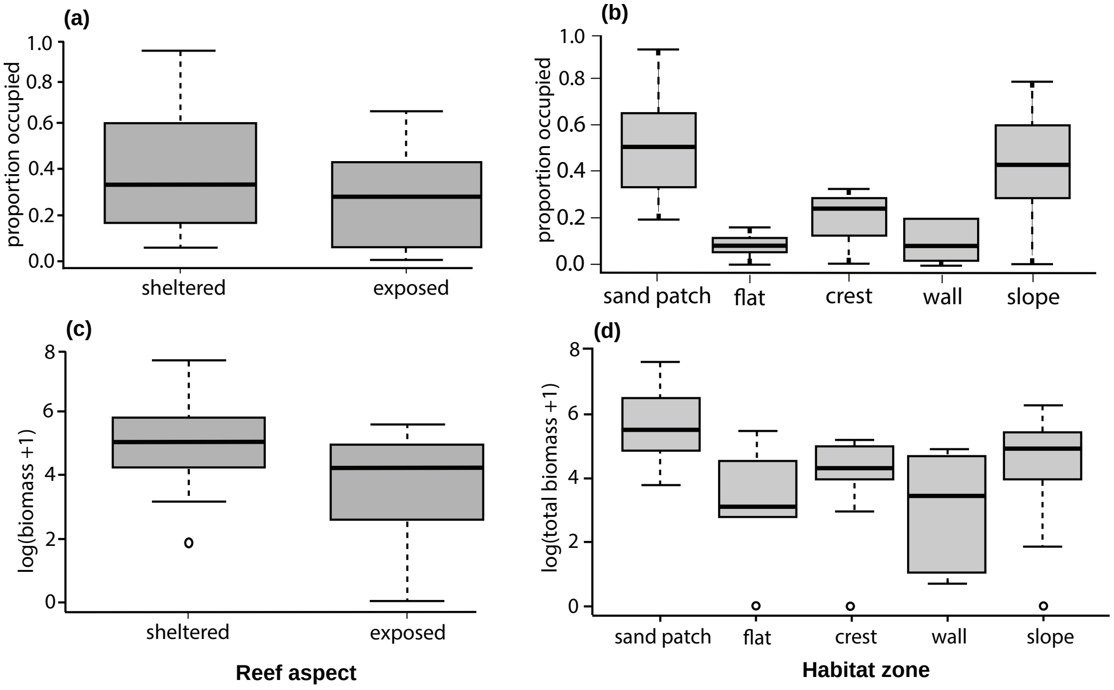


Figure 2.2 Boxplots (horizontal lines show median; boxes indicate 25th and 75th percentiles; vertical dotted lines show range; data points show outliers) of colonies occupied (reef seascape level) **(a, b)** and damselfishes' biomass (log +1) abundance **(c, d)** on five species of branching coral (*A. spathulata*, *A. intermedia, P. damicornis, S hystrix*, and *S, pistillata)* in relation to aspect category (exposed or sheltered) and reef habitat (sand patches, flat, crest, wall, and slope/base).

Additionally, occupancy also varied with coral species (binomial GLM, significant effect of species, $p < 0.05$). Both *P. damicornis* (34% occupancy) and *S. pistillata* (33% occupancy) had the highest average occupancy, when compared with *A.*

spathulata (30%), *S. hystrix* (23%), and *A. intermedia* (22%) (see Table 2.3 for *post-hoc* comparisons and Table S2.1 for the binomial GLM output in Appendix S2). These damselfish specific occupancy patterns translated into different fish communities and damselfishes biomasses on each coral species (Appendix S2, Tables S2.2 and S2.3); for instance, *A. intermedia*, *P. damicornis*, and S. *pistillata* hosted mainly *D. aruanus* and *P. moluccensis* aggregations, while *A. spathulata* hosted *C. viridis* and *P. moluccensis* heterospecific groups.

Table 2.3 Multiple comparisons of coral-species, with p-values, (Tukey's HSD *post-hoc*) based on a binomial generalized linear model of colony occupancy with damselfish species pooled (reef seascape): colony occupancy (dependent) and colony species (independent variable). Significant p-values are in bold.

Comparison	**p-value**
A. intermedia – A. spathulata	0.5089
A. intermedia – P. damicornis	**0.0050**
A. intermedia – S. hystrix	0.9996
A. intermedia – S. pistillata	**0.0131**
A. spathulata – P. damicornis	0.8963
A. spathulata – S. hystrix	0.4492
A. spathulata – S. pistillata	0.9588
P. damicornis – S. hystrix	**< 0.001**

2.4.2. Patterns of damselfishes' biomass across reefs on occupied colonies

Damselfishes biomass was broadly similar to occupancy patterns, displaying significant differences in biomass per 250 m^2 depending on aspect (LME (log+1), aspect, $\chi^2 = 6.88$, $p = 0.008$, Figure 2.2c, d). Sheltered sites had three-fold higher biomass (250 ± 71 g 250 m^{-2} for all colonies per site) than exposed sites (86.7 ± 17 g 250 m^{-2}). Biomass per 250 m^2 also varied by habitat zone (LME (log+1), habitat, $\chi^2 = 9.54$ $p = 0.0489$) with the highest biomass in sand patches (404.9. ± 166 g 250 m^{-2}) and slope habitats (161.7 ±

33 g 250 m^{-2}), and lowest biomass on wall habitats (70.1 ± 42 g 250 m^{-2}). Again, latitude (LME (log+1) $\chi^2 = 2.81$, p = 0.42) and coral cover (LME (log+1), $\chi^2 = 0.109$, p = 0.740) were not significant predictors of total fish biomass per site. In the full model, aspect (1) and habitat (2) were the most important variables in predicting fish occupancy (Table 2.2).

P. amboinensis was the most prevalent damselfish species on the coral colonies considered during this study, present on nearly half of all occupied coral colonies (~3 *P. moluccensis* colony^{-1}), and accounting for ~45% of all damselfish biomass on coral hosts (Tables 2.4 and 2.5 and Figures 2.3 and 2.4). Single-species groups of *P. moluccensis* or *D. aruanus* were recorded on 80% of occupied colonies. Among the five fish species, *P. moluccensis* exhibited the most consistent and broadest distribution being present in high biomass in every habitat zone. *Chromis* and *Dascyllus* species almost exclusively inhabited corals on sand patch and slope habitats (Figure 2.4). Damselfishes' biomass per occupied colony ranged from 1.3 g (a single *P. amboinensis*) to 120 g (a school of ~100 *C. viridis* or a large aggregation of ~30 *D. aruanus*). *C. viridis*, *D. aruanus*, and *D. reticulatus* were nearly exclusive to sheltered aspect sites, mainly absent from flat, crest, and wall habitats (Tables 2.3 and 2.4, and Tables S2.2 and S2.3 in Appendix S2). *P. moluccensis* exhibited a broader distribution being present in high biomass in every habitat zone. *S. hystrix* coral colonies hosted the highest fish biomass per occupied colony (12.45 g ± 1.33), with *A. intermedia* having the lowest biomass per occupied colony (6.87 g ± 1.33). As a result, total damselfishes' biomass was significantly different among occupied coral species (LM: $F_{4,926} = 3.224$, p = 0.012, see Appendix S2, Table S2.4 for *post-hoc* comparisons).

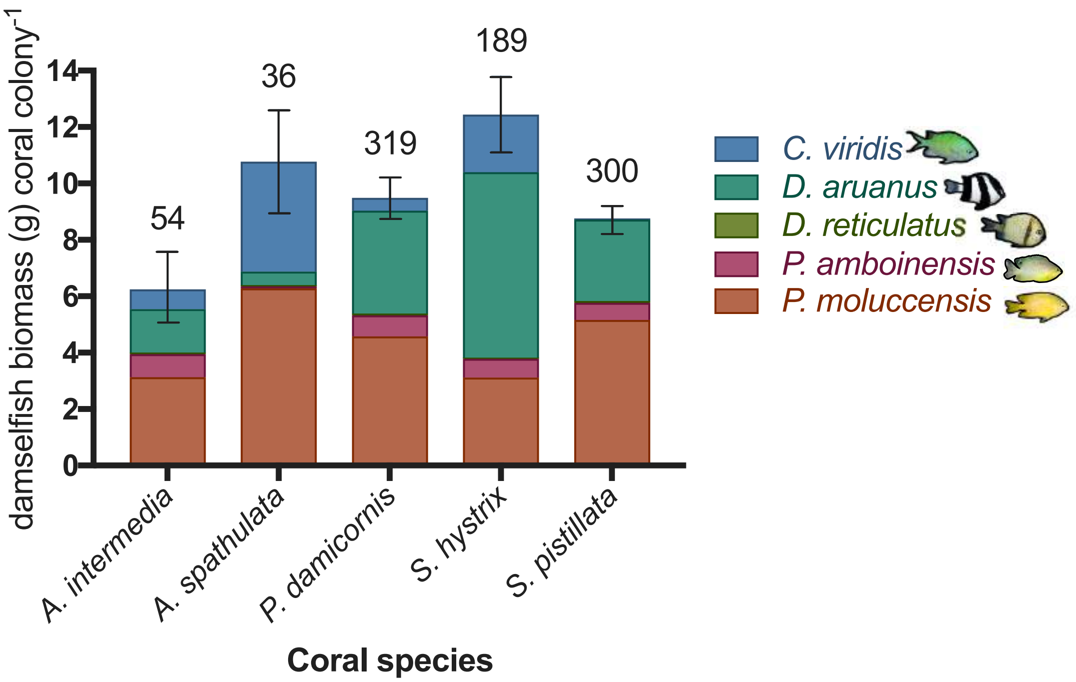


Figure 2.3 Mean reef seascape damselfishes' biomasses per fish species (g ± SE of total biomass of damselfishes) per coral species (*Acropora intermedia*, *Acropora spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*) for all occupied colonies (n = 898) for 5,154 fish (*Chromis viridis*, *Dascyllus aruanus*, *Dascyllus reticulatus*, *Pomacentrus amboinensis*, and *Pomacenturs moluccensis*) at 51 sites. Coral sample sizes per species are displayed above the bars. Note the collapse of *D. reticulatus* and *P. amboinensis* sub-bars for the *A. spathulata* coral bar, and again for *D. reticulatus* on the *S. hystrix* bar, indicating very low biomass values for these fish species on these corals. Further damselfish species-specific and coral species-specific average biomass (± SE) per site aspect, and habitat are displayed in Tables 2.4 and 2.5 and Appendix S2, Tables S2.2 and S2.3).

Table 2.4 Descriptive statistics of reef seascape biomass estimated (mean grams ± SE) for each damselfish species and total biomass pooled for all coral species (per occupied colony of *A. intermedia*, *A. spathulata, P. damicornis, S. hystrix,* and *S. pistillata*) by site aspect (sheltered or exposed).

Aspect	***n***	**Average biomass (g) per coral colony per site aspect**					**Total avg. biomass**
		C. viridis	*D. aruanus*	*D. reticulatus*	*P. amboinensis*	*P. moluccensis*	
Sheltered	627	1.09 ± 0.29	5.36 ± 0.45	0.27 ± 0.08	0.67 ± 0.06	6.96 ± 0.42	11.22 ± 0.56
Exposed	271	0.08 ± 0.07	0.08 ± 0.05	0.59 ± 0.33	0.63 ± 0.09	3.11 ± 0.22	7.29 ± 0.51

Table 2.5 Average reef seascape biomass estimates (mean ± SE) for each damselfish species (*C. viridis, D. aruanus, D. reticulatus, P. amboinensis,* and *P. moluccensis*) on each coral species (*A. intermedia*, *A. spathulata, P. damicornis, S. hystrix,* and *S. pistillata*) on occupied colonies in sheltered and exposed aspect site.

			Average biomass (g) per coral species per site aspect				
Aspect	**Coral species**	***n***	*C. viridis*	*D. aruanus*	*D. reticulatus*	*P. amboinensis*	*P. moluccensis*
Sheltered	*A. intermedia*	38	0.92 ± 0.79	2.21 ± 0.96	0.94 ± 0.89	1.06 ± 0.31	2.80 ± 0.54
	A. spathulata	30	4.66 ± 2.03	0.60 ± 0.48	0.17 ± 0.17	0.09 ± 0.06	5.70 ± 0.96
	P. damicornis	234	0.52 ± 0.22	4.98 ± 0.78	0.26 ± 0.14	0.84 ± 0.12	3.87 ± 0.34
	S. hystrix	147	2.63 ± 1.10	8.49 ± 1.15	0.00 ± 0.00	0.63 ± 0.11	2.47 ± 0.24
	S. pistillata	179	0.22 ± 0.02	4.72 ± 0.64	0.36 ± 0.12	0.50 ± 0.99	4.74 ± 0.51
Exposed	*A. intermedia*	16	0.19 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.24 ± 0.13	3.91 ± 1.06
	A. spathulata	6	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	9.18 ± 3.31
	P. damicornis	114	0.18 ± 0.18	0.00 ± 0.00	1.33 ± 0.79	0.40 ± 0.13	6.57 ± 0.79
	S. hystrix	42	0.00 ± 0.00	0.00 ± 0.00	0.04 ± 0.04	0.84 ± 0.22	5.38 ± 0.89
	S. pistillata	127	0.00 ± 0.00	0.17 ± 0.12	0.21 ± 0.10	0.72 ± 0.15	5.88 ± 0.49

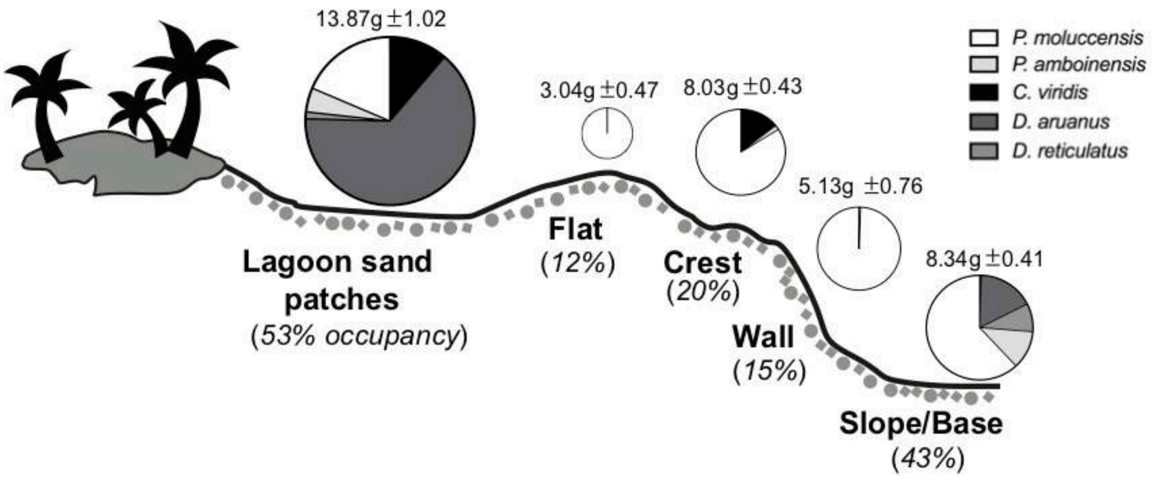


Figure 2.4 Average biomass (g ± SE) of damselfishes per occupied colony on the different reef habitat zones (reef seascape). The areas of each circle are scaled to the overall biomass per zone. The colours of each circle indicate the proportion of biomass per each damselfish species. Overall coral occupancy per 250 m^2 is displayed in italics below each habitat zone.

When data were analysed by fish species, the biomass of each damselfish species significantly varied among host coral species (see Table S2.5 in Appendix S2 for *post-hoc* comparisons), except for *C. virdis* (Kruskal-wallis: $\chi^2 = 9.104$, df = 4, p = 0.0586). *S. hystrix* and *P. damicornis* colonies were favoured by *D. aruanus* (Kruskal-wallis: $\chi^2 = 45.304$, df = 4, $p < 0.001$) and *D. reticulatus* (Kruskal-wallis: $\chi^2 = 29.962$, df = 4, $p < 0.001$). *A. spathulata* and *S. pistillata* colonies were favoured by *P. amboinensis* (Kruskal-wallis: $\chi^2 = 11.715$, df = 4, p = 0.019) and *P. moluccensis* (Kruskal-wallis: $\chi^2 = 29.962$, df = 4, $p < 0.001$).

2.4.3. Colony orientation as a determinant of damselfishes' occupation and biomass

Higher coral occupancy was observed on corals located in reef microhabitats that were either open carbonate pavement or open sandy substratum habitats (GLM: (open) p

= 0.0068) and (sand) $p < 0.0001$, see Table S2.6 for *post-hoc* comparisons in Appendix S2). Similarly, total damselfish biomass on occupied colonies (all fish and all coral species pooled) mirrored occupancy data at the habitat level, varying significantly with colony occupation on the benthos (LM: $F_{3,132} = 5.387$, $p < 0.001$, see Table S2.7 for *post-hoc* comparisons in Appendix S2) with sand (15.3 g ± 2.4) and open (11.4 g ± 1.8) orientation colonies hosting three- to four-fold biomass more than underhang (4.9 g ± 0.8) and crevice (3.8 g ± 0.7) colony position.

2.4.4. Colony structure as a determinant of damselfishes' occupation and biomass

The PCAs of colony attributes (based on the specific subset of corals and study locations where these attributes were measured) of the five coral-dwelling damselfishes (species pooled), revealed distinctive groupings of colonies with and without fish both when data were pooled across coral species and when analysed separately for each coral species. The first two principal components (PC1 and PC2) explained 70% of variance for all colonies pooled (Table 2.6 and Figure 2.5), and between 55% and 77% of variance in colony structure when coral species were analysed individually. Overall, colonies (pooled over species) that were occupied by fish had considerably lower PC1 scores than colonies without fish, and lower PC2 scores (Table 2.6).

Table 2.6 Variance explained and linear models displaying differences between coral colonies with and without fish along principal component analyses PC1 and PC2, for a subset of coral colonies (n = 226) at 15 different sites on 11 reefs (colony level dataset). Significant p-values (PC1 and PC2 scores that are significantly different between colonies with and without fish) are in bold.

Coral species	PC1 variance	PC2 variance	Cumulative variance explained (%)	PC1	PC2
All coral species (pooled)	48.05	19.75	67.8	$F_{1,224}$ = 35.06, **p < 0.001**	$F_{1,224}$ = 16.48, **p < 0.001**
A. intermedia	60.4	16.3	76.7	$F_{1,20}$ = 2.81, p = 0.109	$F_{1,20}$= 2.661, p = 0.119
A. spathulata	51.3	18.2	69.6	$F_{1,30}$ =18.44, **p < 0.001**	$F_{1,30}$ = 0.3362, p = 0.570
P. damicornis	48.3	20.1	68.4	$F_{1,64}$ = 48.75, **p < 0.001**	$F_{1,64}$ = 0.1993, p = 0.661
S. hystrix	39.9	26.5	66.4	$F_{1,42}$ = 35.72, **p < 0.001**	$F_{1,42}$ = 2.431, p = 0.1265
S. pistillata	34.2	20.9	55.13	$F_{1,60}$ = 85.23, **p < 0.001**	$F_{1,60}$ = 4.342, **p = 0.042**

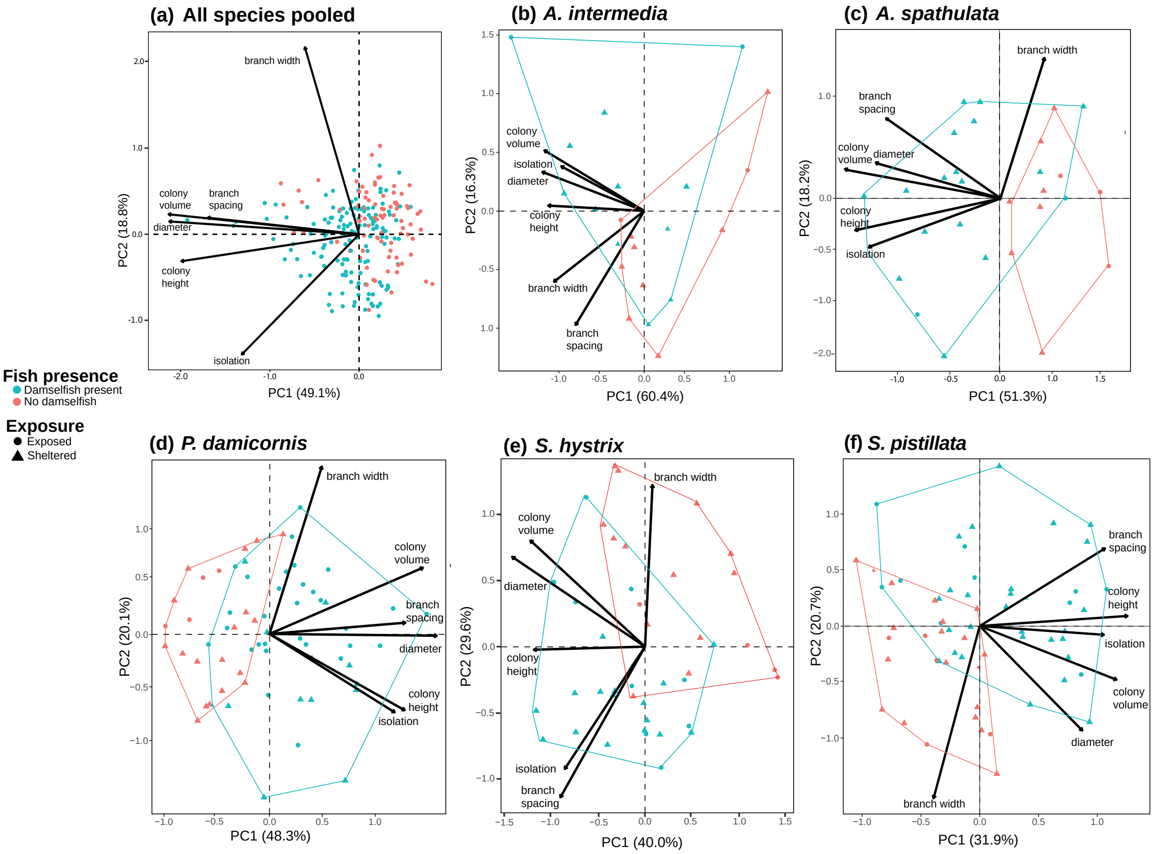


Figure 2.5 Principal component analysis (PCA) of coral colony structure attributes for n = 216 branching corals with and without resident damselfishes along mid-shelf and off-shore reefs of the GBR (colony level dataset). Primary x- and y-axis scales show standardized scores of the coral points. Convex hulls show groupings by occupancy. Eigenvectors of each coral colony structure attribute are overlaid. Principal component analysis (PCA) **(a)** pooled for all colonies and **(b-f)** for each coral species; **(b)** *Acropora intermedia*, **(c)** *A. spathulata*, **(d)** *Pocillopora damicornis*, **(e)** *Seriatopora hystrix*, and **(f)** *Stylophora pistillata*, with convex hulls according to exposure (sheltered and exposed).

In this analysis, PC1 scores were associated with variation in colony diameter and planar areas (dictated by *A. intermedia* colonies), and PC2 scores were associated with variation in branch spacing and colony isolation. When coral colonies were analysed separately by individual species, SIMPER analysis was used to tease out which variables had the most influence on whether or not the colonies had fish, (Table 2.7 and Appendix

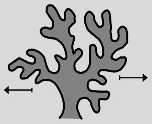
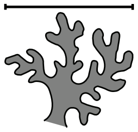
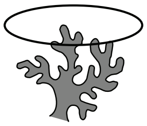
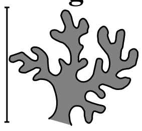
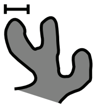
S2, Table S2.8) and revealed isolation was the most influential colony variable for all coral species, with branch spacing and planar area as secondary variables.

Table 2.7 SIMPER analysis results displaying the cumulative contributions of the most influential colony structure variables on coral colony occupation (presence or absence) by damselfishes (colony level dataset). SIMPER analysis was done on the standardized dataset for PCA ordination. A (-) indicates the SIMPER analysis did not identify a particular coral colony structure variable as considerably influential for predicting fish presence.

Coral species	Colony structure variable	Additional variation explained by most influential species	Cumulative contributions of most influential species
All coral species	isolation	0.27	0.27
	branch spacing	0.20	0.47
	colony height	0.16	0.63
	branch width	0.13	0.76
	planar area	-	-
	diameter	-	-
A. intermedia	isolation	0.29	0.29
	planar area	0.20	0.49
	diameter	0.15	0.64
	colony height	0.15	0.79
	branch spacing	-	-
	branch width	-	-
A. spathulata	isolation	0.31	0.31
	planar area	0.20	0.51
	colony height	0.16	0.67
	branch spacing	0.14	0.81
	branch width	-	-
	diameter	-	-
P. damicornis	isolation	0.24	0.24
	branch spacing	0.22	0.46
	planar area	0.19	0.65
	colony height	0.15	0.80
	branch width	-	-
	diameter	-	-
S. hystrix	isolation	0.28	0.28
	branch spacing	0.24	0.52
	planar area	0.15	0.67
	colony height	0.12	0.79
	branch width	-	-
	diameter	-	-
S. pistillata	isolation	0.32	0.32
	planar area	0.16	0.48
	colony height	0.15	0.63
	branch spacing	0.15	0.78
	branch width	-	-
	diameter	-	-

Total damselfishes' biomass per colony followed similar trends with fish occupancy (see linear models in Table 2.8 and Table S2.8 in Appendix S2), with isolation and colony height as the most influential colony structure variables for five of the six coral species, and all structure traits were significant except for branch width, which when analysed individually by species, was only important for *S. pistillata*. Branch spacing, colony diameter, and planar colony area were significant for three coral species. Branch width was only important for predicting fish biomass present on *S. pistillata* colonies

Table 2.8 Series of linear models illustrating variation in total damselfishes' biomass in small branching coral colonies (*A. intermedia*, *A. spathulata*, *P. damicornis, S. hystrix, and S. pistillata*), by damselfishes (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis*, *and P. moluccensis)* for six fine scale indicators of colony attributes (colony level dataset). The first two traits, colony isolation and branch spacing, had the highest importance for determining colony occupation. Significant p-values are in bold.

Coral species	**n**	**Isolation** 	**Branch spacing** 	**Colony diameter** 	**Planar area** 	**Colony height** 	**Branch width** 
A. intermedia	22	**< 0.001**	0.527	**0.019**	**< 0.001**	0.068	0.185
A. spathulata	32	0.099	0.357	**0.020**	**< 0.001**	**0.008**	0.416
P. damicornis	66	**0.014**	**0.002**	**< 0.001**	**< 0.001**	**< 0.001**	0.423
S. hystrix	44	**0.002**	**< 0.001**	0.304	0.809	**0.018**	0.198
S. pistillata	62	**< 0.001**	**< 0.001**	0.734	0.357	**0.015**	**< 0.001**
All colonies	226	**< 0.001**	**0.007**	< **0.001**	**< 0.001**	**< 0.001**	0.176

2.5. Discussion

2.5.1 Reasoning for variations in damselfishes' occupation and biomass

This chapter demonstrates substantial variation in the occupancy rates of small-branching coral hosts by five species of coral-dwelling damselfishes, with between 0-93% of coral colonies being occupied per transect, depending on reef habitat zone and exposure. Within habitats, small-scale differences in the morphology and orientation of coral colonies also contributed to occupancy and biomass of fishes. Previous studies have suggested that variations in coral colony structure and health are likely to play important roles in determining the population dynamics of coral-associated fishes and invertebrates (Noonan et al. 2012; Pereira and Munday 2017), as well as the persistence of fish communities. This study provides new insight into the factors that control the presence and abundance of individual damselfish species (and associated group biomass, distribution across parts of the GBR) and provides context for understanding the potential impacts of aggregating damselfishes on coral populations and reef ecosystem function.

Overall rates of occupancy (30%) are higher than have been reported previously (13% and 27%, see Nadler et al. 2014 (restricted to seven *Acropora* spp); Chase et al. 2014 (not restricted to species)), but exhibit congruent patterns of high occupancy and high biomass on patchy sheltered aspect sites and significantly lower values on continuous, exposed aspect sites. These results indicate that colony morphology and orientation contribute to variation in occupancy (discussed below), however coral occupancy of 30% may be an underestimate, as it excludes additional common fish families that can inhabit coral colonies (i.e. Apogonidae, Gobiidae, Haemulidae), and coral sizes (> 100 cm), and coral species (i.e. *Porites* and *Echinopora*). However, no fish species larger than 25 cm were observed interacting with coral hosts in any survey reported here, which indicates that these other fishes are not consistently associated with the coral species considered herein. Although structural complexity and subsequent coral cover are often positively associated with fish biodiversity (Friedlander and Parrish 1998; Graham and Nash 2013), results of this study showed that these two variables did not predict occupancy of biomass of coral-dwelling damselfishes that closely associate with corals, consistent with previous studies (Ault and Johnson 1998; Bergman et al. 2000; Darling et al. 2017). Furthermore, latitude did not significantly affect colony occupancy or biomass; consistent with studies reporting distribution and abundance of planktivorous damselfish patterns along the Great Barrier Reef (Emslie et al. 2019). It is possible that increased sample sizes across certain latitudes and geographic ranges could reveal subtle patterns present within this dataset.

The coral species considered within this study (*A. intermedia*, *A. spathulata*, *P. damicornis*, *S. hystrix*, and *S. pistillata*) are among the most preferred coral hosts for coral-dwelling damselfishes (Holbrook et al. 2000; Coker et al. 2014), yet 68% of colonies were unoccupied. This suggests that either abundance of these damselfishes is not limited by coral host availability (Doherty and Fowler 1994; Forrester 1995), or that there are colony attributes beyond species identity that determine their suitability as host corals (Noonan et al. 2012; Holbrook and Schmitt 2003). For certain sites, it is possible that low occupancy is a function of a lack of preferred coral habitats, resulting in lower fish abundance, however, surveys in this chapter demonstrate the drivers of damselfishes' occupancies to be more complex. This chapter reveals a suite of factors at small scale (< 1 m) that influence occupation rates, including colony height, and orientation on the benthos as well as the distance to other potential host corals. These attributes do not necessarily distinguish suitable versus unsuitable micro-habitats, but given the choice of host corals, it would be expected that damselfishes would select hosts that maximize individual fitness. Colonies with more elevated growth forms, raised above the seafloor, may also enhance fishes' abilities to stay higher in the water column, containing more enriched plankton, yet still close to refuge (Motro et al. 2005; Zikova et al. 2011). Elevated and isolated colonies, often in open orientations or on sandy substrates, allow for feeding with reduced danger due to visibility and enhanced colony structure complexity for refuge. Furthermore, damselfish species may respond differently to different species and morphologies of corals, with colony structure likely being important to small-bodied fish (Kane et al. 2009; Nash et al. 2013). For instance, *P. moluccensis* 45nalysin corals with more of a flat, two-dimensional shape (*A. spathulata* and *S. pistillata*), while *D. aruanus* prefer colonies with additional height (*P. damicornis*) and more open branch spacing (*S. pistillata*). Branch spacing of corals limits occupancy only in tighter branching species (*A. spathulata, P. damicornis*, and *S. hystrix*) and may lead to variations in species interactions (Chamberlain et al. 2014) between damselfishes with their competitors and/or predators, and services (i.e. nutrient retention, see Holbrook et al. 2008).

Colony isolation was consistently the most important attribute predicting damselfishes' presence and biomass. Many damselfish species exhibit 'clumped' or 'patchy' distributions, leading to increased fish-coral interactions with increased fish abundance (Chase et al. 2014). Edge habitats (i.e. sand patch and slope/base) with lower coral cover host more fish-coral interactions and allow for more 'open' colonies, rather than nested corals along continuous reefs (Nanami and Nishihira 2003; Nadler et al. 2014; Sambrook et al. 2016). The isolation and spacing of colonies occupied may allow for: a) continual use and residency by fish (i.e. distance to nearest available habitat is beyond the fish's home range); b) increased impacts of association defense and reduction of fish predation (Shpigel 1982; Sale 1972b); c) access to plankton resources and reduced competition; and d) larger borders with sandy substrates as an alternative foraging substrate (Wen et al. 2013). Competition between damselfish species is also responsible for the ecological partitioning of theses species along gradients (Eurich et al. 2004) leading to differential use and fish-derived benefits to coral hosts (Komyakova et al. 2013; Chapter 3). The fish-coral holobiont may be enhanced due to elevated levels of fish presence, reduced corallivores, and damselfishes' predators on isolated, patch habitats.

These results suggest that generalist damselfish species may be better able to exploit corals as refuge in high-flow environments than other species (Johansen et al. 2008). For instance, *P. moluccensis* was by far the most prevalent damselfish species recorded and contributed disproportionally to the fish biomass present on occupied colonies on exposed sites. While most coral-dwelling damselfishes are found in sheltered habitats (i.e. flow < 21.2 cm s^{-1}), the body shape and fin morphology (and aspect ratio) of *P. moluccensis* may make them more adapted to higher current velocities, while *D. aruanus* may be more suited to lower currents (Fulton et al. 2005; Johansen et al. 2015). Other abiotic (i.e. water temperature, salinity), and biotic features (i.e. predators, conspecifics) are likely to influence the distribution and abundance of damselfishes, independent of the abundance or availability of suitable coral hosts. In order to explicity disentangle small scale depth patterns of these damsefishes, more precise standardization across local reef zones and habitat complexity is warranted.

While damselfishes are present in nearly all coral reef habitats, fish-coral interactions may vary in the sign or magnitude of the effect on their coral host (Chamberlain et al. 2014; Chase et al. 2014), with certain colony-habitats (i.e. lagoon sand patch, and slope/base zones) acting as small-scale interaction hotspots with high occupancy and biomass patterns. Fish-derived nutrient hotspots are generally infrequent across seascapes, with average damselfishes' biomass low per site (this study: 205 ± 48 g 250 m^{-2}), compared with specialized, high biomass Haemulidae (grunts) aggregations (Meyer et al. 1983). In comparison to large *A. hyacinthus* hosting diurnal biomass concentrations of > 4.7 kg m^{-2} (Kerry and Bellwood 2016), damselfishes' biomass on small branching corals in this study is considerably smaller at 10.03 ± 0.43 g $colony^{-1}$.

As a result, certain density-dependent services in the field, such as nutrient subsidy, may be limited to high biomass colonies (i.e. > 15 g) seen in studies focusing on larger-bodied or more abundant fish species (Meyer and Schultz 1985a, b; Holbrook et al. 2008) or in high density colonies (small coral to high fish biomass present) or certain habitats (i.e. sand patch and slope) where average colony biomass is high. Additionally, large fish resting under table corals interacting with their host coral are considerably different from smaller-bodied fish around branching corals. It is likely fewer fish-derived services generated by resident large fish, as tissue aeration and slowing of disease progression have only been identified in Pomacentrid species. Overall, different coral species have important effects on the biodiversity and function of resident fishes, with several colony structure traits directly associated with fish-derived services (i.e. hosting fish, retention of nutrients, see Darling et al. 2017).

Specific fish-coral associations can produce discernible benefits for host corals through fish services, such as increased photosynthesis (Garcia-Herrera et al. 2017) and colony growth (Meyer et al. 1983). By determining the spatial extent and relative frequencies of these interactions, this study aids in quantifying a measurable link between fish services and coral populations. The focal damselfish and coral species in these surveys are commonly studied in relation to the temporal nature of fish-coral interactions, fish-derived services to corals, and impacts of fish on coral health (Holbrook et al. 2008; Chase et al. 2014, 2018b). With 68% of corals vacant, it is clear that many colonies do not receive potential beneficial effects of resident damselfishes. However, certain provided benefits may be more necessary within specific habitats (i.e. deeper sand patch and slope habitats) or under specific environmental conditions (i.e. low flow habitats) For example, the effect of damselfish on coral growth increases at great depth and under lower light intensity, but diminishes under conditions of high nutrient supply or high water flow (Chase et al. 2014). Furthermore, not all damselfish species produce the same services, suggesting smaller portion of colonies benefit from fish symbionts. For instance, as a majority of interactions in this study solely involved *P. moluccensis,* this species only provides one of the five documented fish-derived coral benefits. Conversely, *D. aruanus* present on only 14% of damselfish occupied corals and in select habitats, provides at least four services (Holbrook et al. 2008; Chase et al. 2014), thereby having a stronger impact on coral health for a smaller proportion of the population of fish-coral interactions.

2.5.2 Conclusions

By analysing the occupancy and biomass of damselfishes, one of the most abundant and important reef fish families that make an important contribution to reef foodwebs (Frédérich et al. 2009), this research illustrates that both large-scale features of reef habitats and fine-scale coral morphological traits contribute to fish-coral association. Several coral-dwelling damselfish species are constrained to certain reef habitats likely due to the physical constraints of the habitat, such as high-water energy. However, even after accounting for extrinsic factors there are important colony traits that influence colony use; fish presence and use must be measured at scales relevant to fish size and coral association (Nash 2013). Clearly, studies of coral-associated fauna across multiple spatial scales, that go beyond simply quantifying fauna presence-absence are necessary to understand the population dynamics of corals and symbiotic fauna. Quantifying the monitoring, establishment, and maintenance of such symbiotic associations with scleractinian corals, will be essential to predicting how these complex networks operate under global environmental stress. Moreover, the high degree of spatial variation in the strength of fish-coral interactions and other symbiotic interactions will make it challenging to predict their ecological functioning and cost-benefit ratios.

CHAPTER 3: Intensity and importance of coral host associations involving coral-dwelling damselfishes (family Pomacentridae)

The content of this chapter has been submitted as:

Chase TJ, Pratchett MS, Hoogenboom MO (in press) Behavioural trade-offs and habitat association of coral-dwelling damselfishes (family Pomacentridae). Marine Ecology Progress Series

3.1 Synopsis

Many coral reef fishes are intimately associated with branching corals. While these fishes rely on their host corals for shelter, fishes may exhibit behavioural trade-offs linked to spatial and temporal variations in their association with corals. This chapter quantified variation in coral use by five species of damselfishes, assessing key behavioural traits that determine the extent to which damselfishes interact with their host colonies. *In-situ* behavioural observations revealed marked interspecific differences in diurnal and nocturnal behaviour among five damselfish species. *Dascyllus aruanus* and *Dascyllus reticulatus* consistently displayed frequent and sustained interactions with and around corals (i.e. frequent colony visits and high aggressiveness towards other fishes), compared to *Chromis viridis, Pomacentrus moluccensis,* and *Pomacentrus amboinensis* that exhibited weaker associations (i.e. few colony visits and low aggression) with host colonies. Coral bleaching impacted modal diurnal swimming positions, thereby altering damselfish-coral interactions under thermal stress. This research demonstrates that coral-associated damselfishes utilize host colonies in very different ways with complex variation in behaviour which extends beyond simple proximity to host coral. Such among-species variation is likely the result of behavioural trade-offs related to coral

association. Understanding species-specific foraging and colony use behaviour is important because habitat degradation may undermine habitat-associations of coral-damselfish and associated mutualistic services.

3.2 Introduction

Scleractinian (hard) corals, and primarily branching corals, are critically important habitat-forming organisms on coral reefs. For example, > 320 species (8%) of reef fishes world-wide associate with live scleractinian corals (Coker 2012; Coker et al. 2014), though many more species (60-65%) are reliant on coral-rich habitats and are adversely affected by coral loss (Jones et al. 2004; Wilson et al. 2006; Pratchett et al. 2008, 2018). Reef fishes, along with many reef-associated motile invertebrates, rely on corals for food and/or shelter (Holbrook & Schmitt 2002, Cole et al. 2008; Stella et al. 2011; Coker et al. 2014), as an egg-laying substrate (Munday & Jones 1998; Coker 2012a), and as temporary refuge from water currents or predation (Johansen et al. 2008). Moreover, corals modulate fish competition, predation and other biological interactions, contributing to the high number of species that co-exist within coral reef environments (Almany 2004; Messmer et al. 2011). The fundamental reliance of reef fishes on coral habitats is most evident during major environmental disturbances and episodes of coral loss, whereby severe (> 60%) coral loss is linked to declines in abundance, biomass and diversity of reef fishes (Wilson et al. 2006; Pratchett et al. 2016). Severe episodes of mass-coral bleaching, which almost invariably lead to elevated levels of coral mortality (e.g., Hughes et al. 2018), have been linked to extensive declines in abundance of fishes, with concomitant effects on the structure, function and productivity of reef fish assemblages (Pratchett et al. 2011, 2018).

The nature and variation within fish-coral associations depends upon: i) densities of fishes within individual coral hosts (Chase et al. 2014; Shantz et al. 2015); ii) levels of site fidelity and use (Jones et al. 2004; Munday 2004; Coker et al. 2014); iii) the position and persistence of fishes relative to coral colonies (Garcia-Herrera et al. 2017); iv) body size or overall biomass of resident fishes (Holbrook et al. 2008; Chase et al. 2014); and v) behavioural trade-offs. These facets are dictated by species prioritizing essential fitness-enhancing processes of growth, reproduction, and survival. The ecological consequences of these behavioural trade-offs (Caley & Munday 2003; Sih et al. 2012) are linked to the nature of fish-coral interactions with a regard to a fishes' specialization to different environmental conditions, social structure, and positive growth/size feedbacks. For example, small-bodied coral-dwelling damselfishes can enhance the growth of their host coral, which in turn promotes fidelity by those fishes to the same coral, thus promoting residency of more fishes to larger, healthy shelters, compared with overcrowded, unhealthy corals (see Holbrook et al. 2011). Furthermore, fish-habitat associations are provisional on environmental conditions. Abiotic factors such as increased sea-surface temperatures, water flow conditions (Johansen et al. 2008), and sediments (Wenger & McCormick 2013) can reduce fishes' foraging distance and movement, and lead to confusion over preferred coral habitats. Alteration of fishes' behaviours, physiology, and survival due to reduced visibility, altered olfactory cues, and increased temperature could alter the selection and location of preferred colonies by fishes (Munday et al. 2008; Nagelkerken & Munday 2016; Boström-Einarsson et al. 2018). The health status of coral hosts, which can be impacted by coral bleaching (Bonin et al. 2009; Coker et al. 2014), disease (Casey et al. 2014), or degradation (algae overgrowth, loss of complexity due to breakage or death) can also lead to dramatic changes in fishes' behaviours, potentially undermining positive effects that fishes can have for host corals, such as enhanced growth and survival (Meyer & Shultz 1985b; Holbrook et al. 2008; Shantz et al. 2015).

Aside from differences in coral reliance and habitat preferences (Wilson et al. 2006, 2008), reef fishes vary in their diurnal patterns of movement, foraging, and habitat-associations. For example, coral-dwelling damselfishes forage actively during the day, and often shelter among the branches of specific host corals throughout the night (Holbrook & Schmitt 2002). Conversely, juvenile haemulids forage mainly at night, and they do exhibit strong site-fidelity, generally resting on the periphery of specific branching coral colonies during the day (Meyer et al. 1983). Therefore, the extent to which fishes interact with, and influence conditions for, host corals varies taxonomically, spatially and temporally (Liberman et al. 1995; Garcia-Herrera et al. 2017). For instance, fish-derived services, like coral tissue aeration by damselfishes, are particularly important at night when coral photosynthesis is absent and hypoxic conditions can develop among the coral branches (Shashar et al. 1993; Kühl et al. 1995; Goldshmid et al. 2004; Garcia-Herrera et al. 2017). Fishes also vary in their associations with different coral species, largely based on different colony morphologies, which afford different levels of shelter, shade, and protection from predation (Kerry & Bellwood 2012). As a result, taxonomic differences in coral use will influence the overall fish-coral feedback.

Obligate coral-associated fishes, such as coral-dwelling damselfishes, not only have direct interactions with host corals, but may also moderate the interactions and effects of other, more transient fishes, based on their level of aggression (McCormick & Meekan 2007). Aggressive interactions, associated with territory or social dynamics, especially those that involve chases, could lead to enhanced water flow and mixing within the colony (Goldshmid et al. 2004), deter corallivores (Cole et al. 2011), as well as potentially cause abrasion damage to coral tissues. Again, aggression may be influenced by coral bleaching or thermal stress (Coker et al. 2012b) and can differ between climate-sensitive and climate-robust coral assemblages (Kok et al. 2016). During crepuscular and nocturnal hours, aggressive individuals can relegate subordinate individuals towards the branch ends or outside the colony (Holbrook & Schmitt 2002; Coker et al. 2012b), likely reducing the input of fish-derived nutrients to the coral colony. Colony usage traits (e.g. nocturnal position, conspecific and heterospecific aggressive interactions, and frequency of colony visits) represent tangible metrics for determining the nature of fish-coral interactions.

This chapter quantified spatial and temporal variations in associations between coral-dwelling damselfishes and their host corals, by examining colony associated (1) behaviours (i.e. territoriality and foraging) and (2) usage traits (i.e. roosting grounds or shelter). While previous studies have demonstrated the importance of corals for resident damselfishes (Pratchett et al. 2012; Coker et al. 2014), and the benefits that these fishes may confer to corals (Holbrook et al. 2008; Chase et al. 2014), interspecific variations in damselfishes'movement and behavioural strategies has not been fully considered. Importantly, species-specific differences in the nature of fishes' associations with their host corals (e.g., frequency and extent of colony visits) is directly linked with their survival strategies and potential benefits provided to host colonies. In this chapter, key diurnal and nocturnal behavioural traits, were quantified *in situ* for five Pomacentrid species to assess their usage and interaction with host colonies (Table 3.1). As a bleaching event occurred during sampling, the impact of colony bleaching/thermal stress on variation in fishes' behaviour, was also examined. As subtle variations in behaviours can impact the outcome of interactions between fish species and association with their coral hosts, this research provides new insight into the importance of fish-coral interactions for coral reef fish populations and communities (e.g., Pruitt & Ferrari 2011; Chamberlain et al. 2014).

3.3 Materials and Methods

3.3.1 Study system

This chapter considered five species of damselfishes (*Chromis viridis*, *Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis and P. moluccensis*) that associate with corals, but vary in their habitat preferences and reliance on live corals (Wilson et al. 2008; Pratchett et al. 2012). These species settle preferentially in reef habitats and in coral hosts containing conspecifics and exhibit high levels of site fidelity (Booth et al. 2000; Booth 2002; Holbrook & Schmitt 2002), often associating with the same coral colony throughout their lives (Sale 1971; Sweatman 1983). These fishes mostly occur in groups, with the number of conspecifics cohabitating a coral colony dependent on the size and complexity of coral hosts (Chase et al. 2014; Holbrook et al. 2000). Average body size and biomass varied slightly by species, but all species were naturally size-matched to fit within the branches of the sampled coral colonies (Allen et al. 2003; Chase et al. 2014; Coker et al. 2014), due to their selection of their host coral over another for residency. Additionally, these species do co-occur on the same coral hosts (Nadler et al. 2014).

Rather than considering the full suite of potential host corals, this chapter focused on five coral species: *Acropora intermedia*, *A. spathulata*, *Pocillopora damicornis*, *Seriatopora hystrix*, and *Stylophora pistillata*. These corals are widely distributed on the Great Barrier Reef (GBR), are locally abundant, and are often occupied by coral-dwelling damselfishes (Holbrook et al. 2000; Pratchett et al. 2012; Coker et al. 2014). Relatively small (~20-80 cm in diameter) coral colonies were selected to standardize for colony size. *In-situ* coral surveys and behavioural observations took place between February - April 2016, which coincided with mass-bleaching in the northern GBR (Hughes et al. 2017, 2018). Behavioural observations were conducted at the following locations (Fig. 1a): northern sites around Ferguson reef (12°33'S, 143°49E, Fig. 1b) and the Lizard Island region (14°41'S, 145°27'E, Figure 3.1c, and see Table 3.1), where bleaching among these coral species was relatively similar (Hoogenboom et al. 2017; Hughes et al. 2017) at shallow depths. All colonies were located on sandy patch and slope/base habitat zones at a depth of 0-12 m (further details regarding locations, coral colony details, and damselfish group sizes in Table 3.1). Coral colonies were considered to be bleached wherever there was anomalous coloration on > 50% of the colony (following Hoegh-Guldberg 1999; Baird et al. 2009; Hughes et al. 2017), whereas colonies with normal pigmentation were considered to be healthy, or at least, not bleached.

Table 3.1 Summary of research objectives, behaviours measured, sampling data design, research locations, and coral colony details. Additional information regarding specific sample sizes of damselfishes per coral species is listed with the Chi-square (χ^2) analysis in the Results. Aspects of mid- and offshore sites are either sheltered (lagoonal or western aspect sites) or exposed (eastern aspect sites) with generally low flow or medium low flow environments, respectively. Letters H (healthy) and B (bleached) signify the number of colonies per species per coral bleaching status. Fish numbers per coral species are listed in parenthesis next to coral species bleaching status.

Research Approach	Specific Behaviours	Sampling	Data points	Locations	Coral colony details
(i) *In-situ diurnal observations of damselfishes on coral hosts*					
In situ filming branching coral colonies (20-80 cm) for 20-40 min to determine species-specific behaviours *bleaching status of the colony was included as a co-factor for behaviours 1-6	(1) Average distance from host colony (cm)	Representative individual	10 observation points	Sand patch and slope/base habitats of Lizard Island (14°41'S, 145°27'E) and Ferguson reef sites (12°33'S, 143°49E)	Semi-isolated (non-bleached and bleached) branching corals (0-14 m, lowest astronomical tide (LAT)) hosting 1400 damselfishes. 34 exposed colonies and 38 sheltered colonies: *A. intermedia* (n = 11: 4H, 8B | Fish = 184) *A. spathulata* (n = 17; 4H, 11B | Fish = 550) *P. damicornis* (n = 27: 18H, 8B | Fish = 557) *S. hystrix* (n = 10: 1H, 9B | Fish = 68) *S. pistillata* (n = 9: 2H, 7B | Fish = 77) Multi-species group size range: 2-105 damselfishes Average group: 20 damselfishes Damselfish group size mode: 7 (0-20 fishes: 43 colonies | 21+ fishes: 29 colonies) Average damselfish diversity per colony: 2 species Colonies were healthy (n =29) and bleached (n = 43)
	(2) Maximum distance (above and side) from host colony	Maximum distance of any fishes	Once		
	(3) Colony visits	All fishes	All visits		
	(4) Within colony conspecific aggression	All fishes	All aggressions per fish species per conspecifics		
	(5) Heterospecific aggression	All fishes	All aggressions per fish species per other fish present		
	(6) Modal diurnal spatial position (above, under, or side)	Representative individual per species per colony	10 time-points (coral colonies pooled)		
	(7) Algae eating behaviour	12 colonies	All bites, expressed as proportion of algae colonies		
Short-term reaction to startle stimulus response	(1) Refuge position in relation to host coral colonies (in colony, under, outside colony)	All fishes	All fishes' positions summed over 4 startle stimulus trials (coral colonies pooled)	Sand patch and slope/base habitats of Lizard Island (14°41'S, 145°27'E) and Ferguson reef sites (12°33'S, 143°49E)	43 Semi-isolated (non-bleached) branching corals (0-5 m LAT)), in sheltered locations, hosting 1023 damselfishes: *A. intermedia* (n = 7) *A. spathulata* (n = 12) *P. damicornis* (n = 13) *S. hystrix* (n = 5) *S. pistillata* (n = 6)

						Multi-species group size range: 1-111 damselfishes Average group size: 25 damselfishes Damselfish group size mode: 6, 9, 10 (0-20 fishes: 24 colonies | 21+ fishes: 16 colonies) Average damselfish diversity per colony: 2.5 species
(ii) In-situ nocturnal observation of damselfishes on coral hosts						
Recording position of damselfishes on colonies *all colonies observed during the day (0800 - 1700) to record the number of resident fishes per species for nocturnal comparison	(1)	Modal nocturnal sleeping (‘roosting’) position between 2000 – 2300 h	All fishes	Modal position	Sheltered and patch and slope/base habitats of Lizard Island (14°41’S, 145°27’E)	25 semi-isolated (healthy, non-bleached), small (~50 cm diameter) *P. damicornis* colonies (0-6 m LAT), hosting 311 damselfishes. Multi-species group size range: 3-36 damselfishes Average group size: 13 damselfishes Damselfish group size mode: 9 (0-20 fishes: 17 colonies | 21+ fishes: 9 colonies) Average diversity per colony: 2 species

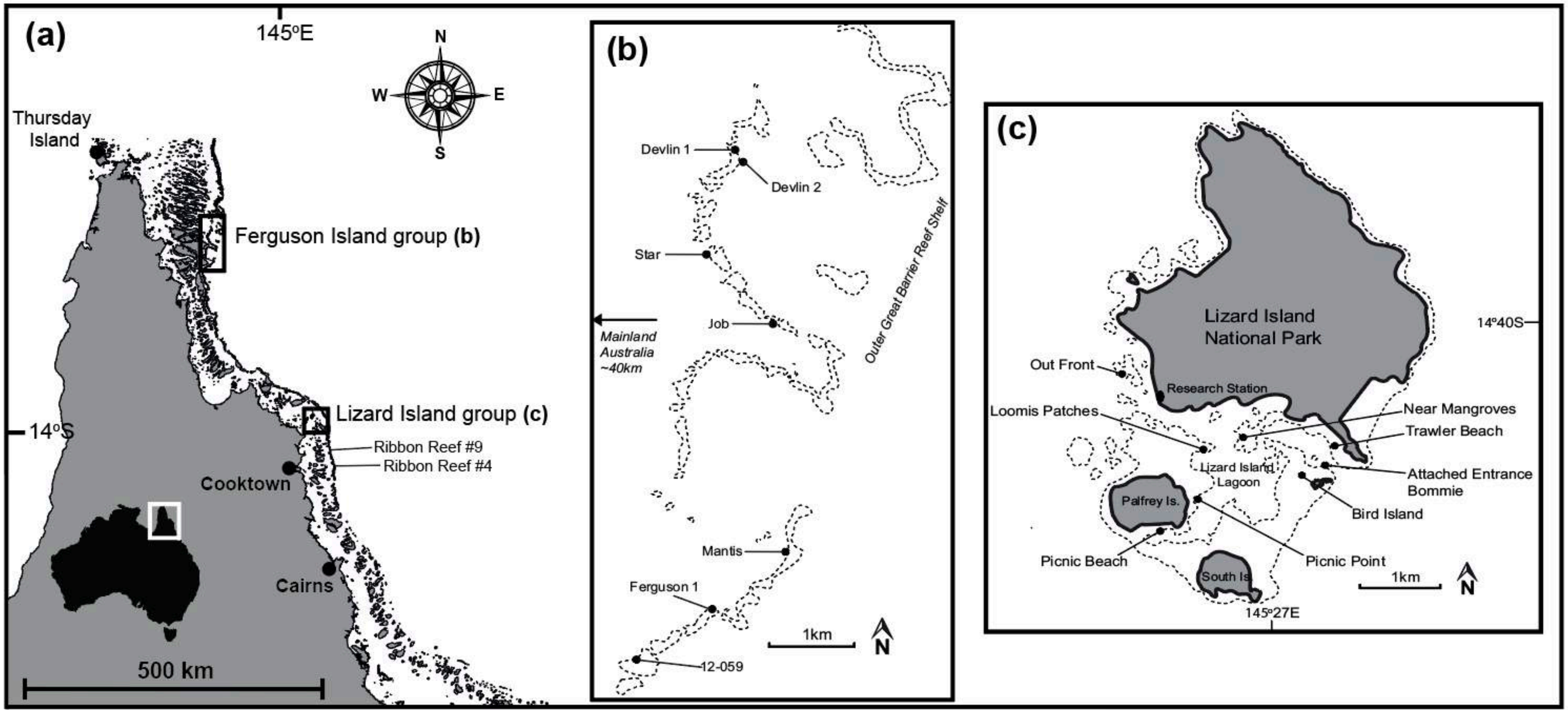


Figure 3.1 Location of study sites along the **(a)** northern Great Barrier Reef for the two study regions, **(b)** the northern Ferguson Reef region and **(c)** Lizard Island region. Dashed lines represent reefs and solid grey areas represent land. Diurnal and nocturnal behavioural observations were conducted on five species of damselfish on five species (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis*, *and P. moluccensis*) of coral (*A. spathulata*, *A. intermedia, P. damicornis, S. hystrix*, and *S. pistillata)* in sand patch and slope/base habitats ranging from 0-12 m below lowest astronomical tide. Map template is provided by Geoscience Australia under Creative Commons Attribution 4.0 International License.

3.3.2 Behavioural Observations

A series of behavioural traits relating to movement, diurnal and nocturnal position, and aggression were recorded for individual fishes (non-juvenile, minimum 2 cm length, group size ranged from 3-105) of each species during *in-situ* observations (SCUBA diver observations and underwater video camera recordings, see Longo and Floeter 2012; Branconi et al. 2018). The focal fish behavioural traits were (1) average distance from host colony; (2) maximum distance from host colony; (3) colony visits; (4) conspecific aggression; (5) heterospecific aggression; (6) modal diurnal orientation; (7) algae eating behaviour; (8) refuge position, and (9) modal sleeping position (see Table 3.1). This chapter focused on behaviours that are linked with important foraging versus survival trade-offs as well as key benefits that fishes provide to coral colonies.

i. Diurnal variation in colony use

Behavioural observations were conducted on mid-shelf and outer-shelf reefs (Table 3.1 and Figure 3.1) on the GBR, from February – April 2016. *In-situ* video recordings were used to quantify the behavioural differences between the five species of aggregating fishes. Semi-isolated colonies (~20-80 cm diameter) of *A. intermedia* (n = 12), *A. spathulata* (n =17), *P. damicornis* (n = 27), *S. hystrix* (n = 10) and *S. pistillata* (n = 9) were filmed for approximately 20-40 minutes each, between 0800 and 1700 h, using high-definition digital video cameras in underwater housings (Hero4 1080p; GoPro). These coral-dwelling species exhibited home ranges that encompassed a single branching coral or small reef structure; nearby suitable branching coral colonies (> 1 m) were beyond average swimming distances. Two GoPro cameras on tripods were situated around the coral colony; one 1 m to the side of the colony and the other 1 m above the colony, to allow for a 360° view of fishes' movement around the coral colony (note, due to standardization of colonies to LAT, all GoPro cameras were underwater during recording). Two, 1 m tape measures were affixed to aluminum poles and positioned adjacent to the focal coral colony for the duration of the observations, serving as scale bars to estimate coral size, fishes' movement, and fishes' size. For each video, a random 10-minute section was selected, excluding the first and last 5 minutes of the video recording in order to exclude any potential disturbances to the fishes due to diver presence during camera deployment and retrieval. This buffer time also allowed fishes to acclimate to the presence of the cameras and scale bars; this acclimation time was deemed appropriate due to fishes resuming natural foraging distances as observed in undisturbed colonies and from previous literature (Chase et al. 2014; Eurich et al. 2018).

Average distance was calculated as the average of the 10 observations for one individual damselfish per each species present on a colony throughout a 10-minute observation period (colony level as the replication unit) and maximum distances were measured by a single observation of the maximum distance of one haphazardly selected damselfish per species within the 10-minute observations. This method of taking either the average or maximum from 10 observations per fish was needed to get a reliable indication a fish's average distance, due to their ever-changing movements. To avoid pseudoreplication the multiple observations were collapsed into a single data point (averaged) prior to statistical analysis. Maximum distances on top of the coral and to the side are connected with fishes' home range (side position = patrolling their areas and exploring new habitat, see Kent et al 2016; Branconi et al. 2019) and foraging behaviours (top position = accessing plankton above the colony, or access to more/better resources, see Noda et al. 1992; Mann & Sancho 2007). These maximum distances were measured by a single observation of the maximum distance of any one damselfish per species within the 10-minute observations.

Diurnal swimming position categories included: “in colony branches” (within branching structure), “above colony” (vertically on top of colony) “under” (under colony structure), and “side” (to the side of the colony). These categories are directly related to foraging for plankton in surrounding water currents (Liberman et al. 1995), and predator avoidance (Boström-Einarsson 2018; Boström-Einarsson et al. 2018; Gauff et al. 2018), along with the nature of certain fish-derived benefits to coral colonies (Goldshmid et al. 2004; Layman et al. 2013). Modal diurnal position was determined by recording the most commonly occupied position relative to host coral of one fish per species, per individual coral colony (a “representative individual”) over ten observations during the 10-minute video periods for each coral colony, see Table 3.1). Coral species were pooled to increase sample sizes for each damselfish species. These methods were determined appropriate due to the fluctuating movement by fishes (10 observation points as replicate counts rather than repeated time points), and the directional orientation and grouping of many of the damselfishes.

Aggressive interactions were characterized by a rapid movement in the direction of another fish often leading to fin flaring, nips, defensive darting towards unwanted visitors (Sale 1970; Parmentier et al. 2009) and/or chases around the colony (see Kok et al. 2016). Counts of aggressive interactions and colony visits were standardized to per fish per 10 minutes. Colony visits were used as a proxy for diurnal colony use and is defined as when a fish completely entered the colony. These visits are typically short in duration (all fishes exited the colony within 10 seconds of entering), but constitute episodes of close interaction between fish and colony. Due to the natural variation in abundance of heterospecific damselfishes on the colony and local predators, heterospecific aggressiveness was also standardized by numbers of heterospecifics present on each colony, as well as any outside fishes that interacted with the colony during the observation period (five outsider fishes interacted with the 72 focal colonies in this experiment).

In addition, fishes' behaviour was quantified to determine whether it differed between bleached and unbleached colonies, to assess if colony bleaching/thermal stress was a factor in driving variations in fish behaviour, and colony usage. Very low levels of partial colony mortality (< 5%) were observed on 12 bleached colonies, and for these colonies algal eating (biting), by damselfishes was recorded per damselfish species and are presented as averages in the Results. Average colony diameter was measured for each colony using ImageJ software (Schneider et al. 2012), which was then used to calculate colony volume, assuming each colony was hemispherical in shape; colony diameter was also included in the measure of fish density and included in statistical models for each of the behavioural traits analyses.

ii. Nocturnal colony use

In-situ behavioural observations were used to compare modal diurnal and modal nocturnal colony occupancy by the same five species of fishes. Within the Lizard Island lagoon, a separate set of *P. damicornis* colonies (n = 25), with aggregating fishes, were tagged and monitored. These corals were tagged during the day using cattle tags, and the positions of aggregating fishes present on coral colonies were observed and recorded via SCUBA both during the day (0800 – 1700 h) and night (2000 – 2300 h), to ensure accurate fish numbers on each colony at night. During nocturnal observations, each tagged coral colony was inspected by SCUBA divers utilizing an underwater torch (using white and UV light) for illumination. The colony was illuminated for less than 20 seconds and this did not induce movement by any of the resident fishes. Due to the sedentary nature of the damselfishes at night, the position of each individual fish was recorded. Nocturnal positions of all individuals of each damselfish species were measured once for each colony of *P. damicornis*. The position of each fish relative to the coral colony was categorized as: “in colony branches”, “under colony”, or “reef” (not visible around colony or located in rubble beneath/near colony) to differentiate fishes’ positions.

iii. Short-term reaction to startle stimulus response

To further quantify the association between aggregating fishes and their host colonies, reaction to startle stimulus trials were performed *in situ*, on natural, non-manipulated coral colonies (n = 43), hosting 1023 damselfishes in the field. On SCUBA, a diver rapidly approached a coral colony with aggregating fishes present until the diver was within 25 cm of the colony, at which point the fishes moved to their selected point of refuge. A point of refuge was categorized as: “in colony branches” (retreat within physical colony structure or branches), “under colony” (retreat to under the colony or into substrate structure), or “outside colony” (swimming away into the water column). Startle stimulus trials were performed in replicates of four (see Table 3.1), to fully capture the refuge position of these continually moving damselfishes, with 90 seconds between replicates to allow focal fishes to return to normal behaviour. Fishes resumed normal foraging behaviours within 30 seconds of startle stimulus; no equipment was placed near the colony, the startle stimulus was similar to a diver swimming over the colony (minimal colony interference), and the interval of 90 seconds between replicates was included as an extra precaution.

3.3.3 Data Analysis

Behavioural observations were analysed using R statistical software (R Development Core Team 2018). Behavioural traits of fishes (average distance, maximum above and maximum side distance from colony) were analysed using Gaussian generalized linear models (GLM) with each behavioural trait as the dependent variable (log+1 transformed), and fish species, colony health, and fish density as independent variables, and colony number as a random factor (to account for any repeated measures of multiple fish within individual coral colonies). Bleaching category was included as a co-factor in select analyses based on evidence of behavioural changes due to bleaching/thermal stress and associated changes in colony health (Coker et al. 2009, Pratchett et al. 2018). Fish density (total number of resident fishes per unit colony volume) was included in these analyses as swimming distances of damselfish can be influenced by both colony size and total number of fishes per colony (Forrester 1991). Model selection was based on Akaike Information Criteria (AIC) values after Burnham and Anderson (2002), and Zuur et al. 2009, 2010; Zuur & Ieno 2016). Assumptions for model validity were checked through residual plots (QQ-normal plot for normality and scatter plots of residuals vs fitted for linearity), as well as calculations of dispersion (comparing model mean with variance). Statistical results were interpreted using the numerical output of the statistical model, after model validation. Following formal model selection, inclusion of colony health and fish density did not significantly improve the fit of the model to the data. As a result, for average distance, maximum distance above and maximum side distance, the best model only included fish species as an independent variable (see model comparison Tables 3.2, 3.3, 3.4). Based on generalized linear models, differences among the five fish species were assessed using estimated marginal means (R package 'emmeans') multiple comparison *post-hoc* (with a Tukey's HSD correction).

Colony visits were analysed using a Poisson distribution GLM, with colony visits (dependent variable), colony health (independent variable), colony number as a random factor (1 | colony), and fish number per species as an offset. The Poisson distribution was selected following AIC model comparison, and because the data were counts of events (visits). Fish number per species and fish density per colony were included as offsets in the model to standardize these counts (Yan et al. 2009).

Aggression data were analysed using GLMs, to determine if conspecific and heterospecific aggressions were different among species and influenced by colony health. In conspecific aggression models, fish species, colony volume, and colony health were included as covariables, and the number of fishes per species as an offset, to standardize conspecific aggressions per individual fish, per the number of conspecifics, to whom they could display aggression. For heterospecific aggression, fish species, colony health, and colony volume were covariables, and the number of fishes per species and the number of other fishes on the colony (number of heterospecific fish available to be aggressed towards) as an offset. Accordingly, figures for conspecific aggression data are displayed as standardized per number of conspecifics, and heterospecific aggression figure data are displayed as standardized per number of fishes per colony and number heterospecifics. Model selection was again performed by comparing AIC values (Zuur et al. 2009, 2010; Zuur & Ieno 2016); and including colony health and fish species did not significantly improve either model for conspecific or heterospecific aggression. Assumptions for model validity were again checked through residual plots, as well as calculations of dispersion.

Diurnal behavioural observational data were converted into modal position categories to represent the area around host colonies in which the fish were most often located. Modal positions were analysed using Chi-square (χ^2) tests comparing the number of observations of occupancy in each position within healthy and bleached colonies to expectations based on random chance (null hypothesis: fish spent equal time in each of the position categories, see Pearson 1990). Again, the multiple initial observations of diurnal position (10 observation points during observation period per fish species) were converted to a single value (mode) to avoid pseudoreplicaton of the data whilst accounting for variability in colony occupancy over time due to normal swimming and foraging activities. Modal diurnal position figures are displayed as proportions of all colonies per fish species with two different health categories: healthy and bleached. Modal nocturnal positions (observed on 25 colonies, separate from the diurnal colonies), with coral colonies pooled were analysed with separate a Chi-square tests (χ^2) by damselfish species. Colony bleaching was not included in the tests as all selected colonies for nocturnal behaviours were healthy (non-bleached) during the observation period. Data for nocturnal positions are presented as average proportion of time in each position category.

Startle refuge responses were analysed using a zero-inflated generalized linear mixed model (GLMM) with a negative binomial distribution to account for the over-dispersed (zero-inflated) count data; it combines the negative binomial distribution and a logit distribution. In the GLMM, the number of fish per shelter position was the dependent variable with fish species and shelter position as fixed factors (additive model), colony number as a random factor and startle number nested within colony (1 | colony / startle number), and total fish per species per colony as an offset. This model included all observation of all of the fish present on each colony whilst accounting for the repeated measures of individual fish within colonies. Colony bleaching was not included in tests as all selected colonies were healthy (non-bleached) during the observation period). Again, Tukey's HSD *post-hocs* were used to compare the startle refuge positions of the five fish species around host colonies.

All modelling was performed in the statistical software R (R Development Core Team, 2018) using the *MASS* (Venables and Ripley 2002), nnet (Venables and Ripley 2002), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), *glmmTMB* (Brooks et al. 2017), *nlme* (Pinheiro et al. 2014) and *emmeans* (Searle et al. 1980).

3.4 Results

3.4.1 Diurnal and nocturnal positions

All damselfish species considered in this chapter (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis and P. moluccensis*) spent the majority of daylight hours (>

80% of time) swimming within 30 cm of their host corals, presumably feeding in the adjacent water column (Fig. 3.2a), while sheltering on or within coral hosts during the night (Fig. 3.2b). The different species of fishes occupied different regions of the space above and around coral colonies, and there was strong evidence that the modal spatial position of fish relative to colonies was non-random (Fig. 3.2a). Three of the species (*C. viridis*, *D. aruanus*, and *D. reticulatus*) spent > 50% of their time positioned directly above the colony (pooled over colony health status). In contrast, *P. amboinensis* spent most of its time to the side or under the colony. Coral bleaching/thermal stress had an impact on the position of all damselfish species (Figure 3.3 and Table S3.1 in Appendix S3), with use of the side spatial position becoming more prevalent. Specifically, *C. viridi*s, *D. aruanus, and D. reticulatus* mostly swam above healthy colonies, but when on bleached colonies displayed weaker preference for the above position and increased swimming to the side and under the colony (*C. viridis*, n = 17 colonies, Chi-square: (bleaching status) $\chi^2 = 29.33$, df = 3 $p < 0.001$; *D. aruanus*, n = 46 colonies, Chi-square: $\chi^2 = 41.06$, df = 3, $p < 0.001$; *D. reticulatus*, n = 20 colonies, Chi-square: $\chi^2 = 16.50$, df = 3, $p < 0.001$). *P. amboinensis* spent most of the time to the side and under healthy colonies and switched to having a stronger preference for swimming above bleached colonies (n = 27 colonies, Chi-square: (bleaching status) $\chi^2 = 25.05$, df = 3, $p < 0.000$). *P. moluccensis* preferred swimming to the side and under healthy colonies, but demonstrated a stronger preference for swimming above and within the branches of bleached colonies, and a weaker preference for swimming under bleached colonies (n = 34 colonies, Chi-square: (bleaching status) $\chi^2 = 23.98$, df = 3, $p < 0.001$)).

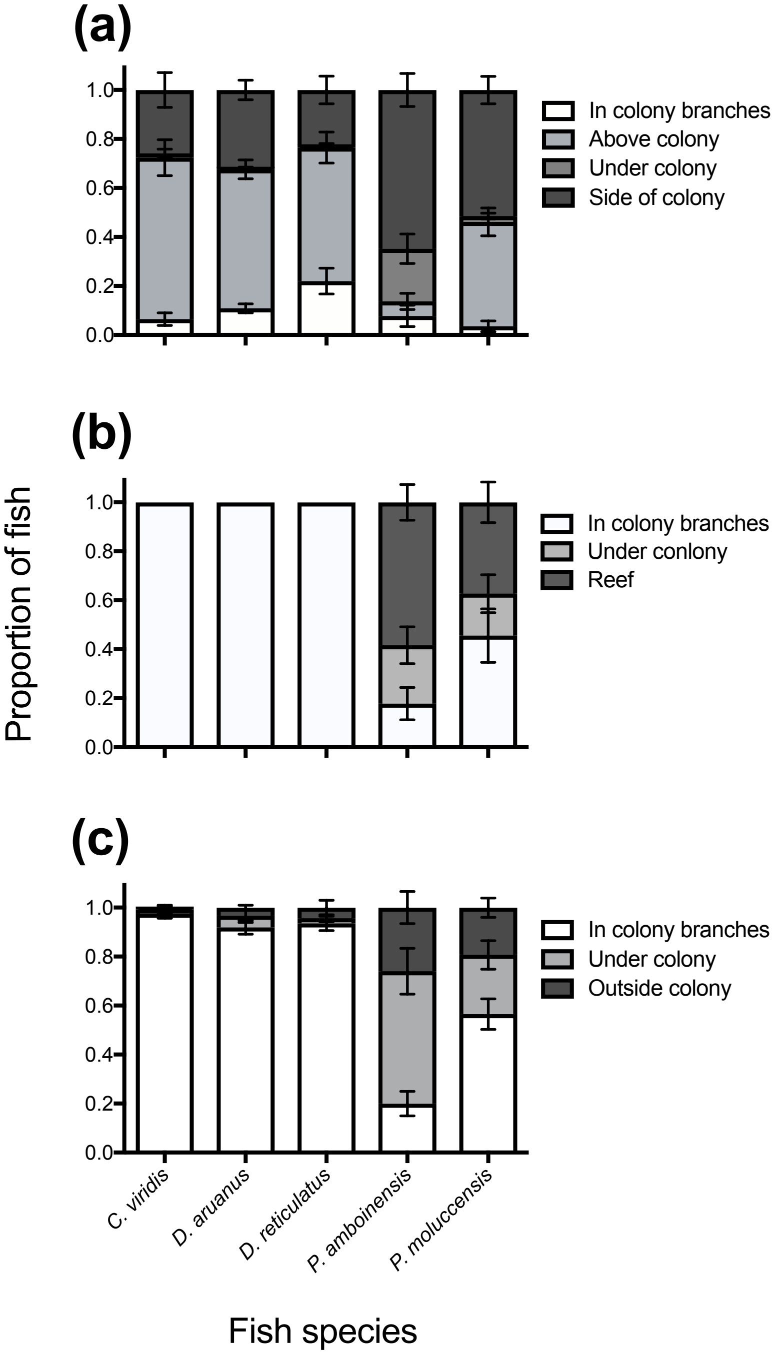


Figure 3.2 Average position (proportion ± standard error) of five damselfish species in relation to natural host colonies of small branching coral colonies (*Acropora intermedia, Acropora spathulata, Pocillopora damicornis, Seriatopora hystrix*, and *Stylophora pistillata*): **(a)** modal diurnal (~0800 – 1700 h) swimming positions, **(b)** modal nocturnal (~2000 – 2300 h) roosting positions, and **(c)** startle refuge positions.

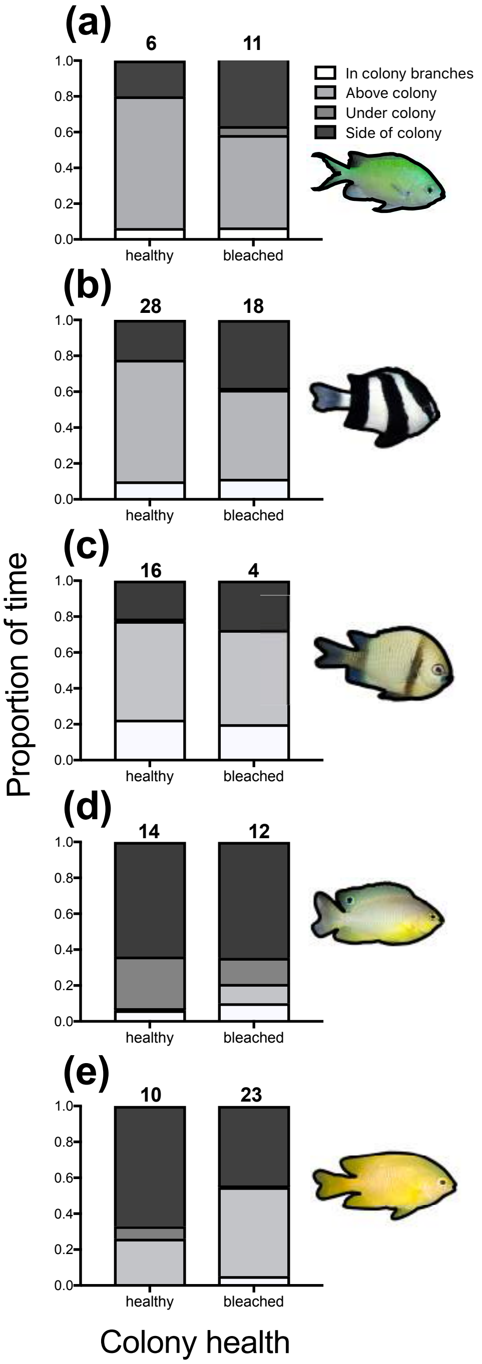


Figure 3.3 Average diurnal (~0800 – 1700 h) position of: **(a)** *Chromis viridis*, **(b)** *Dascyllus aruanus*, **(c)** *D. reticulatus*, **(d)** *Pomacentrus amboinensis*, and **(e)** *P. moluccensis* in relation to host colonies (*Acropora intermedia, A. spathulata, Pocillopora damicornis, Seriatopora hystrix*, *Stylophora pistillata)* of two different health categories: healthy and bleached. Coral sample size per coral health category are displayed above bars.

Targeted algae eating behaviour was observed on 66% of the bleached colonies with partial filamentous algae growth (8 out of 12 colonies). Algae eaten varied by damselfish species with *Dascyllus* species engaged in algae eating on 83% (bites on 6/9 and 1/1 colonies for *D. auranus* and *D. reticulatus*, respectively) of affected colonies and Pomacentrus species only on 58% (2/3 and 3/6 colonies for *P. amboinensis* and *P. moluccensis*, respectively) filamentous algae colonies; sample sizes were too low (zero bites on one algae-covered colonies) to report accurate *C. viridis* algae eating behaviours.

Nocturnal modal position (all damselfishes measured once on 25 colonies) around the colony was species-specific (Fig. 2b). *C. viridis, D. aruanus*, and *D. reticulatus* slept exclusively within the colony branches (*C. viridis*, $n = 103$ fish on 5 colonies, Chi-square: $\chi^2 = 8.50$, $df = 2$, $p = 0.014$; *D. aruanus*, $n = 120$ fish on 24 colonies, Chi-square: $\chi^2 = 48.00$, $df = 2$, $p < 0.001$; and *D. reticulatus*, $n = 28$ fish on 6 colonies, Chi-square: $\chi^2 = 12$, $df = 2$, $p = 0.0025$). *P. amboinensis* ($n = 31$ fish on 10 colonies, Chi-square: $\chi^2 = 1.50$, $df = 2$, $p < 0.027$) and *P. moluccensis* ($n = 39$ fish on 9 colonies, Chi-square: $\chi^2 = 2.67$, $df = 2$, $p = 0.264$) did not display strong preferences in modal position of the three roosting positions. *P. amboinensis* and *P. moluccensis* were both found more commonly outside the colony branches at night, often sleeping semi-motionless within the surrounding reef structure or under the colony.

Modal diurnal and modal nocturnal positions were congruent with startle refuge, with fish species exhibiting preference for refuge location (GLMM: $p < 0.001$, Figure 3.2c, and Tables S3.2 and S3.3 in Appendix S3). When startled, *C. viridis* ($n = 544$ fish on 15 colonies), *D. aruanus* ($n = 190$ fish on 28 colonies) and *D. reticulatus* ($n = 67$ fish on 10 colonies) all retreated into the colony branches > 91% of the time. *P. moluccensis* (n = 148 fish on 31 colonies) and *P. amboinensis* (n = 74 fish on 17 colonies) showed more variance in their refuge position, with *P. amboinensis* preferring to hide under the colony and *P. moluccensis* only retreating into the colony branches ~50% of the time. but still favoured retreating into the colony 57% of the time and displaying equal preference between under or outside the colony as secondary refuge positions (Figure 3.2c, Tables S3.2 and S3.3 in Appendix S3).

The number of colony visits (within the branches of the host colony) were significantly different between damselfish species (GLM: $p < 0.001$, see Table S3.4 in Appendix S3). Neither colony bleaching or fish density affected colony visits for any damselfish species (GLM: (bleaching status, $p > 0.05$), (fish density, $p > 0.05$)). *D. aruanus* and *D. reticulatus* displayed the highest mean (±SE) number of colony visits with 14.5 ± SE 1.8 and 15.3 ± SE 2.9 visits 10 min^{-1} respectively (Figure 3.4). *C. viridis* (4.6 ± SE 1.3 visits 10 min^{-1}), *P. amboinensis* (1.3 ± SE 0.3 visits 10 min^{-1}), and *P. moluccensis* (1.7 ± SE 0.4 visits 10 min^{-1}) exhibited fewer than 5 colony visits fish^{-1} 10 min^{-1}, indicating that these species spend less overall time within the colony branches during daylight hours. Overall *C. viridis*, *D. aruanus*, and *D. reticulatus* exhibited significantly higher visits than *P. amboinensis* or *P. moluccensis* (Table 3.2 for *post-hoc* comparisons).

Table 3.2. *Post-hoc* test (R package 'emmean') for multiple comparisons of colony visits (log + 1) per fish 10 min^{-1}, for each damselfish species from host branching coral colonies, with p-values. Values are based off model selection practice using degrees of freedom and Akaike information criteria (AIC) scores; the best model included colony visits (dependent variable), fish species (independent variable), coral colony (random factor), and fish number per each species as an offset. Significant p-values are in bold.

Comparison	P. adjusted
C. viridis – D. aruanus	**< 0.0001**
C. viridis - D. reticulatus	**< 0.0001**
C. viridis – P. amboinensis	**< 0.0001**
C. viridis - P. moluccensis	**< 0.0001**
D. aruanus - D. reticulatus	0.9999
D. aruanus - P. amboinensis	**< 0.0001**
D. aruanus – P. moluccensis	**< 0.0001**
D. reticulatus - P. amboinensis	**< 0.0001**
D. reticulatus - P. moluccensis	**< 0.0001**
P. amboinensis - P. moluccensis	0.9990

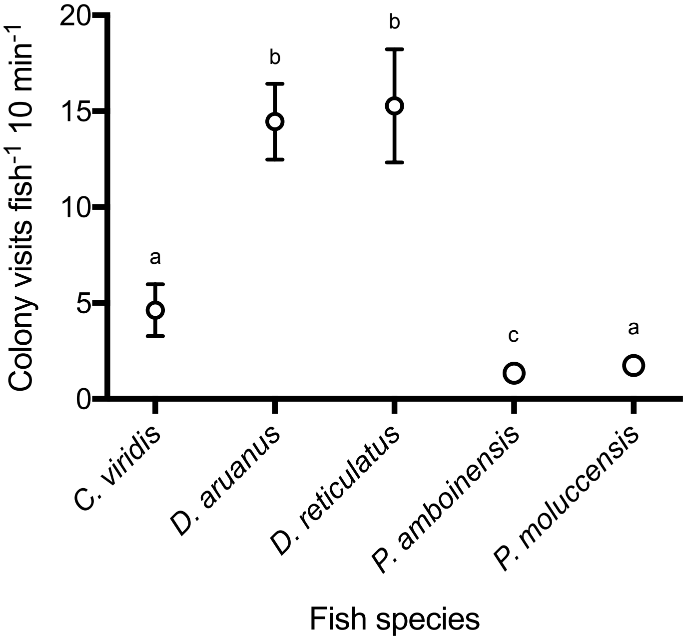


Figure 3.4 Numbers of visits of fish species to coral colonies. Data are standardized per fish, per coral colony and per 10-minute observation period. Letters above points denote a significant difference between fish treatments. *Error bars* show SE.

3.4.2 Proximity of fishes to coral colonies

During the day, fishes were observed continually swimming, eating plankton in the water column, and darting into the colonies to avoid nearby predators. Activity levels ranged from continual swimming due to foraging behaviour, to resting and stationary behaviour where fishes would remain nearly motionless within 10 cm of their host coral (Fig. 5). Average distance from host colony was significantly different between damselfish species (GLM: $p < 0.05$, see Table 3.3, Figure 3.5a, Table S3.5 in Appendix S3), and neither colony bleaching status ($p > 0.05$) nor fish density ($p < 0.05$) influenced this aspect of fish behaviour for any of the five damselfish species (Tables S3.5, S3.6, S3.7 in Appendix S3). *C. viridis* and *D. aruanus* generally had significantly larger average distances from their host colony compared with the two Pomacentrus species (see Table 3.3 for *post-hoc comparisons*).

Table 3.3 *Post-hoc* test ('emmean') for multiple comparisons with adjusted p-values for each species distance from resident colony: average distance, maximum distance above the colony, and maximum distance from the side of the colony; based on a lognormal generalized linear model (GLM) of average distance, maximum distance above, maximum distance to the side (dependent) and fish species (independent variable). Significant p-values are in bold.

Comparison	**Average distance**	**Max distance above**	**Max distance side**
C. viridis – D. aruanus	1.0000	1.0000	0.2019
C. viridis - D. reticulatus	0.8401	0.9954	0.6999
C. viridis – P. amboinensis	**0.0193**	**< 0.0001**	0.9950
C. viridis - P. moluccensis	**0.0063**	**0.0001**	0.9978
D. aruanus - D. reticulatus	0.7679	0.9996	0.9556
D. aruanus - P. amboinensis	**0.0015**	**< 0.0001**	**0.0267**
D. aruanus – P. moluccensis	**0.0002**	**< 0.0001**	**0.0197**
D. reticulatus - P. amboinensis	0.2095	**< 0.0001**	0.3568
D. reticulatus - P. moluccensis	0.1248	**0.0002**	0.3604
P. amboinensis - P. moluccensis	0.9995	**< 0.0001**	0.9999

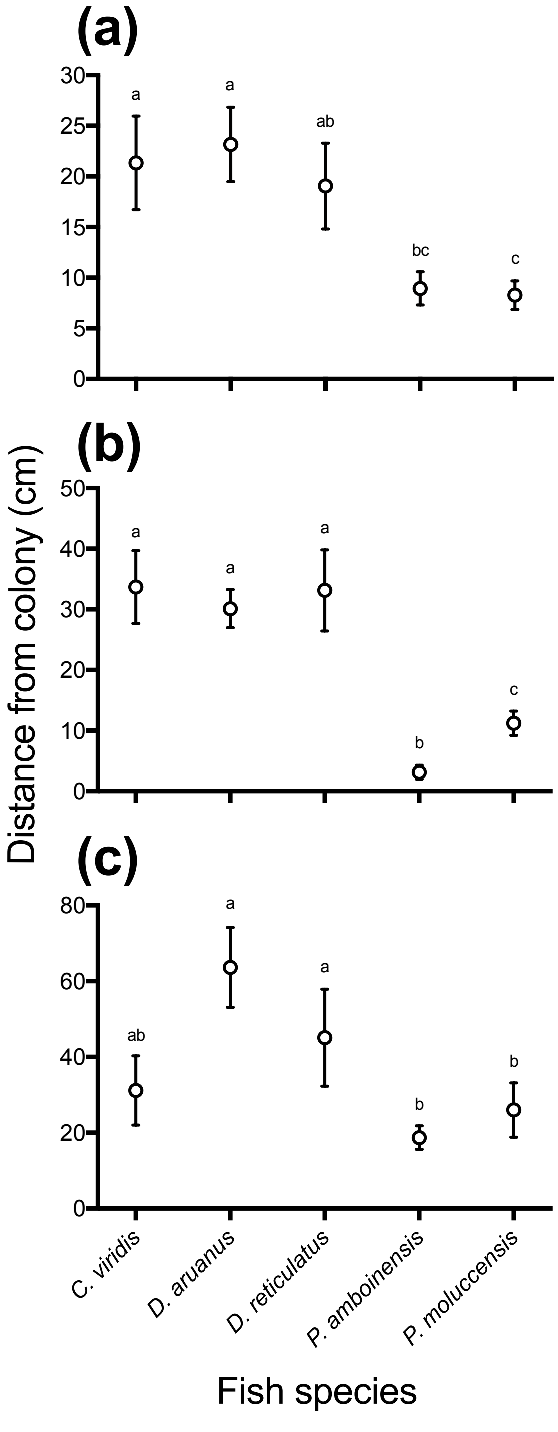


Figure 3.5 Species-specific distances from host colony: **(a)** average distance (cm), **(b)** maximum distance above (cm), and **(c)** maximum side distance (cm) from coral colony. Letters above points denote a significant difference between fish treatments. *Error bars* show SE. Note different y-axis for panels **a-c** to allow for visualization of variance between fish species.

The maximum distance that fishes moved above the colony (Fig. 5b), and the maximum distance moved from the side of the colony (Figure 3.5c, Table S3.6 and S3.7 in Appendix S3) displayed similar differences among species to the average distance each species maintained away from the colony (GLM: above, $p < 0.001$; side, $p < 0.05$). *C. viridis* (21 ± SE 4.6 cm), *D. aruanus* (23 ± SE 3.6 cm), and *D. reticulatus* (19 ± SE 4.2 cm) all displayed considerably further average (see Table 3.3 and Figure 3.4a) and maximum positions away from their host colony compared to *P. amboinensis* (8.9 ± SE 1.6 cm) and *P. moluccensis* (8.3 ± SE 1.4 cm, see Table 3.2 for *post-hoc* comparisons among species). Diver observations also recorded some *D. aruanus* temporarily moving > 3 m to neighbouring colonies. Again, colony bleaching, and fish density did not impact maximum distance to the above (GLM: $p > 0.05$) or side (GLM: $p > 0.05$) positions for any damselfish species.

3.4.3 Aggressiveness and territoriality

The frequency of aggression towards conspecifics was highest for *D. aruanus* (1.1 interactions fish^{-1} 10 min^{-1} ± SE 0.13, standardized to the number of conspecifics, Fig. 6a) and *D. reticulatus* (0.67 ± SE 0.13 interactions fish^{-1} 10 min^{-1}), which were significantly higher than for the other damselfishes (GLM: $p > 0.05$, see Table S3.8 in Appendix S3, and see Table 3.4 for *post-hoc* comparisons), and indicative of territorial damselfishes. *C. viridis* and *P. amboinensis* display particularly low aggression towards conspecifics, both with < 0.1 interactions fish^{-1} 10 min^{-1}. *P. moluccensis* displayed medium levels of aggression (0.29 ± SE 0.08 interactions fish^{-1} 10 min^{-1}). Colony bleaching ($p > 0.992$) and colony volume ($p > 0.962$) had no effect on total aggressive interactions.

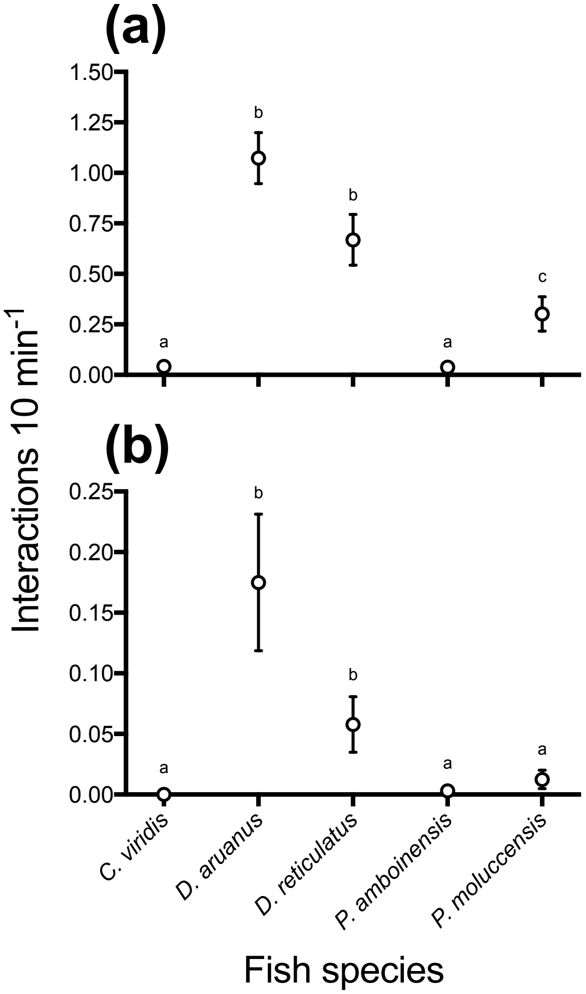


Figure 3.6 Aggressive interactions per species: **(a)** aggressive interactions with conspecifics 10-min^{-1}, standardized to number of conspecifics present, and **(b)** aggressive interactions with heterospecifics 10-min^{-1}, standardized to number of conspecifics and number of heterospecifics. *Error bars* show SE.

Aggressiveness with heterospecifics was also significantly different among species (GLM: $p < 0.05$, Table S3.9 in Appendix S3), with *D. aruanus* again displaying 2 to 10-fold more aggressive interactions than other damselfish species (0.17 ± SE 0.06

interactions fish^{-1} 10 min^{-1}). All other damselfish species displayed low heterospecific aggressive interactions, with *C. viridis* displaying zero interactions (Fig. 6b). *Post-hoc* analysis revealed significant differences for both *D. aruanus* and *D. reticulatus* and all other damselfish species (Table 3.4). *D. reticulatus* (0.057 ± SE 0.02 interactions fish^{-1} 10 min^{-1}) and *P. moluccensis* (0.12 ± SE 0.01 interactions fish^{-1} 10 min^{-1}) had medium scores for aggression, while *C. viridis* and *P. amboinensis* had nearly zero heterospecific interactions (0.00 ± SE 0.00 interactions fish^{-1} 10 min^{-1} and 0.003 ± SE 0.002 interactions fish^{-1} 10 min^{-1}, respectively). Neither colony bleaching nor colony volume both had any effect on heterospecific aggressive interactions ($p > 0.05$).

Table 3.4. *Post-hoc* test ('emmean') for multiple comparisons of conspecific and heterospecific aggressions, per fish 10 min^{-1} for each damselfish species from host branching coral colonies, with p-values. Values are based off model selection practice using degrees of freedom and Akaike information criteria (AIC) scores. The most parsimonious model was based on a lognormal generalized linear model (GLM) that included aggressions as the (dependent variable), fish species (independent variable), coral colony (random factor). Both conspecific and heterospecific aggression were standardized to number of each fish species; heterospecific aggressions included the offset term other fish on the colony. Significant p-values are in bold.

Comparison	**Conspecific aggression**	**Heterospecific aggression**
C. viridis – D. aruanus	**< 0.0001**	**< 0.0001**
C. viridis - D. reticulatus	**0.0499**	**< 0.0015**
C. viridis – P. amboinensis	**0.9996**	0.7543
C. viridis - P. moluccensis	0.6798	0.5527
D. aruanus - D. reticulatus	**0.0231**	0.6141
D. aruanus - P. amboinensis	**< 0.001**	**< 0.0001**
D. aruanus – P. moluccensis	**< 0.001**	**< 0.0001**
D. reticulatus - P. amboinensis	0.0120	**0.0497**
D. reticulatus - P. moluccensis	0.3818	0.2081
P. amboinensis - P. moluccensis	0.4343	0.9961

3.5 Discussion

3.5.1 Investigating variations among damselfishes' behaviours and trade-offs

While coral-dwelling damselfishes have known affinities for specific species of branching corals (e.g., Wilson et al. 2008; Pratchett et al. 2012), this chapter demonstrates that there are important interspecific differences in the nature of these habitat associations. Importantly, the five species of damselfishes considered in this chapter (*Chromis viridis, Dascyllus aruanus*, *D. reticulatus*, *Pomacentrus amboinensis* and *P. moluccensis*) exhibited marked differences in the proportion of time spent inside host colonies, the frequency with which they returned to host colonies, and the distance they ventured away from host colonies. These different behavioural strategies are likely linked to trade-offs (e.g. choosing between feeding versus sheltering), and the functional reliance on corals (discussed below). *D. aruanus and D. reticulatus* exhibited high usage and interactions with their coral hosts; their tight social network is likely derived from the physical structure of their host coral and their swimming positions and usage (Forrester 1991; Booth 1995) with priorities of foraging. *Pomacentrus* spp. showed less colony usage (i.e. maintenance or submissive behaviours involving the coral) and may have prioritized other fitness-enhancing behaviours such as survival or feeding, with less dependency on coral hosts (Fricke 1980; Fishelson 1998; Branconi et al. 2019). Differences in direct (distance from colony or colony visits) and indirect (aggressive) behavioural strategies with respect to fishes interacting with their shelter resource may also be linked to fishes' habitat specialization (Eurich et al. 2018), dependency upon the coral used for the habitat structure (Bay et al. 2001), shelter, swimming ability (Johansen et al. 2008) and foraging (Liberman et al. 1995). *P. amboinensis* are observed to use a small subset of live coral taxa, yet used individual colonies much less compared to the other four Pomacentrus species (this study, and Pratchett et al. 2012). Conversely, *D. reticulatus* was the most specialized species of the focal species and exhibited very high usage and dependency (Wilson et al. 2008; Pratchett et al. 2012). By measuring the nature of the damselfish-coral interaction, this research highlights the potential functional importance of particular species of damselfishes, their strategies of habitat use, and the prevalence of the interaction on coral reefs at the colony and seascape levels.

Apparent differences in behavioural modes and habitat associations among coral dwelling damselfishes most likely relate to fundamental cost-benefit trade-offs among foraging (i.e. position and access to prey, see Coates 1980; Foster et al. 1985; Biro et al. 2006; Wen et al. 2013; White et al. 2013), proximity to shelter and vulnerability to predation (Coker et al. 2009), mating/reproduction (i.e. increased breeding partners and egg-laying substrate, but high aggression/competition, see Forrester 1991, Coker 2012a, b), and social requirements (Fricke 1988, Forrester 1991). While close association with host colonies may reduce vulnerability to predation (Coker et al. 2009), constrained movement reduces prey access for plankton feeders and also increases vulnerability to habitat loss (Pratchett et al. 2012; 2016), while also increasing competition for resources and aggression (Sale 1972; Jones 1987; Coker 2012a). Variations in the average and maximum distance that fishes venture from host colonies are also linked to processes of group living, zooplankton foraging, and territories (Fricke 1977; Shpigel & Fishelson 1986; Fishelson 1998; Meekan 2010). As such, additional traits measured in this chapter (e.g., frequency of colony visits, nocturnal roosting position, and territoriality) may be better functional indicators of colony use. Although *D. aruanus* and *D. reticulatus* often ventured furthest from their host corals, they exhibited high colony usage behaviours (e.g. high colony visits, preferentially roosted within the colony branches, and actively defended the colony). Furthermore, of the fish species in this chapter that showed the lowest usage behaviours with their host corals, *P. amboinensis*, stayed the closest to the coral, yet barely interacted with the colony for shelter or sleeping and did not defend coral colonies within their home range. When associated with colonies *Dascyllus* spp. trade-off increased foraging distances with predator protection, while *Pomacentrus* spp. may trade-off optimal plankton feeding locations (top of colony) for alterative foraging areas around the base of the colony that are more protected (Wen et al. 2013) with lower flow, thereby conserving energy (Johansen et al. 2008, 2015). Additionally, the average size or boldness of these two species may be less compared to the *Dascyllus* spp., reducing their average distance from shelter (Biro et al. 2010).

Aggression of these damselfish species links to the strength of the dominance hierarchies, and how persistent they are in maintaining their colony (i.e. territoriality, see Harrington 1993; Leal et al 2015). With high conspecific and heterospecific aggression, it is evident that host colony is entrenched in the social networks of these two *Dascyllus* spp. For instance, alpha male territory is demarcated by the optimal foraging with respect to the host colony and surrounding currents (Fricke 1977; Shpigel & Fishelson 1986; Fishelson 1998; Meekan 2010); which in-turn explains the average and maximum distances ventured by these damselfishes. Furthermore, this strong usage and interactions by *Dascyllus* spp. is exampled by their high heterospecific aggression; these damselfishes challenge outsiders or large corallivorous predators that pose a threat to their coral-interaction (Gochfeld 2010; Cole et al. 2011) and foraging/mating territory. The other three damselfish species examined in this chapter stayed much closer to their host corals (consistent with low boldness levels), rely less on the physical coral colony for mediating social hierarchies and shelter, and are more flexible to temporarily exploit or re-colonize nearby colonies if other damselfishes or predators exclude them from particular colonies. Although bleaching/thermal stress did not impact any aspect of the measured damselfishes' aggression, it is likely that aggressive behaviour would considerably change with coral mortality or coral re-organization, due to increased competition of habitat and altered territory boundaries (Coker et al. 2009, 2012b; Boström-Einarsson 2018; Kok et al. 2016).

While many reef fishes are fundamentally reliant on coral habitats, there is also evidence that fishes confer important benefits on host corals, such as nutrient subsidies (Meyer et al. 1983; Meyer & Schultz 1985a; Holbrook et al. 2008), hydrodynamic modulation/ventilation (Goldshmid et al. 2004; Garcia-Herrera et al. 2017), and colony defense (Gochfeld 2010; Chase et al. 2014), resulting in enhanced coral health and growth (Meyer & Shultz 1985b; Holbrook et al. 2011; Shantz et al. 2015). Services are likely species-specific; although not explicitly quantified, among the fishes considered in this chapter, *C. viridis*, *D. aruanus*, and *D. reticulatus* are likely to contribute the most to nutrient provision, enhancing water flow and aeration of colony tissues, due to their species-specific nocturnal roosting (where aeration is the most effective (Goldshmid et al. 2004; Berenshtein et al. 2015) within colony branches and frequent diurnal colony visits (or diurnal chases around the colony, see Kok et al. 2016). Coral associated fishes are increasingly vulnerable to ongoing coral loss, mainly caused by climate-induced coral bleaching (Jones et al. 2004; Pratchett et al. 2012); however, these fishes may be important in providing resilience to coral bleaching (Suefuji & van Woesik 2001; Chase et al. 2018b; Chapter 4). Several fishes were observed on bleached colonies that had filamentous algae growing on them, which is consistent with other studies showing fishes remaining with their hosts during partial degradation (as observed by Feary et al. 2007; Bonin et al. 2009; Coker et al. 2009). In this chapter, targeted biting of algae, by *D. aruanus*, *D. reticulatus*, *P. amboinensis*, and *P. moluccensis* on bleached corals was recorded, a behaviour which has previously been documented only in coral-dwelling gobies (Dixson & Hay 2012). Although probably not sufficient to prevent algae growing on the coral colony, target algae biting could help slow rates of algal overgrowth and limit partial mortality of coral tissues after bleaching. Furthermore, subtle differences with swimming position due to colony bleaching may lead to different association strengths with less time spent within colony branches (Coker et al. 2009), reduction in refuge from predators on dead and algae covered colonies (Boström-Einarsson et al. 2018), with interaction breakdown during colony death and subsequent structural degradation.

A previous study of a Red Sea damselfish species found that *D. marginatus* spent 18-34% of its time between coral branches during the day, and 100% at night, for a total 68-84% of its time within the colony (Garcia-Herrera et al. 2017). These values are estimated to be similar to *C. viridis*, *D. aruanus* and *D. reticulatus* (this study estimates: 60-80% within colony time due to 50% of time within branches at night and high colony visits, corresponding with high sheltering time). *P. amboinensis* and *P. moluccensis* would likely spend less time within colony branches (30-50% within colony time, due to lower roosting within colonies and fewer colony visits, corresponding with lower sheltering time, see Garcia-Herrera et al. 2017). This higher residency time is likely to be a major factor in determining the extent by which fishes are dependent upon corals and possible fish-derived services. For example, large schools of generalist fishes (e.g. Haemulidae or Lutjanidae spp.), while representing significant biomass, are likely to have little impact on the health of numerous corals contained within their large foraging areas. By comparison the persistence of a few, small-bodied coral-dwelling damselfishes, on and with specific host corals, can have significant effects on nutrient provisioning and growth of host colonies (Holbrook et al. 2008; Chase et al. 2014). Finally, it is possible that fishes' behavioural strategies, trade-offs and potential benefits differ around colonies of various coral species and in different water flow environments (Holbrook et al. 2008). For instance, distance of fish from substrate would likely vary between larger branched *A. intermedia* colonies, compared with more compact *S. hystrix*. However, distance from colony branches and colony visits remain unchanged, likely due to abundance of food and startle refuge distance (see Table S3.4 and Table S3.5 in Supplement). Distinguishing the foraging distance of fishes around different size (Pereira et al. 2015; Pereira & Munday 2016) and species of corals may elucidate fine-scale patterns of occupancy and usage, as well as survival of these interactions after habitat loss (Pratchett et al. 2012).

3.5.2 Conclusions

This chapter illustrates that coral-dwelling fishes vary in their associations with host corals, which is likely to influence their cost-benefit ratios associated with colony usage (i.e. roosting location, foraging ground, social group network). These behavioural variations are exemplified by contrasting the association of *D. aruanus*, which shelters within the coral throughout the night and regularly returns to the coral even during feeding, compared to *P. amboinensis,* which infrequently visits the colony and exhibits less fidelity for roosting within the colony. This interspecific trait variation (as well as intraspecific variations) between aggregating damselfish species at the colony level could alter community dynamics through reduced fish-coral interaction abundances and interaction strengths (Bolnick et al. 2011; Pruitt & Ferrari 2011). Nevertheless, changes in coral colony health (bleaching), can alter key behaviours, such as swimming position around coral colonies, fish-interaction strengths, and fish survival during and after bleaching events. This research emphasizes that fishes utilize colonies in different ways and for different purposes; there is a need to consider not only which fish species are present, but also a range of diurnal and nocturnal movements, and social fish behavioural traits dictating the mechanisms impacting their coral use. Scientific literature currently focuses on how changes in coral complexity influence fish communities, but limited information exists on the reverse feedback of how fish-derived behaviours translate into beneficial services for coral colonies and populations. The results of this chapter highlight the complexity of quantifying the nature of fish-coral interactions (how fishes utilize colonies), its species-specific variations, the context-dependency across temporal scales, and how it will respond to current and future global environmental change. These abiotic stressors will disrupt habitat associations (Pratchett et al. 2018), and eventually erode the function of fishes within reef habitats (Graham et al. 2006; Kiers et al. 2010).

CHAPTER 4: Fishes alleviate the impacts of sediments on host corals

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4.1 Synopsis

Mutualisms play a critical role in ecological communities, however the importance and prevalence of mutualistic associations can be modified by external stressors. On coral reefs, elevated sediment deposition can be a major stressor, reducing the health of corals and damaging reef resilience. Here, I investigated the influence of high levels of severe sedimentation on the mutualistic relationship between small, aggregating damselfishes (*Dascyllus aruanus* and *Pomacentrus moluccensis*) and their coral host (*Pocillopora damicorni*s). In an aquaria experiment, corals were exposed to sedimentation rates of ~100 mg cm^{-2} day^{-1}, with and without symbiont fishes present to test whether: (1) fishes influence the accumulation of sediments on coral hosts, and (2) fishes moderate partial colony mortality and/or coral tissue condition. Colonies with symbiont fishes accumulated much less sediment compared to colonies without fishes, and this effect was strongest for colonies with *D. aruanus* (five-fold less sediment than controls) as opposed to *P. moluccensis* (two-fold less sediment than controls). Colonies with symbiont fishes also had 10-fold less sediment-induced partial mortality, as well as higher chlorophyll and protein concentrations. Differences in the effects of different damselfish species suggests that proximity of fish to their host corals determines the strength of mutualistic benefits. These results demonstrate that fish mutualisms may be

critical for maintaining coral health and resilience under high sediment stress and indicate that some mutualistic or facilitative interactions might become more important for species persistence as stress levels increase.

4.2 Introduction

Positive species interactions play a critical role in community assembly, species coexistence, and ecosystem function, by enhancing fitness (Stachowicz 2001; Bruno et al. 2003; Schmitt and Holbrook 2003). Mutualistic and facilitative relationships range from tightly co-evolved symbioses (e.g. lichens, legumes, and zooxanthellate corals) to looser associations whereby certain taxa derive benefit from others in close proximity (e.g. plants-pollinators, and clownfish-sea anemones), both forming critical components of community interaction networks (Bruno et al. 2003). Many positive interactions arise from the ability of species to modify the local environment through nutrient enrichment or habitat modification, and therefore ameliorate stress for the benefit of their neighbours (Wright et al. 2017). However, studies from a range of systems demonstrate that the role of positive interactions increases under high-stress conditions (Mulder et al. 2001; Callaway et al. 2002; He et al. 2013), and interaction networks may shift to a "survival mode", with a greater reliance on mutualism and facilitation. A major challenge, therefore, is to understand how positive interactions are likely to fare in the face of global environmental change, and how they might help communities deal with these stressors.

Coral reefs are hotspots of mutualistic and facilitative interactions (Stella et al. 2010; Stier and Leray 2014; Thompson et al. 2015; Barlow et al. 2018). Reef-building corals, for example, foster numerous interactions with obligate coral-dwelling invertebrates (e.g. *Trapezia sp.* crabs and other cryptofauna) and associated fish species that use corals for habitat or temporary refuge. Many of these interactions are mutualistic; augmenting the growth and overall health of their coral hosts (Lassig 1977; Stewart et al. 2006; Pollock et al. 2013). Aggregative damselfishes, such as *Chromis* spp., and *Dascyllus* spp., provide beneficial services to corals, including increases in coral growth rates by up to 40% (Holbrook et al. 2008), reductions in black-band disease progression (Chong-Seng et al. 2011; Dixson and Hay 2012), subsidies of nitrogen and phosphorous, and increases in colony aeration by 60% (Goldshmid et al. 2004; Holbrook et al. 2011). Thus, although many studies highlight the breakdown of coral reef mutualisms during extreme stress (Hughes et al. 2017a; 2018a, b), it is also possible that positive interactions could enhance system resilience by moderating effects of stressors on reef organisms (Kiers et al. 2010; Marquis et al. 2014; Chase et al. 2018b).

Inputs of sediment to coastal environments and coral reefs have increased rapidly in recent times due to altered land-use practices (McCulloch et al. 2003; Bainbridge et al. 2018), coastal development (Wolanski et al. 2009; Brodie et al. 2012), and dredging (Pollock et al. 2014; Fisher et al. 2018). For example, high sediment levels can erode coral reef resilience via lethal and sub-lethal impacts on reef organisms (Fabricious 2005; Erftemeijer et al. 2012; Jones et al. 2015). Sediment reduces light levels, damages coral tissue, smothers polyps, and reduces coral growth (Dodge et al. 1974; Dodge and Vaisnys 1977; Rogers 1990; Sweet and Brown 2016). Furthermore, corals under high sediment levels are physiologically stressed (Sweet and Brown 2016), with reduced heterotrophy, the death of symbiotic algae (*Symbiodiniacea spp.* see LaJeunesse et al. 2018), and the production of excess mucus to remove sediment (Crossland et al. 1980; Stafford-Smith and Ormond 1992; Philipp and Fabricius 2003; Sweet and Brown 2016). While profound effects of sediment on the coral holobiont are evident, the potential for fish-derived benefits to assist corals stressed by sediments remains relatively unexplored. Indeed, behaviours of symbiont damselfishes such as “water stirring” within colony branches and nocturnal aeration of stagnant inner colony areas (Liberman et al. 1995) suggest that mutualistic associations may greatly enhance the capacity of host corals to withstand sediment stress.

The objective of this chapter was to test whether coral-dwelling damselfishes can alleviate the deleterious effects of high sediment stress on their host coral colonies, by (1) reducing the accumulation of sediments within host colonies; and/or (2) moderating physiological damage, localised tissue loss and partial colony mortality. I hypothesised that fish movement and fish-derived services (i.e. “water stirring” and nutrient subsidy) would assist corals under long-term, severe sediment stress (e.g. during sediment deposition following sustained dredging activity, storms, or natural resuspension events) through sediment removal, and that the varying behaviours (e.g. roosting position and colony visits, see Chapter 3) of different damselfish species would benefit host corals to different extents. To assess this, a laboratory-based experiment was used to examine the responses of corals to chronic sedimentation while hosting or not hosting aggregative damselfishes. Understanding the impacts of sedimentation on coral colonies within the context of coral-fish associations will provide new insights into the importance of mutualistic associations and their contributions to resilience in an increasingly modified environment.

4.3 Materials and Methods

4.3.1 Study site and specimen collection

Field sampling and the aquaria experiment were conducted between April – June 2017 on Orpheus Island, an inner-shelf, continental island of the Great Barrier Reef (GBR) (Figure S4.1). Orpheus Island is located ~20 km from the Queensland coast and close to the Herbert (~20 km) and Burdekin rivers (~150 km) where seasonal flood plumes, storms, agricultural runoff, and dredging activities deposit and resuspend high amounts of sediment onto the GBR (Furnas 2003). Colonies of *Pocillopora damicornis* (averaging 13.5 cm in diameter) were collected from around the Palm Islands. *P. damicornis* is widely distributed on inshore and offshore reefs of the GBR and exhibits high levels of occupancy by coral-dwelling damselfishes (Pomacentridae, see Holbrook et al. 2000; Coker et al. 2014). Two damselfish species, *Dascyllus aruanus* and *Pomacentrus moluccensis*, were collected from nearby reefs using a weak solution of clove oil (Boyer et al. 2009; Javahery et al. 2012) and hand nets. These two damselfish species are common on the GBR and exhibit high levels of coral occupancy (Holbrook et al. 2000; Coker et al. 2014). Fishes and corals were transported to the research station aquaria and transferred to 25 L flow-through seawater tanks. Corals and fishes were then allowed to acclimate to aquaria conditions for one week. All fishes were subjected to a brief freshwater rinse to remove contaminants (Pironet and Jones 2000) and weighed (wet weight, Kern PCB, John Morris Scientific balance, precision 0.001 g) to determine treatment group biomass. Resident coral cryptofauna (i.e. *Trapezia sp.* crabs and *Alpheus sp.* shrimp) remained within their host colonies to simulate a natural coral holobiont system; coral colonies were haphazardly assigned to different treatments so that any influence of these resident cryptofauna and/or other variability among individual coral colonies on the coral processes examined (i.e. sedimentation stress on corals) was factored out.

4.3.2 Aquaria sediment deposition experiment

To test whether coral-dwelling damselfishes reduce the accumulation of sediments within occupied colonies, and thereby moderate deleterious effects of sediment on corals, 72 coral colonies were collected and subjected to one of six treatments (12 corals per treatment, with each coral in their own tank): 1) no sediment, no fish; 2) no sediment with *P. moluccensis*, 3) no sediment with *D. aruanus*, 4) sediment added with no fish, 5) sediment added with *P. moluccensis*, and 6) sediment added with *D. aruanus.* Fish treatments contained 4 individual damselfish from either of the two fish species, with biomass representative of colonies naturally found in the field (Chase et al. 2014, 2018b). *D. aruanus* ranged in size from 20 - 70 mm and weighed from 0.5 to 10.3 g, with an average group biomass of 11.9 ± 0.3 g. *P. moluccensis* ranged in size from 17 to 59 mm and weighed from 0.3 to 5.7 g, with an average group biomass of 8.5 ± 0.6 g. Diurnal (13:00 – 16:00 h) and nocturnal (20:00 – 22:00 h) fishes' behaviours in experimental aquaria were observed four to five times for each fish in each coral colony (n = 24 colonies with 96 fish per fish treatments, per time period), during the course of the experiment. Swimming positions of all *D. aruanus* or *P. moluccensis* in each replicate aquaria were recorded during spot checks (n = 5 diurnal checks, per colony, and n = 4 nocturnal spot checks per colony, each spread out over the course of the experiment), where the observer did not interfere with the fish's behaviours. Nocturnal spot checks utilized a white light torch for illumination – each colony was illuminated for less than 10 seconds and did not induce movement by any of the resident fishes (see Chapter 3 for similar methods). Positional categories included: "in colony branches" (within branching structure), "outside colony" (vertically on top or to the side of colony), and "under" (under colony structure).

Corals and fishes were maintained in outdoor aquaria (25 L volume), that received an inflow of new ambient filtered seawater (~15 L hr^{-1}, re-circulating slowly enough to prevent sediment disruption). This water flow is a common flow rate on coral reefs and at the study sites around Orpheus Island (Patterson et al. 1991; McWilliam et al. 2018). Aquaria were also fitted with an air stone to maintain oxygen saturation of the water, but with sufficiently low air-flow rates to avoid disrupting sediments. Corals and fishes were fed daily to satiation with enriched *Artemia salina* nauplii; any additional nutrients in each tank system would be limited to the exosymbiont invertebrates and damselfishes. One coral fragment per colony, ~5 cm in length, was collected from each colony, during acclimation (prior to adding fish or sediment) and again after 28 days of treatment exposure. Fragments (n = 144) were subsequently frozen in liquid nitrogen, transported to James Cook University, and coral tissues were analysed for chlorophyll density, protein density, and tissue biomass (Chase et al. 2018b). Additional measurements of partial mortality were quantified from photos taken from above the coral at the beginning of the experiment and again after 28 days, after all sediment was removed. The two-dimensional area of the bleached or dead coral tissue was measured using ImageJ software (Schneider et al. 2012).

A dose of 14 g of sediment was added to each tank using a funnel to spread the sediment evenly over the coral surface, daily for 28 days. This equated to standardized sedimentation rates of ~100 mg cm^{-2} day^{-1}, which is slightly higher than the range measured on nearby inshore reefs (e.g. averages of 50-80 mg cm^{-2} day^{-1}, with maximums of >100 mg cm^{-2} day^{-1} around Magnetic Island reefs (see Stewart et al. 2006; Whinney et al. 2017, for sedimentation in nearshore lagoons). This was similar to sedimentation observed in the field around the Palm Islands (this study, all sediment traps at sites pooled: average ~137 mg cm^{-2} day^{-1}, see Appendix S4, Text S1 for specifications on design and deployment, Tables S4.1, S4.2, S4.3, S.4.4, S4.5, S4.6, Figures S4.1, S4.2, S4,3, S4.4, S4.5), as well as published sediment experiments (Rogers 1985; Stewart et al. 2006; 2013; Duckworth et al. 2017) investigating the impacts of sediment on coral tissues from 0.5 – 600 mg cm^{-2} day^{-1} in natural and controlled *ex situ* aquaria conditions (allowing for direct comparison with this experiment). High sediment loads, such as > 80 mg cm^{-1} day^{-1}, in inshore reef environments are common and will likely increase in occurrence due to associated impacts of dredging, post-wet season sediment runoff and other recurring natural resuspension events including storm and water current movements (Storlazzi et al. 2004; 2011; Duckworth et al. 2017). The experiment was designed to examine the amount of sediment contacting (temporarily contacting or settling/depositing) live coral branches, which can be approximated using certain *in-situ* sedimentation methodology (Storlazzi et al. 2011). In addition, a level of 100 mg cm^{-2} day^{-1} was chosen to facilitate comparion with previous research that has explored the impacts of sediment deposition on corals under deposition rates ranging 0.5 – 600 mg cm^{-2} day^{-1} in natural and controlled *ex situ* aquaria conditions (Rogers 1983; Stewart et al.

2006; Erftemeijer et al. 2012; Stewart et al. 2013; Duckworth et al. 2017). However, while maximum sedimentation rates of >100 mg cm^{-2} day^{-1} have been reported from around Magnetic Island, near Orpheus Island on the inner-shelf of the GBR (Whinney et al. 2017), in general sedimentation rates of 100 mg cm^{-2} day^{-1} over prolonged periods are considered severe within the context of coral reef ecosystems. Moreover, many published studies have relied on sediment trap data to set their experiemtnal treatments, and while this method is commonly used to quantify sediment accumulation rates it can overestimate or underestimatehow much sediment is actually deposited on natural benthos (Storlazzi et al. 2011; Latrille et al. 2019). As such, the sedimentation rate used herein (100 mg cm^{-2} day^{-1}) should be viewed as a severe sediment deposition event such as may be experienced during dredging activities, and/or wave driven resuspension during tropical storms (Storlazzi et al. 2004; Duckworth et al. 2017) Added sediment consisted of a combination of silicate, carbonate, and organic particulates with grain sizes between 63 – 4000 µm, in a ratio of 4 (carbonate sediment, 63 µm): 1 (siliciclastic sediment, 63 µm): 2 (90-355 µm): 3 (355-1400 µm): 1 (1400-4000 µm), which is consistent with settled inshore sediments around the Palm Islands (see Gordon et al. 2016; Jones et al. 2016) for justification of size classes and sedimentation rates). Sediments were collected from local reefs, dried at 60°C for > 24 hours and sieved into size classes prior to experimental use (see Esslemont 2000; Ricardo et al. 2015, 2016 and Appendix S4, Table S4.8 for sediment description and composition). Airstone and water flow were turned off directly before sediment addition and remained off for 1 hour to enable sediment settlement.

Sediments were carefully removed from the bottom of the tank every 3-4 days to mimic natural substrate clearing and to prevent any anoxic microbial build-up in experimental tanks (see Appendix S4, Table S4.9 and Figure S4.6). To determine the amount of sediment remaining on the coral at the end of the experiment, each coral was carefully removed from its aquarium, placed into a labelled container full of seawater and shaken until all sediment was removed from the colony. Sediments were allowed to settle for > 6 hours in temporary collection buckets, transferred into labelled containers and transported to James Cook University for further processing. All collected sediments were rinsed with freshwater three times to remove salts, dried at 60°C (Axyos Microdigital Incubator) for > 4 days, weighed for constant weight (g), sieved into three factions (Wentworth 1992): < 125 µm (very fine sand and silt), 125-500 µm (fine to medium sand), 500-4000 µm (coarse sand to gravel) and weighed (using Kern PCB, John Morris Scientific balance, precision 0.001 g).

4.3.3 Data Analysis

Variation in the total sediment load remaining on *P. damicornis* colonies after 28 days in aquaria was examined using a lognormal linear model. In the model, 'fish presence' (no fish, *P. moluccensis*, *D. aruanus*) was treated as a fixed factor and only 'sediment added' treatment colonies were included in the analysis, as all colonies in the 'no sediment' treatment exhibited very low (< 0.3 g) sediment accumulation during the experiment. Tukey's HSD comparisons were employed *post-hoc* to assess differences among factor levels. Model fit was assessed using residual plots (QQ-normal plot for normality and scatter plots of residuals vs fitted for linearity), all of which were satisfactory (normal and homogenous). To assess whether the grain size distribution of sediments remaining on *P. damicornis* colonies differed among treatments, a permutational multivariate analysis of variance (PERMANOVA) was used. The PERMANOVA was based on a Euclidean distance matrix of standardised data, and once again fish presence was treated as a fixed factor. Pair-wise tests were utilised to determine where between level differences occurred. Homogeneity of dispersions for the PERMANOVA was tested using a permutation analysis of multivariate dispersions (PERMDISP). A canonical analysis of principle components (CAP) was employed following the PERMANOVA to visualise significant groupings, although grain size distributions were better visualized as bar graphs (see electronic supplementary material, figure S4).

Partial colony mortality of host *P. damicornis* colonies was analysed using a beta regression model with sediment and fish as interacting fixed factors. Due to the proportional nature of the data, the beta binomial distribution with a logit-link was the most appropriate (Cribari-Neto and Zeileis 2010). However, as this distribution is bounded between 0 and 1, a small constant (0.001) was added across the data set. Model fit was assessed using residual plots, as above. Following the beta regression model, treatment comparison differences were assessed using Least Square Means (lsmeans) multiple comparison *post-hoc* (with a Tukey's correction).

Differences in coral tissue components (total chlorophyll, proteins, and tissue biomass) were examined using two-way ANOVAs with sediment and fish treatments initially fitted as interacting fixed factors. Coral tissue components data was log transformed. Tukey's HSD *post-hoc* comparisons were used to examine between treatment differences. When interaction terms were not significant, additive models (sediment treatment + fish treatment) were performed. Model fit was assessed using residual plots, all of which were satisfactory (normal and homogenous). Tissue components at the start of the experiment and after 28 days (end) were analysed separately, as all tissue component comparisons at the beginning were not-significantly different.

Pearson's chi-squared goodness-of-fit tests (χ^2) were used separately for each damselfish species to determine non-random variation in diurnal and nocturnal fish position around host coral colonies in aquaria. Diurnal and nocturnal positions were the count of multiple observations (the sum of $n = 5$, and $n = 4$ observations, respectively, treated as replicates rather than repetitive time points) and was deemed appropriate for the categorical nature of the spatial position data.

All analysis was performed in the statistical software R (R Development Core Team 2018) using the *betareg* (Cribari-Neto and Zeileis 2010), *multcomp* (Hothorn et al. 2008) and *lsmeans* (Lenth 2016) packages. Multivariate analysis was performed in PRIMER 7.0 PERMANOVA+.

4.4 Results

4.4.1 Fishes removal of sediment in aquaria

The total weight of accumulated sediment on host corals varied among the different fish treatments (LM: $F_{2,33} = 28.22$, $p < 0.001$, Figure 4.1a). Sediment commonly pooled on the upper horizontal surfaces of the coral colonies, with the majority becoming trapped within branch connection points.

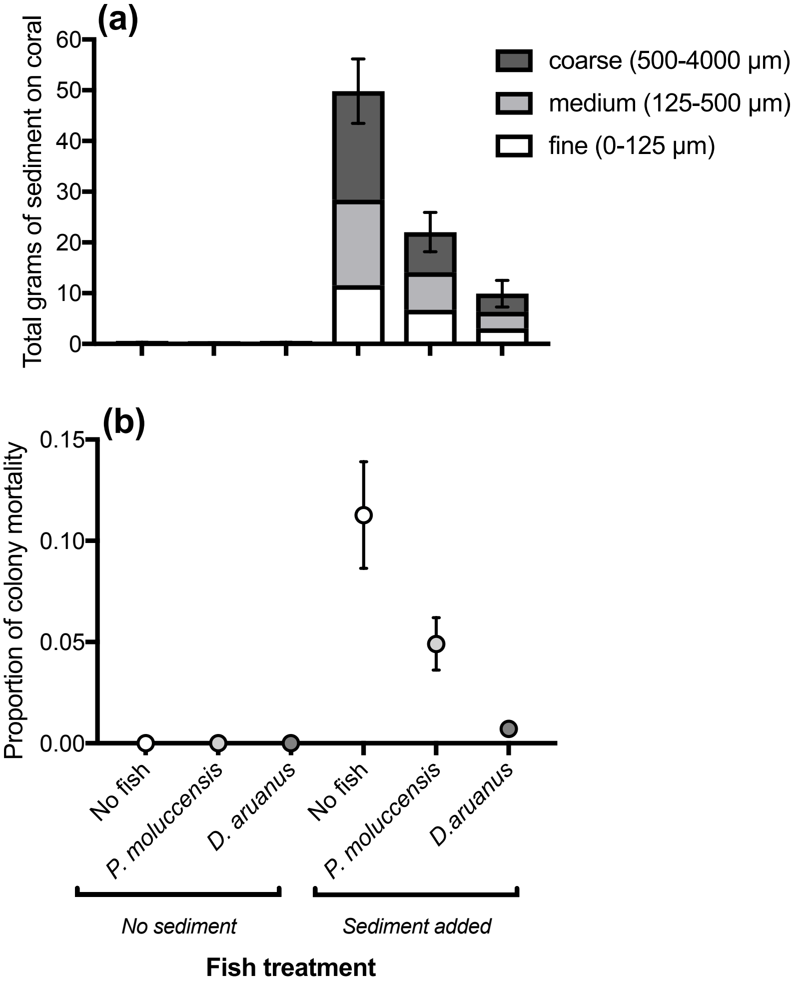

Figure 4.1 (a) Remaining sediment on *P. damicornis* colonies (~13.5 cm diameter) after 28 days of ~14 g of sediment deposition in experimental aquaria. n = 12 corals for all treatments, except corals with sediment added, in which a colony died on day 25 and was removed from analysis. Treatments included colonies with different fishes (no fish, 3 *P. moluccensis*, and 3 *D. aruanus*) and sediment (no sediment and with sediment added at a rate of ~100 mg cm^{-2} day^{-1} for 28 days). *Error bars* show SE and values for no sediment treatments are absorbed into the x-axis. Bar colours represent grain size fractions as follows: dark grey is coarse (500-4000 µm), grey is medium (125-500 µm) and white is fine (0-125 µm) sediment. **(b)** Average levels of whole *P. damicornis* colony partial mortality, measured after 28 days of experimental fish and sediment treatments.

Sediment treatment colonies of *P. damicornis* hosting *D. aruanus* exhibited the lowest levels of accumulated sediment (~10 ± 2.6 g), which was two-fold less than sediment treatment colonies hosting *P. moluccensis* (~22 ± 3.9 g, Tukey's HSD: p =

0.002) and nearly five-fold less than sediment treatment vacant colonies (~49 ± 6.3 g, Tukey's HSD: (*D. aruanus*) $p < 0.001$, (*P. moluccensis*, $p = 0.002$, Table 4.1, Appendix S4, Figure S4.7). Sediment grain size fractions left on *P. damicornis* colonies after 28 days varied by treatment (PERMANOVA: Pseudo-$F_{2,33} = 3.0615$, p(perm) = 0.0485; Appendix S4, Table S4.10 for homogeneity of sediment grain size distributions), with higher amounts of medium and coarse sediments removed from fish treatment colonies. Pairwise tests revealed that grain size fractions of sediment remaining on colonies were significantly different between fish-absent colonies and *D. aruanus* present colonies (*pairwise test*, $t = 2.061$, p(perm) = 0.041) and *P. moluccensis* present colonies (*pairwise test*, $t = 2.177$, $p = 0.028$). However, grain size fractions on colonies did not differ between colonies with *D. aruanus* and *P. moluccensis* (*pairwise test*, $t = 1.304$, p(perm) = 0.2095). Sediment in non-sediment treatment colonies was very low (< 0.29 g) for all three treatments and was likely a result of residual treatments within the aquaria system.

Table 4.1 Tukey's HSD *post-hoc* multiple comparisons table (including confidence intervals) for total sediment, log (x+1) transformed, left on experimental *P. damicornis* colonies in the manipulative sediment experiment. Only 'sediment added' treatment colonies were included in the analysis and subsequent Tukey HSD post-hoc tests, as all colonies in the 'no sediment' treatment exhibited very low (< 0.3 g) sediment accumulation over 28 days in aquaria. Significant p-values are in bold.

Treatment comparison	Lower	Upper	P adjusted
Sediment *P. moluccensis* – Sediment *D. aruanus*	0.2714	1.36110	**0.0023**
Sediment No fish – Sediment *D. aruanus*	1.1231	2.2128	**< 0.0001**
Sediment No fish – Sediment *P. moluccensis*	0.3069	1.3966	**0.0015**

Partial colony mortality was explained by the presence or absence of fish under sediment stress (Appendix S4, Table S4.11, S4.12 and Figure S4.8). Sediment-free colonies of *P. damicornis* did not exhibit any signs of partial mortality, and colonies subjected to daily sediment treatments exhibited an average of 5.6% partial mortality over the course of 28 days, ranging from < 1% to 32% (Figure 4.1b). Areas of partial mortality were usually limited to the site where sediments directly settled, and generally, no visible impacts on the healthy coral tissue < 1 cm away from the impacted tissue. The highest average partial mortality (11.2% ± 0.03) was observed in the sediment with no fish treatment (Figure 4.1b), which was two-fold higher than the partial mortality of colonies with *P. moluccensis* (4.9% ± 0.01), which was significantly different (*lsmeans*: (no fish vs *P. moluccensis)* $p = 0.046$), and four-fold more than colonies with *D. aruanus* (*lsmeans*: (no fish vs. *D. aruanus*) $p < 0.001$). Host colonies with sediment added and *D. aruanus* exhibited very low partial mortality (< 1%). Indeed, partial colony mortality on sediment-added colonies with *D. aruanus* was not-significantly different from that of sediment-free colonies (Appendix S4, Table S4.12).

4.4.2 Impacts of sediment and fishes on coral tissues

Prior to sediment and fish treatments, chlorophyll density ($\bar{x} = 5.4 \pm 0.4$ μg cm^{-2}), protein concentration ($\bar{x} = 1.8 \pm 0.5$ mg cm^{-2}) and tissue biomass ($\bar{x} = 1.9 \pm 0.0$ mg cm^{-2}) were not significantly different among treatments (ANOVA, total chlorophyll (sediment*fish): $F_{2,59} = 0.165$, $p = 0.849$), total protein (sediment*fish): $F_{2,66} = 1.486$, $p = 0.234$; tissue biomass (sediment*fish): $F_{2,66} = 1.244$, $p = 0.295$) ($p > 0.05$ for all other factors for the three tissue components, see Table S4.13 in Appendix S4).

After 28 days of sediment and fish treatments, there were reductions in coral tissue components in sediment-added colonies with no damselfish (Figure 4.2). Overall, corals exposed to sediments and hosting *D. aruanus* exhibited the lowest coral tissue stress. Specifically, chlorophyll levels in colonies stressed by sediments and hosting *D. aruanus* were two-fold higher (7.37 ± 1.18 µg cm^{-2}) compared to colonies stressed with sediment but not hosting fish (3.24 ± 0.59 µg cm^{-2}), which was statistically significant (Tukey's HSD *post-hoc*: $p = 0.017$, $r^2 = 0.12$, see Figure 4.2a). By contrast to *D. aruanus*, *P. moluccensis* had no significant effect on chlorophyll levels (Table 4.2; Appendix S4, Table S4.13). The interaction between sediments and fish treatment was not significant for chlorophyll (ANOVA: $F_{2,61} = 1.216$, $p = 0.304$).

Table 4.2 Tukey's HSD *post-hoc* for multiple comparisons of tissue components (total chlorophyll, total protein, and tissue biomass) from two-way additive ANOVAS (sediment treatment + fish treatment) with significant p-values in bold.

Tissue component	Comparison	p-value
Total chlorophyll	*P. moluccensis* – *D. aruanus*	0.5154
	P. moluccensis – no fish	0.1492
	D. aruanus – no fish	**0.0117**
Total protein	*P. moluccensis* – *D. aruanus*	0.1686
	P. moluccensis – no fish	0.2667
	D. aruanus – no fish	**0.0063**
Tissue Biomass	*P. moluccensis* – *D. aruanus*	0.4217
	P. moluccensis – no fish	0.9128
	D. aruanus – no fish	0.2263

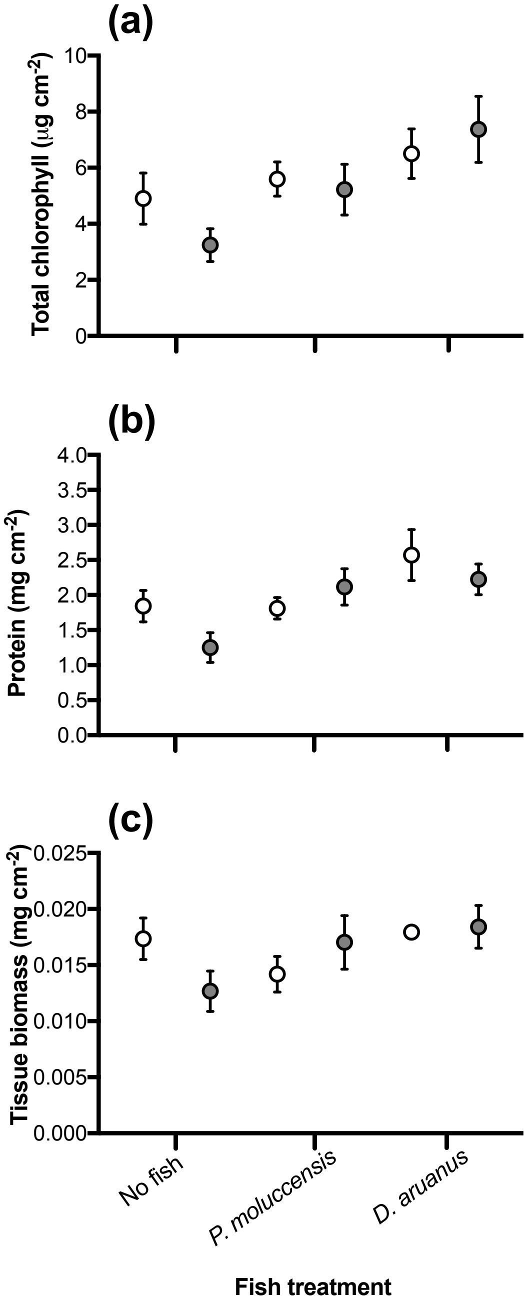

Figure 4.2 Sample fragment tissue compositions at the end of 28 days of experimental sediment and fish treatments: **(a)** total chlorophyll (chl *a* + chl *c,* μg cm^{-2}), **(b)** protein (mg cm^{-2}), **(c)** tissue biomass (mg ash free dry weight) for *P. damicorni*s colonies in experimental aquaria with different fishes (no fish, 3 *P. moluccensis* , and 3 *D. aruanus*) and sediment treatments (no sediment: white dots and with sediment added at a rate of ~100 mg cm^{-2} day^{-1}: grey dots for 28 days). *Error bars* show SE Refer to Table 4.2 and Table S4.13 in Appendix S4 for sample sizes and for comparisons among treatments

Patterns in total protein concentration at the end of the experiment were similar to those for total chlorophyll in that colonies hosting *D. aruanus* had the highest total protein levels (Figure 4.2b). Despite the higher protein levels in colonies hosting *D. aruanus*, the only statistically significant difference occurred between colonies with no sediment added and hosting *D. aruanus* (2.22 ± 0.2 mg cm^{-2}) and colonies with sediment added, but with no fish (1.25 ± 0.2 mg cm^{-2}, Tukey's HSD *post hoc*: $p < 0.01$, $r^2 = 0.11$, Figure 4.2b, Table 4.2). Again, the interaction between sediments and fish treatment for protein content was not significant (ANOVA: $F_{2,65} = 2.682$, $p = 0.076$). Finally, no significant differences in tissue biomass were detected among treatments at the end of the experiment (ANOVA: (fish effect) $F_{2,65} = 2.631$, $p = 0.079$, $r^2 = 0.00$, Table 4.2 and Figure 4.2c).

4.4.3 Spatial position of damselfishes in aquaria

Diurnal and nocturnal positions differed between *D. aruanus* and *P. moluccensis* (Figure 4.3). During the day *D. aruanus* swam < 80% of its time outside the colony branches, mainly on top of the colony (Chi-square: $\chi^2 = 174$, df = 2, $p < 0.001$). By contrast, *P. moluccensis* spent most of its time within the branches or under the colony (Chi-square: $\chi^2 = 69$, df = 2, $p < 0.001$). However, at night, *D. aruanus* preferentially slept within host colony branches (Chi-square: $\chi^2 = 469$, df = 2, $p < 0.001$), while *P. moluccensis* was less specific about roosting locations, spending nearly equal time in the colony, outside the colony, or under the colony (Chi-square: $\chi^2 = 1.2$, df = 2, $p = 0.56$).

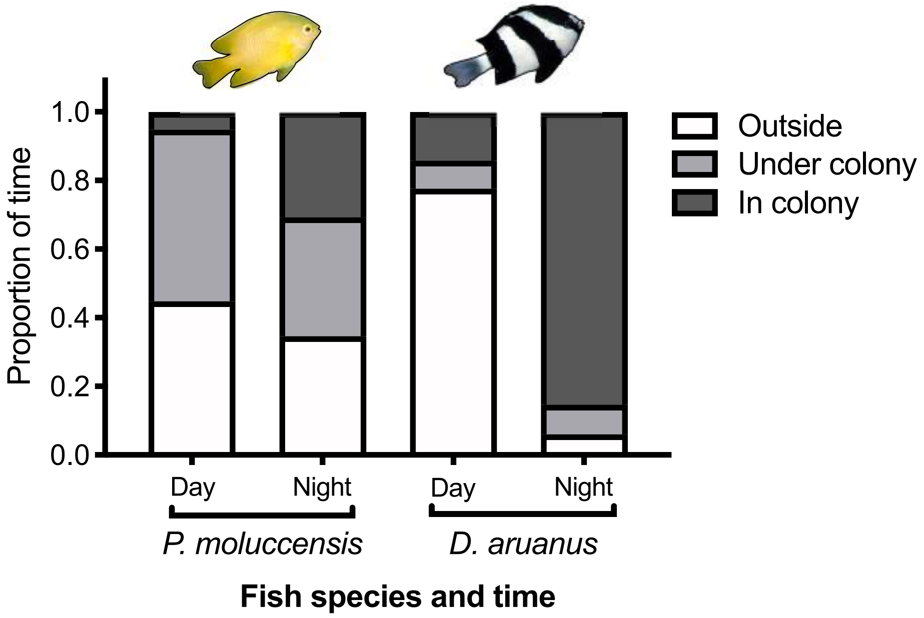

Figure 4.3 Average nocturnal (~2100 h) position (proportion ± standard error) of *P. moluccensis* and *D. aruanus* in relation to small (~13.5 cm diameter) *P. damicornis* colonies in experimental aquaria (25 L cylindrical tanks) at Orpheus Island Research Station. Half of the total coral colonies (n = 72) were exposed to sediment treatments. Fish treatment and numbers: n = 72 *D. aruanus* on 24 colonies and n = 72 *P. moluccensis* on 24 colonies. *Error bars* show SE; note top error bars removed to confine data to 0 – 1 proportions.

4.5 Discussion

4.5.1 Role of symbiont damselfishes in maintaining coral health under high sediment conditions

This chapter demonstrates that the presence of coral-dwelling fishes reduces accumulation of sediment on host corals during high sedimentation conditions, and thereby moderates the localised tissue loss. Moreover, colonies with fishes had higher chlorophyll and protein concentrations compared to unoccupied corals when subjected to severe sediment stress. Results of this study are attributed to the additional direct and indirect effect of fishes (in addition to the coral holobiont, including associated cryptofauna) on coral health and sedimentation. These results suggest that coral-dwelling damselfishes and, potentially, other cryptofauna provide a "housekeeping service" to branching corals, adding to the growing list of recognised indirect and direct services that fishes provide to host corals (Liberman et al. 1995; Goldshmid et al. 2004; Holbrook et al. 2008; Chase et al. 2014). *D. aruanus* in particular had strong mutualistic effects on its coral host, as coral colonies subjected to the high levels of sediment deposition, but hosting *D. aruanus*, had equivalent levels of partial mortality to coral colonies that were not exposed to any sediments. Consequently, fish presence can negate the negative impacts of severe sediment deposition or heavy wave action on coral physiology, potentially leading to higher fitness in corals with associated fish due to larger energy reserves (i.e. nutrients and photosynthetic efficiency), increased overall growth (Holbrook et al. 2008; Shantz et al. 2015; Garcia-Herrera et al. 2017, Chase et al. 2018b), increased reproductive output (Liberman et al. 1995), and enhanced colony resilience.

The removal of sediments from host corals has been demonstrated previously with coral-dwelling crabs (*Trapezia* spp.) and shrimps (*Alpheus* spp.), which can generate significant increases in coral growth in the field (Stewart et al. 2006, 2013; Stier et al. 2012). However, levels of sediment removal (or more precisely, limited accumulation) by *D. aruanus* and *P. moluccensis* (recorded here) were much greater (~95% of sediments removed) than those recorded for *Trapezia* sp. crabs (≤ 60%, as reported in Stewart et al. 2006). While sediment removal by coral-dwelling *Trapezia* sp. crabs may be intentional (Stewart et al. 2006), sediment removal by fish may be more indirect and unintentional, caused primarily by their movements in and around the coral, but also via other mechanisms such as (a) additional coral mucus production through abrasion and impairment (Simon-Blecher and Achituv 1997), (b) enhanced coral polyp expansion and cilia movement (Jones et al. 2000; Stier et al. 2012), (c) inadvertent or passive removal due to capture of sediment in gills (Hess et al. 2015), and (d) attracting additional colony cryptofauna through additional nutrient subsidies (Rothans and Miller 1991; Stier and Leray 2014). Active removal of sediment by damselfishes appears to be less frequent, but not uncommon. Indeed, I observed both damselfish species (although, more frequently, *D. aruanus*) deliberately removing sediment particles by picking them up in their mouths in this experiment (also seen in *D. marginatus*, see Liberman et al. 1995) or blowing them off the coral to clear their preferred roosting areas and tend to their habitat area (Liberman et al. 1995; Branconi et al. 2019), behaviour which is common in certain reef species living on sandy habitats (Moyer 1975). Damselfishes also appear to be effective at clearing sediments around the base of coral colonies, excavating areas under the branches. This activity would allow for further coral expansion around coral attachment points and deter detrimental bacterial activity, anoxia (present in the sand (Flores et al. 2012; Weber et al. 2012) or disease in coral colonies (Pollock et al. 2014).

The effectiveness of damselfishes in moderating sediment deposition varied between the two focal damselfish species, which may be attributable to the strength and intensity of interactions between the fishes and *P. damicornis* colonies. For example, *D. aruanus* exhibited high levels of colony visits (potential water stirring behaviour and nutrient subsidy) and sleeps exclusively within its host colony branches (Chapter 3). By contrast, *P. moluccensis* is less regular in its nocturnal roosting position and exhibits lower colony visits. Furthermore, the impact of fish on clearing sediment is likely most effective and beneficial at the very beginning of sediment exposure, and at night when oxygen levels within the inner branches decline. Indeed, during daily sediment doses and at night, *D. aruanus* retreat or roost within the branches of their colony, subsequently augmenting colony aeration and water flow (Goldshmid et al. 2004).

This study suggests the importance of some mutualistic or facilitative interactions may become greater as abiotic stress levels increase, as seen in terrestrial systems (Callaway et al. 2002; Bruno et al. 2003; He et al. 2013). Consequently, this positive net effect of hosting damselfishes on corals and subsequent buffering mechanisms (Bruno et al. 2003) is likely context-dependent and may be particularly important on sheltered, inshore reefs, where negative impacts of nutrient laden terrigenous sediments are the most pervasive. This notion is supported by previous research which have highlighted that the positive impacts of aggregating damselfish on coral growth are highest in sand patches and reef slope/base areas (Chase et al. 2014). Moreover, *D. aruanus*, *P. moluccensis*, and other coral-inhabiting damselfishes, are most commonly found on corals located in sheltered (flow < 21.2 cm s^{-1}, see Johansen et al. 2015), reef/sand edge environments (Sambrook et al. 2016). Sheltered sites with low hydrodynamic energy facilitate the settlement of finer sediments suspended in the water column (Sweet and Brown 2016; Whinney et al. 2017), maximixing sedimentation rates that can lead to the smothering of corals, a common phenomenon on many inshore (Fabricius 2005), leading to greater positive interactions between fishes and their coral hosts. As a result, there is spatial congruency between where the damselfishes' greater positive coral interactions are located and the strength of their benefits to host coral. Since removal of symbiont fishes lowers coral growth and reproduction rates (Liberman et al. 2005), fishes' removal will likely detrimentally affect coral health under high sedimentation, similar to bleaching conditions (Chase et al. 2018).

4.5.2 Limitations for fish to enhance coral health

It should be noted that explicitly uncoupling the impacts of fish presence and/or cryptofauna presence (i.e. coral benefiting services) with sediment removal on coral health will require additional tests of the physical mechanisms in isolation. While the presence of resident crypofauna has been demonstrated to impact the behaviour of corallivorous fishes and other predators (Pratchett et al. 2000; Chase et al. 2014), no impacts on resident damselfishes have been previously documented. Furthermore, as cryptofauna were standardized across experimental corals (natural cryptofauna left in corals and the coral colonies haphazardly allocated to treatments) to retain ecological relevance (a natural coral holobiont), fish behaviour and impacts on coral health reported here are in addition to the natural coral holobiont processes. While the biomass levels of *P. moluccensis* and *D. aruanus* used in the aquaria experiment are representative of those in the field (Chase et al. 2014, 2018b), it is possible that the disparity in damselfish's biomass (~25% higher group biomass of *D. aruanus* experimental colonies compared with *P. moluccensis*) is partially responsible for the differences among treatments. However, biomass alone cannot be fully responsible for these larger patterns in sediment removal between the two species; respective species behaviours likely drive additional differences in sediment removal and enhancement of coral health. Additional caveats to this experiment can be made regarding how the coral/fish/sediment dynamics could be altered under natural (non-experimental tank) conditions. With these levels of sedimentation, reefs would also experience high turbidity levels (> 20 m l^{-1}), leading to impariments in fish behaviours, such as average foraging distance, leading to variable levels of sediment removed (Wenger & McCormick 2013; Wenger et al. 2013). The small confined aquaria space will enhance fish-coral interactions (closer fish proximity, similar to Chapter 5) resulting in higher levels of sediment removed and greater coral health. In the field, while these damselfishes on average stay close (< 25 cm, which is slighly larger than the tank space) to their host corals, they do roam further from the coral during the day (see diurnal and nocturnal behaviours recorded in Chapter 3) which would reduce the strength of their positive effects for sediment removal. However, certain *in-situ* conditions, not present in aquaria, would augment the coral coral holobiont. For example, increased flow levels and wave action will remove sediment more efficiently (either through water currents, resuspending sediment off the coral surface, or enhancing the coral health/mucus production allowing for sediment removals) in natural conditions. As a result, positive interactions would likely differ in larger tanks or in the field.

The sediment levels used in the present chapter were designed to reflect high concentrations and prolonged sediment deposition, such as would be experienced during storms and reuspension events rather than average background sedimentation levels (Storlazzi 2004; Whinney 2017). However, prior research has documented that select natural coral populations experience sediment deposition rates exceeding 200 mg cm^{-2} day^{-1} (Erftemeijer et al. 2012), which are considerably higher than the sedimentation levels used in the current experiment. Nevertheless, the severe sedimentation levels used herein are relatively uncommon in coral reef ecosystems. These results reveal the positive effects of fishes on corals and should be interpreted within this context. This study represents a step-forward in determining the nature of fish-coral interactions under sediment stress, and highlights that a positive interaction can occur in certain circumstances. There is scope for future research to explore the relationship between fishes and corals under a more nuanced range of sedimentation levels, additional branching morphologies/taxa, and other non-visible and sub-lethal impacts.

The impacts of sediment and fish on total protein, total chlorophyll, and tissue biomass of host coral colonies in this study may have been underestimated for a number of reasons. Firstly, branching corals such as *P. damicornis* are adept at removing sediments (Lasker 1980) from their surfaces and are less susceptible to sediment impacts (Duckworth et al. 2017), potentially leading to greater impacts of sediment in other taxa. While still abundant on inshore, sheltered reefs, branching corals are in generally lower abundance compared with massive and encrusting corals, inferring different interactions exist between damselfishes and these more common coral morphologies (i.e. considerably less interactions and of a different natural with non-branching corals (see Holbrook et al. 2000; Pratchett et al. 2012; Kerry et al. 2012, Chapter 3). Secondly, corals in this experiment may have supplemented their diet (more than *in situ* due to the daily enriched food source) and even augmented coral tissue levels by feeding on the organic component of sediments (Rosenfeld et al. 1999), preventing depletion of energy reserves, thereby masking considerable negative impacts on colony tissue (Philipp and Fabricius 2003). Thirdly, select natural coral populations experience > 200 mg cm^{-2} day^{-1}, with certain coral species tolerating > 300 mg cm^{-2} day^{-1} (supported by published *ex-situ* experiments, Erftemeijer et al. 2012) which are considerably higher than sedimentation levels used in this experiment. Finally, while sedimentation alone has been documented to have minimal sub-lethal and lethal effects on corals under certain conditions (Rogers 1990; Philipp and Fabricius 2003), the additive stress of suspendend sediment (not specifically examined here) can induce larger damage to the holobiont. Detrimental energy expending or non-visible sub-lethal impacts will occur under sediment stress (e.g. mucus production energy), although these facets were not measured in this experiment. Per the natural sediment grain composition around the Palm Islands, corals in the manipulative aquaria experiment were exposed to sand, which has been documented to have little impact on coral photophysiology (Weber et al. 2006). Therefore, future studies could examine whether and how fish presence alters the influence of different sediment types on coral colonies.

4.5.3 Conclusions

Increased sediment inputs are one of the main stressors underpinning ecological degradation on inshore reefs (Done 1982; Rogers 1990; Richmond 1993). The impacts of sediments on these ecosystems range from sub-lethal effects on individual coral colonies, to sediment driven regime-shifts altering the functioning of benthic communities (Goatley et al. 2016). This chapter demonstrates that small aggregating damselfishes can alleviate the negative effects of severe sediment deposition on their host coral colonies, acting as buffers by removing sediments and enhancing colony survival. Such benefits have the potential to act as stabilizing forces, facilitating the persistence and growth (Meyer et al. 1983; Holbrook et al. 2008) of the coral holobiont (including endosymbionts and exosymbionts) in the face of anthropogenic and natural stressors (Kiers et al. 2010; Marquis et al. 2014). These positive interactions link high diversity to high productivity under stressful environmental conditions (Mulder et al. 2001), increasing survivorship of interacting species in the face of certain global climate change conditions. Unfortunately, mutualist damselfishes, those proposed to offer the greatest benefits to corals under high sediment stress, are also some of the most sensitive fishes to environmental changes (Wong and Candolin 2015). As such, these important mutualisms may become less prevalent with ongoing reef degradation, limiting the propensity of fishes to support coral colony health in the face of widespread environmental change. By developing a new understanding of the association between ecologically important aggregating damselfishes and their coral hosts, this chapter sheds new light on the manifestation of context-dependent symbioses in coral reef systems.

CHAPTER 5: Evaluating the influence of coral-dwelling fish on the health of their coral hosts before, during and after a thermal-bleaching event

The context of this chapter has been published as:

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5.1 Synopsis

Global environmental change has the potential to disrupt well established species interactions, with impacts on nutrient cycling and ecosystem function. On coral reefs, fish living within the branches of coral colonies can promote coral performance, and it has been hypothesized that the enhanced water flow and nutrients provided by fish to corals could ameliorate coral bleaching. The aim of this chapter was to evaluate the influence of small, aggregating damselfish on the health of their host corals (physiology, recovery, and survival) before, during, and after a thermal-bleaching event. When comparing coral colonies with and without fish, those with resident fish exhibited higher *Symbiodinium* densities and chlorophyll in both field and experimentally-induced bleaching conditions, and higher protein concentrations in field colonies. Additionally, colonies with damselfish in aquaria exhibited both higher photosynthetic efficiency (F_V/F_M) during bleaching stress and post-bleaching recovery, compared to uninhabited colonies. These results demonstrate that symbiotic damselfish, and the services they provide, translate into measurable impacts on coral tissue, and can influence coral bleaching susceptibility/resilience and recovery. By mediating how external abiotic stressors

influence coral colony health, damselfishes can affect the functional responses of these interspecific interactions in a warming ocean.

5.2 Introduction

Coral reefs are among the most biodiverse and climate change vulnerable ecosystems (Hoegh-Guldberg 1999; Hughes et al. 2017a), largely owing to the thermal sensitivity of habitat-forming scleractinian corals. Aside from causing widespread coral bleaching and coral loss (Hughes et al. 2017a; 2018b), sustained and ongoing changes in environmental conditions may also threaten complex and critical interactions among coral reef organisms (Bellwood et al. 2004; Hughes et al. 2003, 2017a, b). These complex interactions give rise to ecological processes that shape the structure and function of ecosystems, with feedbacks that are critical to reinforce or to destabilize particular species-species and species-environment interactions (Bolker et al. 2003; Bairey et al. 2016; van de Leemput et al. 2016). For instance, aggregating damselfishes and host corals are engaged in a positive feedback loop where symbiont damselfishes increase coral growth, thereby increasing available habitat and attracting more damselfishes (Holbrook et al. 2011). Abnormally high ocean temperatures, however, disrupt the foundation interaction between the coral animal and its photosynthetic endosymbionts (*Symbiodinium* spp.), resulting in coral bleaching and mortality (Lesser 2011; Hoegh-Guldberg 1999; Hughes et al. 2017a; 2018b). Severe bleaching events can lead to the loss of over 90% of local coral populations, especially in thermally-susceptible coral species, such as *Acropora*, *Pocillopora*, and *Stylophora*, (Glynn and D’Croz 1990; Brown 1997; Loya et al. 2001; Graham et al. 2006), altering nearly all reef interactions and feedbacks dependent upon corals. Understanding the causes and impacts of bleaching on coral reef biodiversity and functioning requires knowledge of the environmental factors that stabilize or destabilize the core coral-*Symbiodinium* mutualism.

Coral symbioses are complex, multi-level networks of numerous species wherein the coral animal interacts with *Symbiodinium* with a complex microbial community (Hernandez-Agreda et al. 2016), and with resident invertebrates and site-attached fish (Cantrell et al. 2015). Various mechanisms act to stabilize or destabilize the coral holobiont. While temperature stress is often recognized as the primary driver of coral symbiosis breakdowns (Lesser 2011; Hoegh-Guldberg 1999), other abiotic factors such as nutrient excess, changes in salinity, water flow, and light intensity (Glynn 1991) can also lead to bleaching, and mortality. Increased temperature also impacts symbiotic partners' behaviour and metabolism (Nagelkerken and Munday 2016) as well as the host's demands, leading to shifts in interactions from mutualisms to commensalism or parasitism, or abandonment of the symbiosis, or co-extinction (Six 2009).

Certain coral species, primarily branching corals from the genera *Acropora*, *Pocillopora*, *Seriatopora and Stylophora*, provide critical habitat for small aggregating fishes (Holbrook et al. 2000; Coker et al. 2014). While these fish gain shelter, food, and refuge from coral colonies (Cole et al. 2008; Wilson et al. 2008; Coker et al. 2014) they also provide benefits to corals. Certain fish species can enhance coral health by defending corals from predation (Gochfeld 2010), increasing nutrient concentrations in the water column (Meyer and Shultz 1985a; Shantz and Burkepile 2014; Chase et al. 2014), enhancing tissue aeration and increasing water flow between branches (Berenshtein et al. 2004; Goldshmid et al. 2004; Garcia-Herrera et al. 2017), slowing the progression of coral disease (Chong-Seng et al. 2011), and increasing overall growth (Meyer and Shultz 1985b; Liberman et al. 1995; Shantz et al. 2015). Both increased nutrients (specifically altered nitrogen:phosphorous ratios) and water flow rates can moderate bleaching susceptibility (observed under field conditions) and the rates of recovery of bleached corals (Nakamura et al. 2003; Wiedenmann et al. 2012). As coral-dwelling fishes can alter water flow and nutrient availability for corals, they can potentially influence coral resistance to bleaching and/or coral recovery from bleaching (Doropoulos et al. 2015).

Multiple processes and feedbacks are likely to determine whether and how fish influence bleaching susceptibility and recovery of their host corals. Many damselfish species remain with their coral counterparts during and after thermal stress, even when corals are severely bleached (Bonin et al. 2009; Coker et al. 2012a, b). As a result, the benefits that fish provide to corals can continue to operate during thermal stress conditions. Nutrient provision can lead to a proliferation of symbionts within coral tissue (Meyer and Shultz 1985b), and the nutrients excreted by fish living within coral branches might therefore prevent the collapse of the endosymbiotic algae population during temperature stress. Similarly, enhanced water flow can modulate mass-transfer rates and support gas exchange for photosynthesis; therefore, the swimming activity of fish living within coral branches might also stabilize symbiont population size and lessen the severity of bleaching (Nakamura and van Woesik 2003; Goldshmid et al. 2004; Garcia-Herrera et al. 2017). However, bleaching can alter fish behaviour, physiology and survival (Munday et al. 2008; 2009), and these changes potentially alter the nutrient provision and flow-moderation functions of fish living within corals (Jones et al. 1998).

Whether and how coral-associated fish aid corals in bleaching tolerance and recovery is unknown.

The objective of this chapter was to evaluate the influence of coral-dwelling fishes on the health of their host corals during and after thermal stress. I assessed the hypothesis that nutrient provision, aeration and water stirring by coral-dwelling fish act as "ecological buffers" (Marquis et al. 2014) that enhance coral health during temperature stress. Using a combination of field-based and aquarium experiments, this research aimed to elucidate the impacts of aggregating damselfish on: a) coral health under thermal bleaching conditions in the laboratory and in the field; and (b) coral health under ambient conditions in the field. Multiple physiological traits for the same coral fragments were measured to facilitate direct comparisons within colony bleaching treatments to assess whether fish ameliorate bleaching severity and/or enhance bleaching recovery.

5.3 Materials and Methods

5.3.1 Ethics Statement

All methods and experimental protocols were carried out in accordance with Great Barrier Reef Marine Park Authority permit (G15/37657.1), James Cook University Animal ethical guidelines and regulations (A2186), and James Cook University's General Fisheries permit (170251). All coral and damselfish were returned to the site of collection (following JCU Ethics permit A2186) and select coral fragments (< 8cm in length) were sacrificed for further laboratory tissue analysis, per GBRMPA permit G15/37657.1 None of the corals or damselfish collected were protected species.

5.3.2 Study System and Location

An aquarium experiment and field observations were conducted to determine whether coral-dwelling damselfish enhance coral health before, during, and after thermal bleaching events. The symbiotic interaction between the coral-associated damselfish, *Dascyllus aruanus*, and its coral host was chosen due to the damselfish's site fidelity (Sale 1972a), and its behaviour of aggregating in social groups that remain close to the host coral, sleeping within the branches. *D. aruanus* is abundant within the Lizard Island lagoon (Pratchett et al. 2012) and is commonly found in groups of 2 – 10 fish on colonies of branching corals (Holbrook et al. 2000; Chase et al. 2014). The coral *Pocillopora damicornis* was selected as a focal species for the aquarium experiment as it is a natural host of *D. aruanus* (and other damselfish species), is generally abundant on shallow coral reefs, and has often been used as a focal species in bleaching studies (Marshall and Baird 2000; Pratchett et al. 2012; Sweet and Brown 2016). A different coral species, *Seriatopora hystrix*, was used in the field observations due to its local abundance and trajectory of bleaching at the time of field sampling. Both *P. damicornis* and *S. hystrix* are known to host damselfishes, exist in a range of habitats with adult colonies similar in size ranges, and exhibit high bleaching susceptibilities (Hoegh-Guldberg and Smith 1989; Hughes et al. 2017a). Using previous literature on *S. hystrix* under natural conditions, in combination with *in-situ* exposure to extreme temperatures similar to the aquarium experiment I conducted, provides a deeper understanding of fish impacts on corals during thermal stress.

Research was conducted at Lizard Island Research Station on the northern Great Barrier Reef (GBR), Australia (14˚41'S, 145˚27'E). An aquarium experiment investigating the effects of fish presence on coral bleaching severity and rates of recovery was conducted between June and August 2015, with all corals and fish used in these experiments collected from sites within the Lizard Island lagoon (Appendix S5, Table S5.1). *In-situ* bleaching observations were conducted in February and March of 2016, during the severe mass bleaching event (Hughes et al. 2017a). Colonies of *S. hystrix* were tagged at four sheltered sites of the lagoon at depths between 0-2 m (n = 20 colonies per site, Figure S5.1) and tracked for bleaching progression. These four sites had abundant small branching corals (mainly *S. hystrix*), both with and without target aggregating fish, and displayed bleaching during this timeframe. In contrast, during the observation period, other small branching corals with and without aggregating fish, located at deeper sites, had yet to exhibit signs of bleaching.

Table 5.1 Summary of the research objectives of this study, the general approach, and coral metrics used to investigate each objective.

Research Objective	General approach	Coral metrics analysed
In-situ observations of aggregating damselfish on coral hosts pre- and during bleaching conditions (in the field)		
(i) Condition of *Pocillopora damicornis* with and without *Dascyllus aruanus* symbionts during non-bleaching conditions in the field	Colonies at one site within the Lizard Island lagoon	*Symbiodinium* density Total chlorophyll ($a + c$) Total protein Tissue biomass
(ii) Condition of *Seriatopora hystrix* with and without *D. aruanus* symbionts during bleaching conditions in the field	Colonies at four sites within the Lizard Island lagoon	*Symbiodinium* density Total chlorophyll ($a + c$) Total protein
Impacts of aggregating damselfish on coral hosts under manipulative thermal bleaching experiment (in aquaria)		
(iii) Condition of *P. damicornis* with and without *D. aruanus* symbionts during experimental bleaching temperatures in aquaria	Colonies under four experimental treatments: (i) ambient temp + colonies with fish; (ii) ambient temperature + colonies without fish; (iii) bleaching temperatures + colonies with fish; (iv) bleaching temperatures + colonies without fish.	*Symbiodinium* density Total chlorophyll ($a + c$) Total protein Tissue biomass Photochemical efficiency (F_V/F_M)

5.3.3 In-situ observations pre- and during bleaching conditions

To confirm whether *D. aruanus* influenced the tissue composition of corals under ambient field conditions, fragments were sampled from small (20 – 50 cm diameter) *P. damicornis* colonies during non-bleaching conditions. In May of 2015, *P. damicornis* colonies with *D. aruanus* (n = 5, each with 2 to 10 damselfish) and without *D. aruanus* present (n = 4) were sampled within the Lizard Island lagoon between 0-4 m (similar depths per treatments). One fragment per colony was removed using a hammer and chisel. These fragments were analysed for protein, symbiont density, total chlorophyll density, and tissue biomass (Text S5.2 in Appendix S5) using the methods described below (see "Coral tissue analysis" below). Data were analysed using a one-way analysis of variance (ANOVA) with fish presence as a factor. Statistical assumptions were assessed by analyzing residual plots, homogeneity of variance (Bartlett's test), and normality (Shapiro-Wilks test).

To investigate the impacts of aggregating fish on corals during an *in-situ* bleaching event, 10 colonies were tagged at each of four sites (n = 40 colonies) within the Lizard Island lagoon in March 2016. At each site, *S. hystrix* colonies with *D. aruanus* (n = 5) and without *D. aruanus* (n = 5) were tagged, photographed, and sampled. *S. hystrix* was used, instead of *P. damicornis*, because it was more commonly found to host *D. aruanus* at these sites. One fragment from each colony was collected in March 2016 and analysed for protein, symbiont density and total chlorophyll density. Coral colonies were checked 10 months post-tagging to quantify bleaching-related mortality under natural field conditions (see Text S5.1, Figure S5.1, and Figure S5.2 in Appendix S5). To assess the impacts of fish on coral physiology (proteins, symbiont density, and total chlorophyll density) during *in-situ* thermal bleaching, tissue composition data were analysed using one-way analysis of variances (one-way ANOVAs) with Tukey's HSD *post-hoc* tests (where applicable) using R statistical software.

Statistical assumptions were assessed by analyzing residual plots, homogeneity of variance (Bartlett's test), and normality (Shapiro-Wilks test).

5.3.4 Manipulative thermal bleaching experiment

An aquarium experiment with a factorial design was established with ambient and heated water temperature treatments, and fish present versus absent. Corals were acclimated to aquarium conditions for two weeks prior to the start of the experiment. During this time any dead branches, algae and/or other invertebrates were removed. Ambient and heated sump tanks (1000 L, 2 sumps per temperature treatment) were established in a shaded outdoor area (daily maximum light intensity ~350 μmol photons m^{-2} s^{-1}) with replicate aquaria positioned within each sump. Heated sump tanks each contained a 2400-watt water heater (TECO TK 1000 heaters, accuracy 0.1°C), and were equipped with 2-3 water pumps to ensure an even heat distribution. The two control (unheated) sumps received a supply of ambient seawater from the reef flat (23.5-25°C, dependent upon the time of day) for the entire duration of the experiment. The heated treatment was implemented in phases as follows: (i) Acclimation – corals were held at ambient temperatures for 7 days; (ii) Ramping - temperature was gradually raised from ambient to 32°C (typical of northern GBR summer temperatures, (Hughes et al. 2017a) over the course of 2 weeks (increase of~0.5°C day^{-1}); (iii) Stress – corals were maintained at 32°C for 15 days, and; (iv) Recovery – temperature was decreased back to ambient over 8 days, and then maintained at ambient for 20 days to allow recovery. Spot-check temperature measurements were made for each tank multiple times daily using a handheld water-proof thermometer (±1°C accuracy, Dig-stem-1 Digital Thermometer, Instrument Choice AU). At the end of each of the acclimation, thermal stress, and recovery phases of the experiments, one fragment per colony (n = 114 in total) was sampled for subsequent quantification of tissue protein, symbiont density, total chlorophyll density, and tissue biomass.

Each individual aquarium (25 L volume) received an inflow of ambient seawater (~12 L hr^{-1}) pumped directly from the Lizard Island lagoon and was fitted with an air stone. This low flow rate of ~12 L hr^{-1} is representative of reef flow regimes, often ranging from 1 and 15 cms^{-1} (Patterson et al. 1991). Water from each aquarium flowed into the surrounding sump. This experimental set-up was designed to: a) ensure each replicate aquarium had an individual water supply so that fish-excreted nutrients did not contaminate tanks without fish, and b) ensure stable and equal water temperatures among replicate aquaria within each temperature treatment. Temperatures were maintained within ± 0.5°C of the desired level.

Replicate aquaria with fish and no-fish treatments were divided evenly between the sumps (10 replicates per sump). Each replicate had a small (~20-25 cm diameter) *P. damicornis* colony which was collected from the Lizard Island lagoon and which were naturally devoid of any resident fishes at the time of collection. Treatments with fish present contained six *D. aruanus* with a similar group biomass (individual fish biomass 0.5 to 5.6 g, group biomass 15 g ± 0.56) that were collected from the Lizard Island lagoon using a weak solution of clove oil (see Frisch et al. 2007, Javahery et al. 2012) and hand nets. Damselfish were subject to a brief 'freshwater rinse' to remove any bacteria and parasites prior to being introduced to other fish and corals within each experimental treatment (Pironet and Jones 2000). After 72 hours of acclimation, damselfish were weighed (wet weight, using a MS105 Semi-Micro Balance, Mettler Toledo, accuracy 0.001), measured (total length), and placed in aquaria with live *P. damicornis* colonies. Fish remained with the same conspecifics found in the field to maintain existing social groups and minimize aggressive behaviour in aquaria. Fish number and biomass per aquarium were consistent with natural aggregations. Fish numbers and condition were inspected several times a day throughout the 66-day experimental period, particularly during feeding times when damselfish were actively moving in the water column. All corals and fish were fed multiple times a day to satiation (Chase et al. 2014) with enriched *Artemia salina* nauplii to supplement food naturally available in the seawater pumped from the nearby lagoon.

Linear mixed effects models with experimental phase, fish treatment and temperature treatment as factors, were used to assess whether fish presence affected each of the measured components of tissue composition during thermal stress using the function ‘lme’ in the package ‘nlme’ (Pinheiro et al. 2014; R Core Development Team 2018). For all of these analyses, coral colony was included as a random effect to account for repeated measures of each colony at each phase of the experiment. Selected multiple comparisons (n = 12 *post-hoc* planned contrasts, see Table S5.2 in Appendix S5) were performed using a model contrast matrix to determine: (a) whether the treatments differed immediately after acclimation, (b) effect of fish presence during bleaching, (c) effect of fish presence during recovery, and (d) long-term effect of fish presence two months after bleaching. Adjusted p-values and confidence intervals, to account for multiple contrasts, were utilized to determine which treatment combinations were significantly different from each other. Values in the text are specified as means ± standard error. All statistical analyses were performed using the R statistical software (R Core Development Team 2018).

5.3.5 Photosynthetic efficiency as a proxy for bleaching severity

A Pulse Amplitude Modulated (PAM) fluorometer (Mini-PAM, Walz; for settings see S2 Text in Appendix S5) was used to monitor the onset, severity, and recovery of coral bleaching nightly during the temperature stress, and every five days during acclimation and recovery, with three replicate measurements per colony per day. The dark-adapted F_V/F_M (F_V is minimum fluorescence and F_M is maximum fluorescence), which is a measure of the maximum photochemical efficiency of symbionts present within coral tissue (e.g. Jones et al. 2000), was measured approximately 2.5 hours after sunset (~21:00 h). F_V/F_M was used as a proxy for coral bleaching severity as there is a relationship between the photosynthetic efficiency of symbionts (as measured using PAM fluorometry), symbiont density, and coral bleaching status (Krause and Weis 1991; Jones et al. 1998; Warner et al. 1999; Nir et al. 2011). Photosynthetic efficiency measurements were averaged per colony per night and the change in this metric over time was analysed using piecewise regressions. This piecewise approach was used because the dynamics of F_V/F_M differed during the different phases of the experiment. Linear regression was used to assess changes in F_V/F_M for control (ambient temperature) corals throughout the experiment. For the colonies exposed to heat stress, linear regression was also used to assess changes in F_V/F_M during recovery. Linear regressions were appropriate for analysis of F_V/F_M during this phase of the experiment based on the distribution of the data. During heat stress, however, data from acclimation, ramping and thermal stress were analysed using non-linear regression because changes in F_V/F_M during these phases were strongly non-linear (Table S5.3 in Appendix S5). A sigmoidal equation was chosen based on preliminary observation of the data following Negri and Hoogenboom (2011), as:

$$Y = (mx + a) - \left(\frac{mx}{1 + \exp\left(-\frac{t - x\theta}{\omega}\right)}\right) \tag{1}$$

Where Y is the photosynthetic efficiency (F_V/F_M) on a given day during exposure to elevated temperature, mx is the maximum achievable efficiency, a is the minimum efficiency, t is time, $x\theta$ is the time at which Y is halfway between mx and a, and ω captures the rate at which efficiency declines. Because I was fitting different equations to the different sections of the data, I used a formal model selection process to determine which model best described the dynamics of F_V/F_M. Akaike's Information Criterion (AIC) and subsequent weight ($wAIC_i$) for each potential model (see Table S5.4) were calculated (see Burnham and Anderson 2002; Hoogenboom et al. 2011). The results presented are for equations fitted to the daily mean values for all colonies within each treatment. However, the model fitting was repeated for the data for individual colonies within treatments; that analysis yielded similar results with the same overall conclusions.

5.3.6 Coral tissue analysis

In all three experiments (*in-situ* natural conditions, *in-situ* bleaching conditions, and *ex situ* thermal bleaching experiment) 1-2 coral fragments, approximately 6 cm in length, were collected from each colony. Fragments were subsequently frozen in liquid nitrogen during transport and maintained at -80°C prior to laboratory analysis. Tissue was removed from the skeleton using compressed air in 0.45 µm filtered seawater, collected, and homogenized. The resulting tissue suspensions were divided into aliquots for protein assays (1 ml), symbiont counts (0.9 ml with 0.1 ml of 10% formaldehyde, to preserve samples), total chlorophyll (5 ml), and tissue biomass (8 ml). Coral skeletons were retained to quantify fragment surface areas using the wax dipping technique (Stimson and Kinzie 1991). Five coral colonies, all from the heated treatments in the manipulative thermal bleaching experiment (from colonies with and without fish), died during the recovery phase of the experiment. Tissue composition data for these dead corals were recorded as 0 for all metrics, to represent the biological consequences of coral death during bleaching events. Detailed methods of coral tissue analysis are provided in Appendix S5, Text S5.1 and Text S5.2.

5.4 Results

5.4.1 Effects of fish presence on corals before and during bleaching under natural conditions (in situ)

Under normal temperature conditions in the field, *P. damicornis* colonies with *D. aruanus* had significantly higher densities of *Symbiodinium* (ANOVA, $F_{1,8} = 8.2$, $p = 0.02$) and higher concentrations of total chlorophyll (ANOVA, $F_{1,8} = 6.7$, $p = 0.03$) than unoccupied colonies (Figure 5.1). In contrast, no significant differences were observed in protein concentration (ANOVA, $F_{1,8} = 3.19$ $p = 0.112$) or tissue biomass (ANOVA, $F_{1,8} = 0.04$ $p = 0.85$).

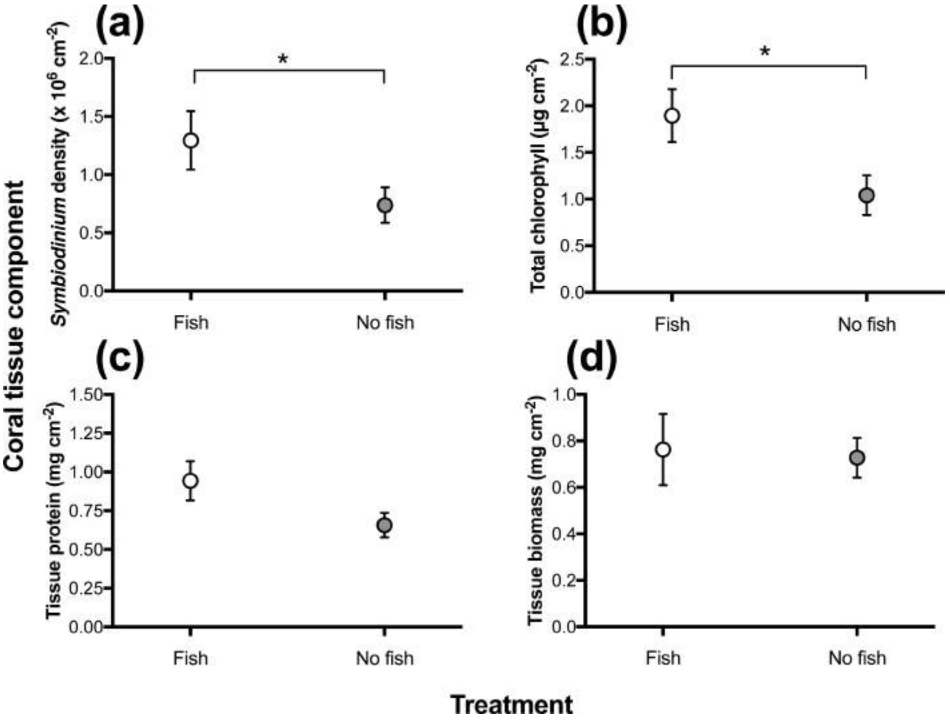


Figure 5.1 *In-situ* levels of **(a)** endosymbionts (*Symbiodinium* density × 10^6 cm^{-2}), **(b)** total chlorophyll (chl *a* + chl *c*, µg cm^{-2}), **(c)** tissue protein (mg cm^{-2}), and **(d)** tissue biomass (calculated via ash-free dry weight, mg cm^{-2}) of naturally occurring *P. damicornis* colonies, with *D. aruanus* (n = 5) and without fish (n = 5) present. (*) denotes a significant difference between fish treatments, and *error bars* show SE.

During the 2016 bleaching event at Lizard Island, *S. hystrix* colonies in the field were exposed to temperatures > 33°C, which led to widespread bleaching and mortality. At the time of collection, *S. hystrix* colonies had an average of 0.32 × 10^6 *Symbiodinium* cm^{-1} ± 0.02 (compared with typical ambient densities of 2.1 × 10^6 *Symbiodinium* cm^{-1} ± 1.0, see Hoegh-Guldberg and Smith 1989). The effects of fish presence were consistent among sites for *Symbiodinium* density (ANOVA(treatment*site): $F_{3,30} = 1.81$, $p = 0.17$, Figure 5.2a). Conjointly, average *Symbiodinium* densities were higher for colonies with fish than for colonies without fish (ANOVA treatment effect: $F_{1,33} = 6.16$, $p = 0.018$). In addition, average *Symbiodinium* densities differed between sites (ANOVA, site effect: $F_{3,33} = 3.75$, $p = 0.02$). No differences in total chlorophyll or proteins were detected among sites, however, both of the tissue variables depended upon fish presence (ANOVA: total chlorophyll, $F_{1,35} = 7.29$, $p = 0.01$, proteins: $F_{1,36} = 4.50$, $p = 0.041$, see Figure 5.2b, c). All colonies were monitored during the bleaching event and after a period of recovery of > 6 months: in September 2016, > 90% of colonies were dead and covered in filamentous algae regardless of fish presence/absence. Due to the severity of the bleaching event and the position of the colonies within a lagoon (higher recorded temperatures, see Hoogenboom et al, 2017), post-bleaching recovery was non-existent, resulting in widespread mortality of *S. hystrix* colonies (post-bleaching > 90% of colonies were recorded as dead) and disappearance of symbiont damselfish.

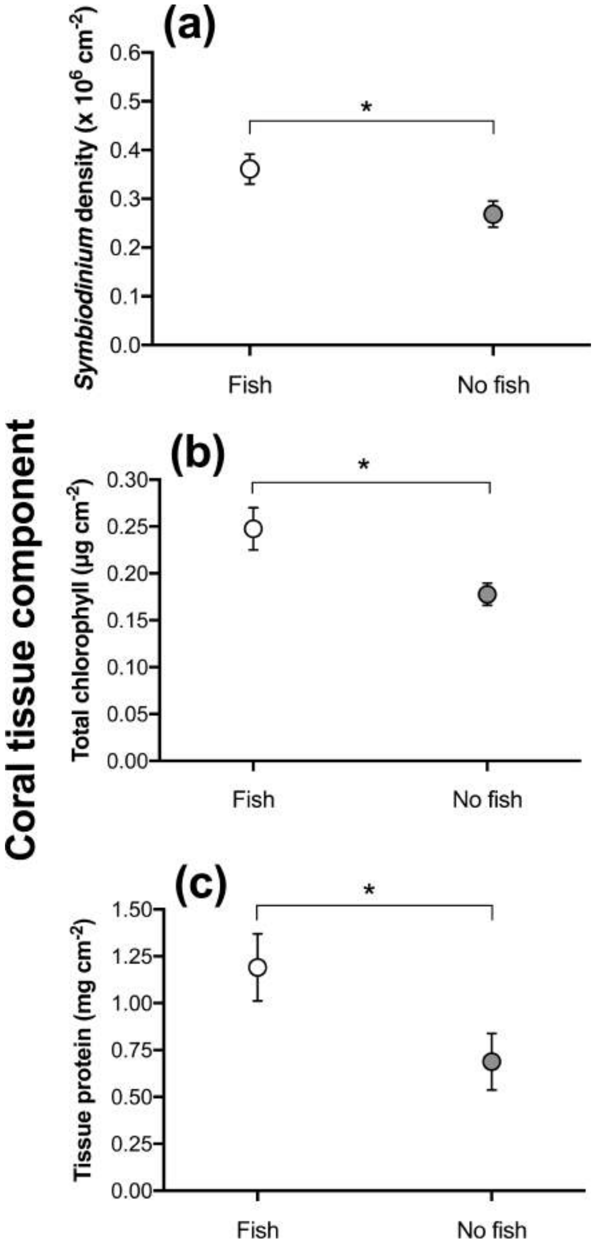


Figure 5.2 Differences in mean (±SE) levels of **(a)** endosymbionts (*Symbiodinium* density × 10^6 cm^{-2}), **(b)** total chlorophyll (chl *a* + chl *c*, µg cm^{-2}), and **(c)** tissue protein (mg cm^{-2}) of naturally occurring *S. hystrix* colonies, with *D. aruanus* (n = 19) and without fish (n = 18) present during a coral bleaching event at Lizard Island. Colonies positioned at 1 - 3 m depth within four lagoonal sites with limited current activity. (*) denotes a significant difference between fish treatments, and *error bars* show SE.

5.4.2 Effects of fish presence during experimental bleaching

At the end of the acclimation phase during the manipulative thermal bleaching experiment, *Symbiodinium* density, chlorophyll density, protein concentration, and tissue biomass were approximately equivalent among all treatments (*in aquaria*: *Symbiodinium*: µ =

0.99 × 10^6 *Symbiodinium* cm^{-2} ± 0.07; total chlorophyll: μ = 1.5 chl *a* + chl *c* μg cm^{-2} ± 0.10; protein: μ = 0.64 mg cm^{-2} ± 0.03; tissue biomass: μ = 7.8 mg cm^{-2} ± 0.048, see Table 5.1, Figure 5.3a, d, g, j, and *planned comparisons* Table S5.6, in Appendix S5). These values (see Figure 5.3a) were approximately the same as those for fragments sampled from the field (*in-situ*: *Symbiodinium*: μ = 1.1 × 10^6 ± 0.17 *Symbiodinium* cm^{-2}; total chlorophyll: μ = 1.02 chl *a* + chl *c* μg cm^{-2} ± 0.15; protein: μ = 0.8 mg cm^{-2} ± 0.09; tissue biomass: μ = 7.5mg cm^{-2} ± 0.08, see Figure 5.1).

Table 5.2 Linear mixed effect model of the effect of phase, temperature, and fish presence (*D. aruanus*) on experimental *P. damicornis* colonies for **(i)** *Symbiodinium* density, **(ii)** total chlorophyll density, **(iii)** total proteins, and **(iv)** and tissue biomass (as part of the manipulative thermal bleaching experiment), where coral colony was included as a random effect.

Coral component and factor	**Df**	***F***	***P***
(i) ***Symbiodinium***			
Phase	2,66	13.6610	< **0.001**
Temperature	1,33	73.0350	< **0.001**
Treatment	1,33	14.5070	< **0.001**
Phase:Temperature	2,66	30.2860	< **0.001**
Phase:Treatment	2,66	6.2300	< **0.001**
Temperature:Treatment	1,33	0.8580	0.360
Phase:Temperature:Treatment	2,66	0.7610	0.470
(ii) *Total Chlorophyll*			
Phase	2,69	10.683	< **0.001**
Temperature	1,41	49.310	< **0.001**
Treatment	1,41	17.059	< **0.001**
Phase:Temperature	2,69	18.651	< **0.001**
Phase:Treatment	2,69	3.4260	**0.038**
Temperature:Treatment	1,33	0.1260	0.730
Phase:Temperature:Treatment	2,69	0.0980	0.910
(iii) *Protein*			
Phase	2,66	12.7377	< **0.001**
Temperature	1,33	16.1734	< **0.001**
Treatment	1,33	0.4165	0.523
Phase:Temperature	2,66	6.7671	< **0.001**
Phase:Treatment	2,66	1.3440	0.268
Temperature:Treatment	1,33	0.4041	0.529
Phase:Temperature:Treatment	2,66	0.4201	0.659
(iv) *Tissue biomass*			
Phase	2,126	15.9175	< **0.001**
Temperature	1,126	12.3097	< **0.001**
Treatment	1,126	0.0002	0.988
Phase:Temperature	2,126	11.3356	< **0.001**
Phase:Treatment	2,126	2.7551	0.067
Temperature:Treatment	1,126	2.8269	0.095
Phase:Temperature:Treatment	2,126	1.1974	0.308

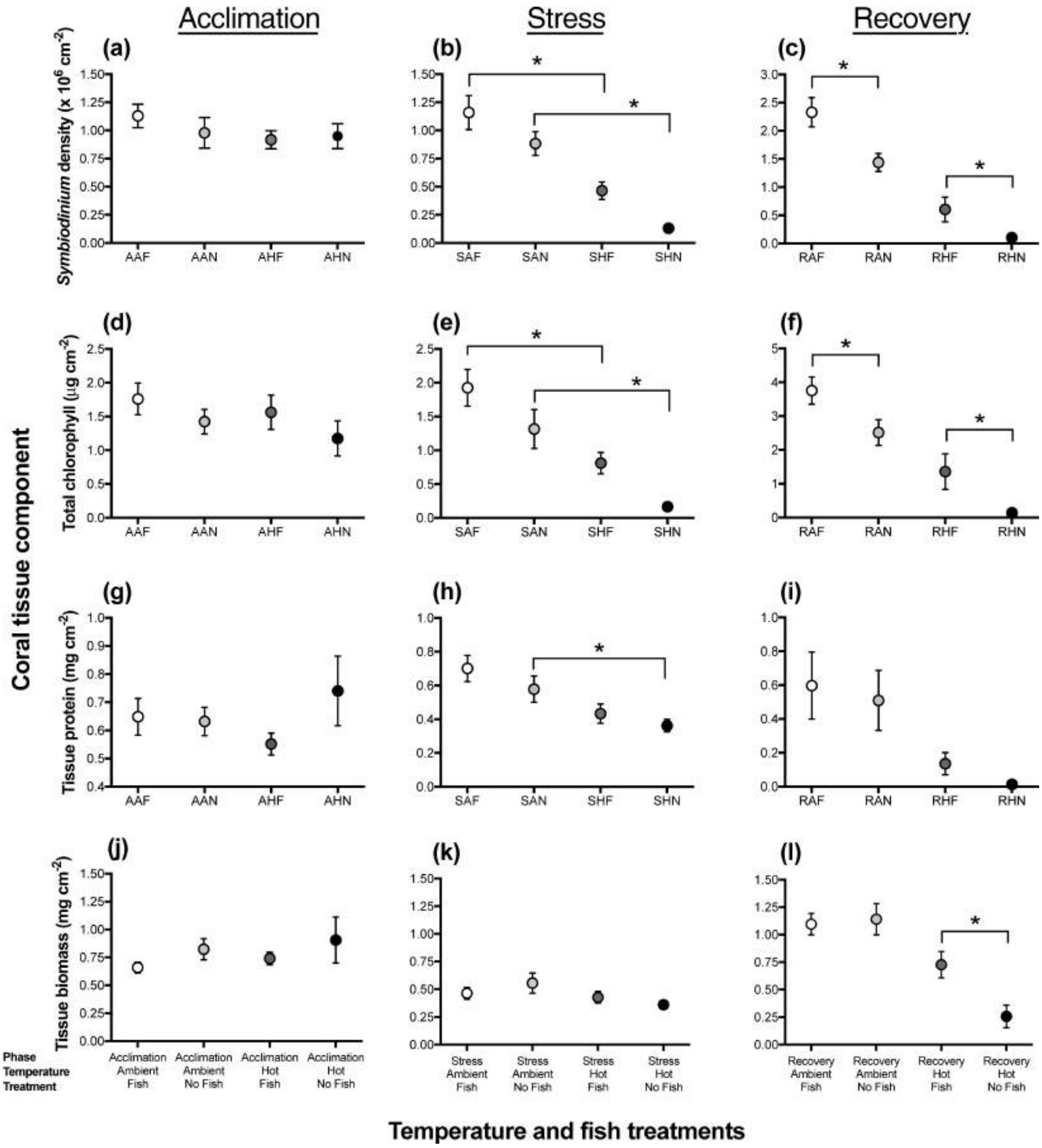


Figure 5.3 Levels of **(a-c)** endosymbionts (*Symbiodinium* density × 10^6 cm^{-2}), **(d-f)** total chlorophyll (chl *a* + chl *c,* µg cm^{-2}), **(g-i)** protein (mg cm^{-2}), **(j-l)** tissue biomass (calculated via grams of ash-free dry weight mg cm^{-2}) in experimental *P. damicornis* colonies, with *D. aruanus* for different temperature and fish treatments (ambient/fish: n = 9, ambient/no fish: n = 9, hot/fish: n = 10 and hot/no fish: n = 9) for three different experimental phases ((Acclimation (25°C), Stress (temperature increased and held at 32°C for four weeks), and Recovery (temperature returned to 25°C)). (*) denotes a significant difference between select comparisons of fish treatments, and *error bars* show SE. Refer to Table S5.2 for results of all 12 planned contrast per coral tissue components in Appendix S5. Note difference in y-axis for panels **(c)** and **(f)**, to allow for visualization of variance between treatments. Data points per phase, temperature, and fish presence have been abbreviated to form 3 letter keys, as follows: A = acclimation, S = stress, R = recovery, A = ambient temperature, H = hot/bleaching temperature, F = fish present, N = fish absent, i.e. SHF = sample collected during stress phase of a hot temperature with fish present colony.

Due to the experimental design, temperature only differed between treatments in certain phases (e.g. in acclimation, all tanks received the same temperature). Consequently, *Symbiodinium* density only differed between treatments during the stress treatment and the recovery phase (significant phase*temperature treatment interaction, Table 5.2). During the stress phase, ambient colonies had significantly higher levels of *Symbiodinium* compared with their counterparts (*comparison*, SAF vs SHF: $p = 0.001$; SAN vs. SHN: $p < 0.001$, Figure 5.3b) and this was observed in both the fish and no-fish treatments. All other planned contrasts for the Stress phase were non-significant (see Table S5.2). After the recovery phase (Figure 5.3c), ambient colonies with fish had significantly higher *Symbiodinium* densities than colonies without fish (*comparison* RAF vs. RAN: $p < 0.001$). After recovery, heated colonies with fish (including dead colonies with 0.0 *Symbiodinium* cm^{-2}) had an average of $0.60 \times 10^6 \pm 0.2$ *Symbiodinium* cm^{-2}, while heated colonies without fish had an average of $0.10 \times 10^6 \pm 0.06$ *Symbiodinium* cm^{-2} (*comparison* RHF vs RHN: $p < 0.021$). Excluding dead corals, heated colonies with fish still had more *Symbiodinium* ($0.67 \times 10^6 \pm 0.23$ *Symbiodinium* cm^{-2}) than heated colonies without fish ($0.19 \times 10^6 \pm 0.09$ *Symbiodinium* cm^{-2}). Between the stress and recovery phases (~30 days), *Symbiodinium* in heated colonies with fish increased ($+0.14 \times 10^6$ *Symbiodinium* cm^{-2}), while *Symbiodinium* in heated colonies without fish decreased slightly (-0.03×10^6 *Symbiodinium* cm^{-2}). Declines in F_V/F_M below 0.7 were associated with declines in *Symbiodinium* concentrations from 1×10^6 cells per cm^2 to $< 0.2 \times 10^6$ cells per cm^2 (Figure S5.3 in Appendix S5).

Similar to *Symbiodinium* densities, the presence of fish had a significant effect on total chlorophyll density in the interactions between phase, temperature, and treatment (Table 5.2) within the manipulative thermal bleaching experiment. During the stress phase, ambient temperature colonies had significantly higher levels of chlorophyll when compared with their heated/bleaching counterparts (comparison, SAF vs SHF: $p = 0.008$; SAN vs. SHN: $p =$

0.007, Figure 5.3e). Additionally, during stress, heated colonies with fish had an average of 0.67 μg cm^{-2} chlorophyll more than heated colonies without fish. During the recovery phase (Figure 5.3e, f), colonies with fish had significantly higher levels of chlorophyll density than colonies without fish (comparison RAF vs. RAN: $p < 0.002$, RHF vs RHN: $p = 0.005$). All other planned comparisons for the Stress phase were non-significant. Analysis further indicated that between stress and recovery phases, total chlorophyll in heated with fish increased greatly (+0.52 μg cm^{-2} chlorophyll), while total chlorophyll in heated colonies without fish only increased slightly (+0.04 μg chlorophyll cm^{-2}). Excluding dead corals, heated colonies with fish still had significantly more chlorophyll (1.49 ± 0.53 μg chlorophyll cm^{-2}) than heated colonies without fish (0.127 ± 0.12 μg chlorophyll cm^{-2}).

While there were no effects of fish presence on tissue protein concentrations or tissue biomass, differences between temperature treatments were evident (Table 5.2 and Figure 5.3g, h, i, j, k, l). Overall, colonies with fish exhibited slightly higher values of protein and tissue biomass than colonies without fish, in both stress and recovery phases. During the stress phase, heated corals contained ~2x less protein than ambient temperature colonies; ambient colonies with fish had 0.27 mg cm^{-2} more protein than stress heated colonies with fish (comparison SAF vs SHF $p = 0.046$). Additionally, during the stress phase, ambient colonies without fish had 0.22 mg cm^{-2} more protein than stress heated corals without fish. These relationships were exaggerated in the recovery phase with ambient corals having ~4 times more protein than heated corals (Figure 5.3i). For tissue biomass, during recovery phase (Figure 5.3l), heated colonies with fish increased in biomass (+ 0.299 mg cm^{-2}), while biomass in heated colonies without fish decreased (- 0.1 mg cm^{-2}); these colonies with fish had significantly higher levels of chlorophyll density than colonies without fish (*planned comparison* RHF vs RHN: $p < 0.012$).

5.4.3 Change in photosynthetic efficiency during and after manipulated temperature stress

Prior to the temperature stress (during acclimation) in the manipulative thermal bleaching experiment, all colonies of *P. damicornis* had approximately equivalent photosynthetic efficiency (F_V/F_M = ~0.7). The best model to explain inter-colony differences in photosynthetic efficiency through the course of the experiment included both temperature treatment and fish treatment (Table 5.3, wAIC for the model which fitted separate responses for all treatments = 1.0 and Figure 5.4a). For colonies with fish and subject to ambient conditions, F_V/F_M increased gradually over time, while colonies subjected to ambient temperature without fish had constant F_V/F_M throughout the entire experiment (Figure 5.4a, b). Overall, ambient corals with fish exhibited slightly higher and more consistent values of F_V/F_M compared with colonies without fish (Figure 5.4b). Irrespective of fish presence, F_V/F_M decreased in heated corals during the stress phase, when temperatures exceeded 30°C, typical of natural bleaching events at Lizard Island (Figure 5.4c, d). However, heated colonies without fish exhibited a more pronounced decline in F_V/F_M to more than half of its initial value (0.7 to ~0.3) when compared with a 30% decrease observed in heated colonies with fish (0.7 to ~0.5). The parameters describing the non-linear relationships between F_V/F_M and time during the experiment (mx, $x\theta$, ω, and α) depended upon temperature treatment and fish presence (Table S5.3 in Appendix S5). During recovery, heated colonies with fish continued to experience a very slight decrease in F_V/F_M (Figure 5.4c and Appendix S5, Table S5.3) for the duration of the experiment. However, F_V/F_M in heated colonies without fish continued to decline (Figure 5.4d) with an average F_V/F_M of close to 0.25 at the end of the experiment. Differences in photosynthetic function were correlated to an increased density of *Symbiodinium* (Figure S5.3 in Appendix S5).

Table 5.3 Comparison of regression models testing the effects of temperature (ambient: 25°C or hot: 32°C) and fish presence (fish or no fish) on *P. damicornis* photosynthetic efficiency (F_V/F_M), fitting the data through the means for colonies within treatments for the Acclimation and Stress experimental periods during the manipulative thermal bleaching experiment. Akaike's information criteria (AIC) and AIC differences (ΔAIC) were calculated per model selection practice (Burnham and Anderson 2002; Hoogenboom et al. 2011; Negri and Hoogenboom 2011). See Table S5.4 in Appendix S5 for calculations with individual points yielding similar results as mean models (mean model results presented here).

No.	Model	N	AIC	delta AIC	wAIC
1	All data	76	-170.44	241.32	0.00
2	By temperature treatment	76	-331.45	80.31	0.00
3	By fish treatment	76	-181.39	230.37	0.00
4	By temperature treatment by fish treatment	76	-411.76	0.00	1.00

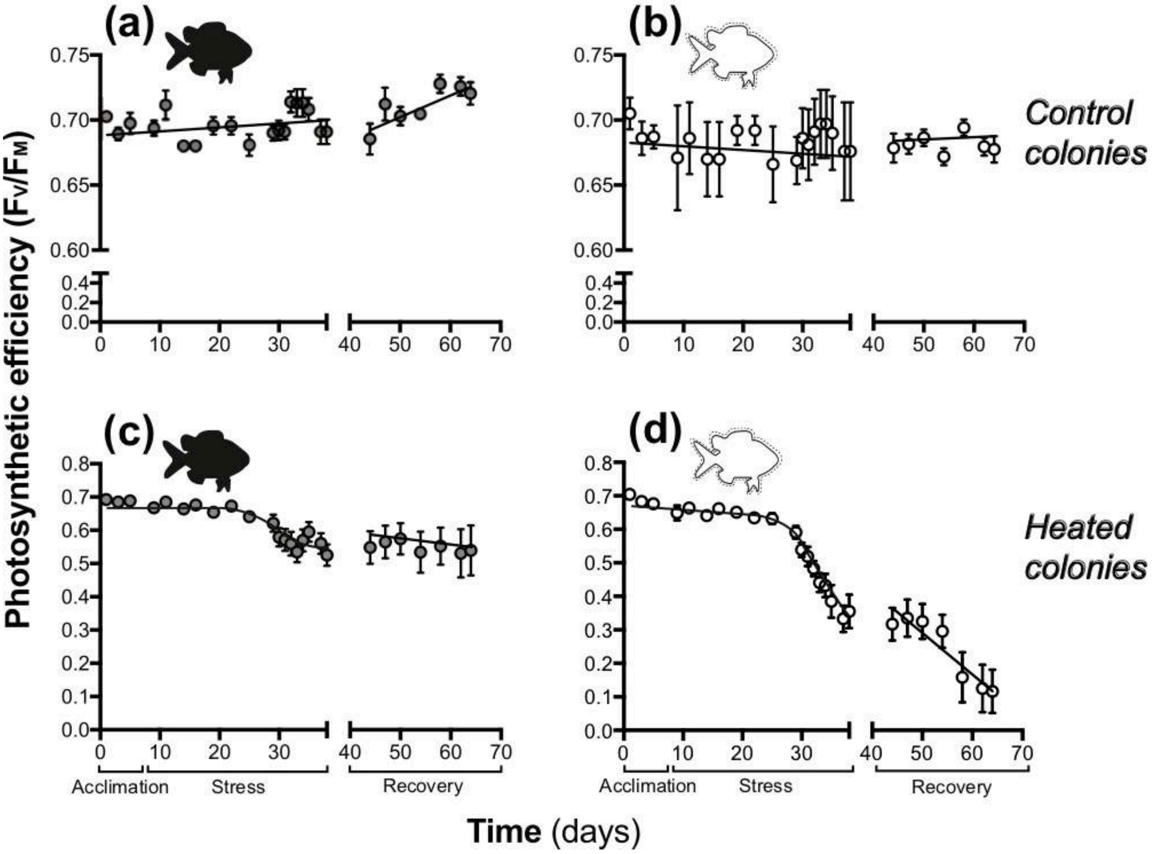


Figure 5.4 Temporal changes in photosynthetic efficiency (F_V/F_M) of *P. damicornis* with (**a** and **c**) and without *D. aruanus* (**b** and **d**) under control (**a** and **b**) and heated (**c** and **d**) treatments. Data are presented for all phases of the experiment: Acclimation (days 1 - 7), Temperature Stress (days 8 - 37) and Recovery (days 38 – 66); and points and error bars show means and SE for n = 9 colonies per treatment group. Solid lines show best fit regression lines (for line equations regression coefficients see Appendix 5, Table S5.3). Black fish symbols represent colonies with fish, and white symbols represent colonies without fish. Note different y-axis ranges were used for visual clarity of effects.

5.5 Discussion

5.5.1 Damselfish's impact on host corals under thermal stress

This chapter demonstrates that coral-dwelling fishes may reduce bleaching severity, as well as enhance post-bleaching recovery, for host corals. Using a combination of field-based observations and aquarium experiments, I show that corals that host fishes have higher *Symbiodinium* densities and chlorophyll concentrations when compared to colonies without resident fishes. When subjected to thermal anomalies, corals hosting fishes continued to have higher *Symbiodinium*, chlorophyll, and tissue protein than colonies without fish. The mechanisms underlying these findings are likely to include inputs of nutrients from fish excretion, and aeration and water stirring from fish swimming within branches, that moderate the effects of thermal stress. However, under severe warming conditions, > 90% bleached corals died regardless of the presence or absence of resident fishes.

Beneficial effects of fishes on *Symbiodinium* densities and chlorophyll concentrations of host corals have been recorded previously (Holbrook et al. 2008; Shantz and Burkepile 2014; Woods 2015). In this study, I observed that colonies maintained in aquaria for 66-days with fish had almost two-fold higher *Symbiodinium* and chlorophyll levels than colonies without fish. The elevated levels of *Symbiodinium* and chlorophyll translate into higher photosynthesis rates (Garcia-Herrera et al. 2017), and faster overall growth rates in colonies with aggregating damselfish (Holbrook et al. 2008; Shantz et al. 2015). While differences in photosynthetic function were directly related to an increased density of *Symbiodinium*, additional physical components and processes associated with fish presence, such as increased net oxygen exchange and reduction of the diffusive boundary layer (Goldshmid et al. 2004) due to water stirring and other specific behaviours of resident fishes, may also explain variations in photosynthetic function.

The benefits that fish can provide to corals have been identified in at least seven fish families (Meyer et al. 1983; Cole et al. 2009; Dixson and Hay 2012; Chase et al. 2014). However, benefits to host corals are best understood for damselfishes (family Pomacentridae) that exhibit some of the highest levels of association with small branching corals (Coker et al. 2014). At the level of the coral population, these benefits for coral health are likely substantial, as aggregating damselfishes are widely distributed across the Indo-Pacific, are present in nearly all reef zones and, in certain habitats, more than 80% of branching corals are engaged in Pomacentrid-coral associations (Holbrook et al. 2000; Chase et al. 2014). Consequently, resident aggregating fish potentially play an important role in buffering coral populations from certain environmental changes.

Higher baseline levels of *Symbiodinium* and chlorophyll in the field due to fish presence may counteract high energy requirements of bleaching before expulsion and coral starvation (Borell and Bischof 2008). The smaller decrease in F_V/F_M of colonies with fish is consistent with a ~22% increase in photosynthesis due to fish ventilation observed in a previous study (Garcia-Herrera et al. 2017). This continual ventilation of the colony interior could reduce holobiont stress during bleaching by enhancing photosynthetic gas exchange and ameliorating oxidative stress. Comparable to other studies, photosynthetic efficiency values (especially in corals without fish) were still considerably low 4 weeks post-bleaching; marked decreases in bleached colonies of *P. damicornis* were reported during the 1998 bleaching event at Heron Island, GBR (Hoegh-Guldberg and Smith 1989; Jones et al. 2000), where *P. damicornis* colonies F_V/F_M values dropped > 25% from ~0.60 to 0.45, similar to this experiment.

Similar to ambient conditions (Meyer et al. 1983; Holbrook et al. 2008; Shantz et al. 2015), fish services continue to enhance coral health under bleaching conditions, as examined in this study. These small-scale feedbacks (i.e. services between damselfishes and corals) influence colony physiology and can accumulate to influence the stability and resilience of coral populations at larger scales (McCann 2000). By increasing functioning in a pre-disturbance state, there is evidence that corals with fish can temporarily experience continued benefits during certain disturbances, along with expedited recovery. However, these benefits require that fish remain with their host colonies during and after disturbance. In the case of bleaching, abandonment of the colony by resident damselfishes has been documented only after the coral died and succumbed to algae overgrowth (Coker et al. 2012b), but not during the states of declining coral health (Feary et al. 2007). In this case, *D. aruanus* is able to maintain swimming performance at high temperatures, (Eme and Bennett 2009; Johansen and Jones 2011) supporting the idea that this species of fish can maintain fish-derived services to host corals (remaining with the colony and swimming within branches, see Coker et al. 2012b), as observed in this study.

Regardless of the presence of fish, these *S. hystrix* colonies still bleached severely and displayed approximately two-fold lower values of *Symbiodinium* compared with those observed under non-bleaching conditions (Hoegh-Guldberg and Smith 1989). The intensity and duration of the bleaching may overwhelm natural resilience limits (McClanahan et al. 2002; Donelson et al. 2011), and result in a loss of advantageous fish services, resulting in severe bleaching and mortality (> 90% whole colony mortality) for field colonies. This is consistent with widespread bleaching events, leading to high coral mortality, resulting in short-term changes such as loss of suitable habitat for aggregating fish, and long-term changes such as loss of complexity and rise of algae-dominated states (Graham et al. 2006).

The benefits accrued to coral colonies from hosting high abundance or biomass of resident fishes is strongly context-dependent (Chamberlain et al. 2014). Most notably, benefits of reef fishes on host corals are most apparent under low-flow conditions (Chase et al. 2014), potentially due to greater capacity for nutrient enrichment, due to increased residency time of water within the host coral colony (Holbrook et al. 2008). Similarly, the positive effects of fish on host corals were generally apparent in aquaria settings, but not in the field. In aquaria, the presence of coral-dwelling fishes resulted in higher survival and partial recovery of coral colonies. It is likely that close interactions between fish and corals, restricted by aquaria space, enhanced effects of fish on corals during temperature stress. Additionally, controlled factors in aquaria, such as high food levels, low flow levels, low light stress, and removal of other external factors (i.e. coral predators) may not fully simulate *in-situ* conditions and may limit comparison to natural field conditions. Nutrient pollution is an increasing global stressor and can result in localized direct effects on corals (Gil 2013; Shantz and Burkepile 2014). Further research is needed to assess whether the nutrient subsidy via fish may continue to produce positive effects for corals, have a negative additive effect with high ambient nitrogen levels (Chase et al. 2014), or neutralize certain fish services.

5.5.2 Conclusions

Global climate change, and especially ocean warming, is greatly altering the structure of coral reef assemblages (Hansen et al. 2001; Tunney et al. 2014; Nagelkerken and Munday 2016), with concomitant effects on species interactions and ecosystem function. In this chapter, the critical symbiotic association between corals and zooxanthellae (*Symbiodinium*) is moderated by the presence and behaviour of coral-dwelling damselfishes. Under certain conditions, the presence of these fishes may actually reduce vulnerability to coral bleaching, thereby ensuring persistence of host corals (van de Leemput et al. 2016). In this study, this feedback was relatively weak, and did not prevent host coral bleaching nor loss during severe thermal stress in the field. However, increased densities of coral-dwelling fishes or stronger associations between fishes and corals may confer increased resilience (van de Leemput 2016; Kiers et al. 2010), thereby buffering the effects of global environmental change.

CHAPTER 6: GENERAL DISCUSSION

6.1 Overview

The research presented in this thesis greatly increases understanding of the nature and significance of interactions between coral-dwelling damselfishes and their coral hosts. Habitat structure and colony traits determine which coral colonies are occupied, and fish species-specific colony-usage behaviour shapes the services that fishes provide to corals. While most previous research on coral-fish interactions has focused on fish behaviour (e.g. boldness, competition, and foraging), my research integrates detailed observations of fish behaviour with broad-scale surveys of colony occupancy and analyses of coral ecophysiology. Overall, I found that these small-scale species interactions and positive feedbacks between coral-dwelling damselfishes and branching scleractinian corals are dynamic and context-dependent. Damselfish-coral interactions are generally restricted to ~30% of small-branching colonies (Chapter 2), and they exhibit differential services due to damselfish-species specific behaviour (Chapter 3). Moreover, damselfishes' occupancy can then alleviate partial mortality from sedimentation (Chapter 4) and help corals to resist bleaching and recover faster (Chapter 5). Clearly, coral reef damselfishes confer considerable growth and survival benefits at the individual colony level through a variety of interactions, manifesting in enhanced coral health (i.e. increases in *Symbiodinium*, chlorophyll, protein, and tissue biomass) and colony resilience (survival and recovery) under environmental stressors (Chapters 4 and 5). Understanding the relationships between coral-dwelling damselfishes and corals, and quantifying how these relationships vary spatially, temporally, and behaviourally (Chapters 2 and 3) provides context for understanding the ramifications of ongoing coral reef stressors for coral health and reef degradation (Bellwood et al. 2004; Ahmadia et al. 2012; Hughes et al. 2017a; 2018b).

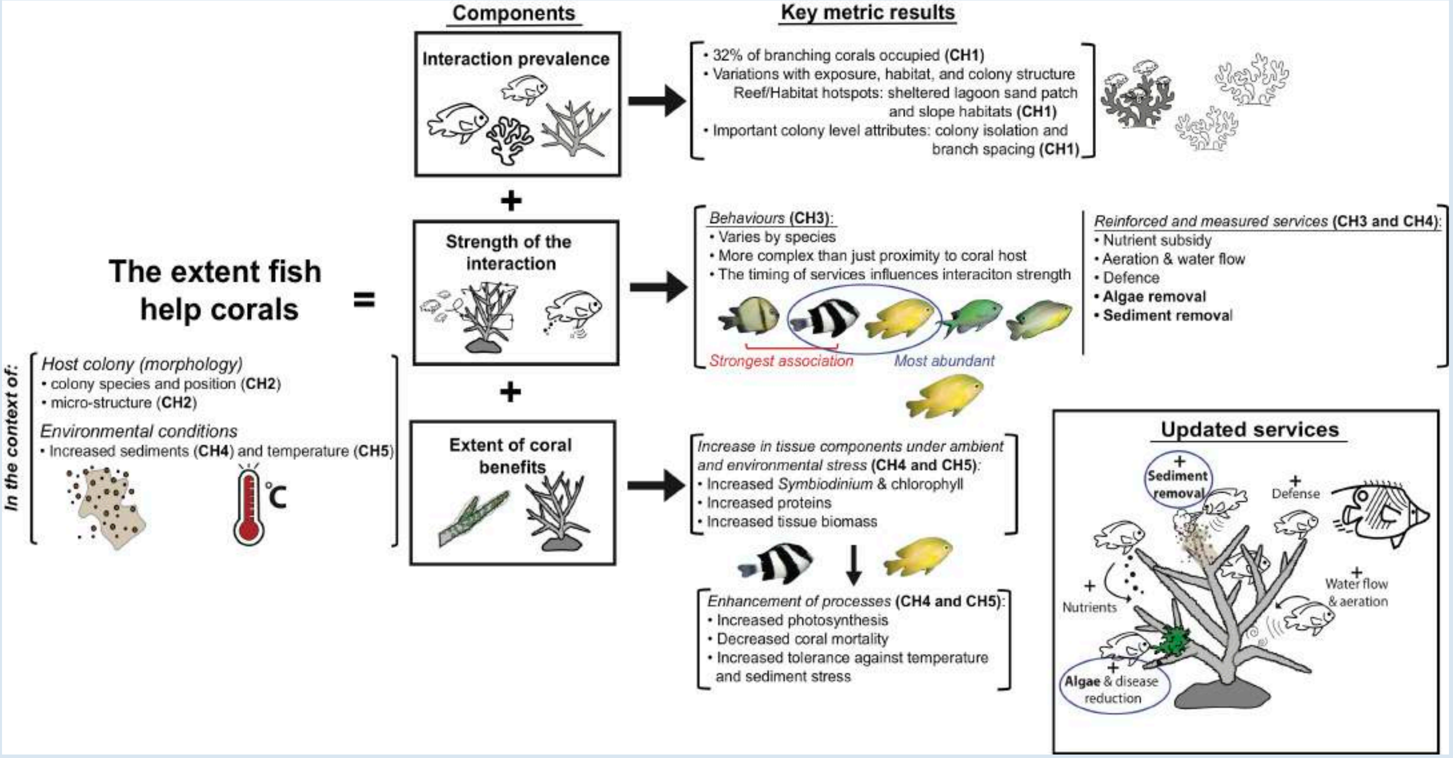
In this concluding chapter, I synthesize the results presented in preceding chapters to identify where and how these fishes benefit corals, the contextual nature of the association, the fish-coral system's resilience under global change, and ability to buffer and enhance trophic interactions. Subsequently, I discuss whether fish contribute to coral population persistence and community stability across space and time and identify future research directions where the results of this thesis can be implemented for continued study of fish-coral interactions, fish-derived services, and how future stressors will impact this association.

6.2 Updated fish-derived services and extent coral-dwelling damselfishes impact coral health

Using laboratory experiments and field observations, this thesis reveals novel aspects of the association between aggregating damselfishes and branching corals, adding the additional benefits of algae reduction and sediment removal to the growing list of recognised services damselfishes provide to host corals (Box 6.1). In the absence of disturbances, damselfishes, notably *D. aruanus*, enhance coral tissue components and aid colony growth and survival (Liberman et al. 1995; Chase et al. 2014). Under moderate abiotic stress, some of these coral-dwelling damselfishes can alleviate the negative effects of sedimentation (Chapter 4), reduce bleaching severity, as well as enhance post-bleaching recovery (Chapter 5), mostly likely through nutrient subsidy and water flow modulation for a subset of host bleaching corals. While it is possible for damselfishes to move between nearby colonies (Chapter 3), potentially to select the healthiest corals, it is more likely that these five site-attached damselfish species remain with their host colonies throughout disturbances, due to their severely limited home-ranges and certain disturbances enacting relatively uniform conditions (i.e. *in-situ P. damicornis* colonies during the 2016 bleaching event) at local scales for the sandy substrate, small branching colonies studied.

Box 6.1 Updated summary of the ways that fishes help corals

Updated summary and visualization of key aspects of interaction prevalence, fish behaviour and services, and the extent of coral benefits provided by coral-dwelling damselfishes, are presented in this thesis. Across seascapes, these partnerships are regulated by reef, habitat, and colony structure factors. The strength of the interaction is based on spatial and temporal species-specific behaviours. Results from field and lab experiments reinforce known and introduce new services present in this system. The first two components contextualize where and how benefits may occur, while the third component quantified what the actual benefits are under stressed and non-stressed conditions. *D. aruanus* and *P. moluccensis* enhance tissue components, thereby conferring increased resilience to host corals. The updated services subpanel illustrates additional, novel services of algae reduction and sediment removal, documented in this thesis.



6.3 Conditional damselfishes' services to corals

Research presented in this thesis illustrates that coral-dwelling damselfishes, such as *D. aruanus* and *P. moluccensis*, can benefit their specific coral hosts, providing multiple services that enhance coral growth and health. However, due to the varying nature of these species' interactions, the services and net benefits to corals may vary in different environmental or biological contexts (Bronstein 1994b: Hopkins et al. 2016). Mutualisms, in particular show a greater variation depending on biotic and abiotic factors than other interactions classes (i.e. predation or competition); there is potential for this interaction to erode to commensalism or parasitism (Bronstein 1994a; Chamberlain et al. 2014). Until now, the only reported service *P. moluccensis* rendered to corals was coral disease eating behaviour (Cole et al. 2009). This thesis reveals *P. moluccensis* assists corals under high sediment stress (Chapter 3) and reduces algae present on bleached colonies (Chapter 2). As a result, the relationship between *P. moluccensis* and their branching hosts may be commensalistic in nature, unless coral disease, algae overgrowth, or high levels of sediment are present, wherein the interaction would have elements of mutualism. Even the *D. aruanus* and coral relationship can vary considerably. Under select conditions, *D. aruanus* can act as parasites, diminishing coral growth under high water flow, and promoting growth of damaging microbes under high nutrient conditions (Garren et al. 2008; Zikova et al. 2011; Chase et al. 2014). Similar to the impact of high nutrients nullifying the dependency of plants on mycorrhiza fungi (Bowen 1980), the services that one fish species provides can be enhanced, buffered, or nullified, depending on which other fish species are present and which resources they provide (Bronstein 1994b; Holland et al. 2002).

Quantifying the nature of coral-fish interactions (i.e., how it manifests in form and strength) is critical for determining impacts of fish on coral health. The intricacies of fishes' impacts on coral growth and health are more complicated than the overall interaction sign/outcome. For instance, both *Dasycllus aruanus* and *Stegastes nigricans* damselfishes protect host colonies from corallivorous fishes and enhance juvenile coral survival (Weber and Woodhead 1970; Suefuji and van Woesik 2001; Chase et al. 2014), however, *S nigricans* continually farms algae, fostering partial colony death and the presence of coral disease microbes (Casey et al. 2014; Schopmeyer and Lirman 2015). Conversely, *D. aruanus* feeds on plankton and has only been observed to negatively impact corals under very specific high flow and nutrient levels (Chase et al. 2014). Despite *S. nigricans* benefit to host colonies, the cost-benefit ratio is more complicated (Suefuji and van Woesik 2001; Kamath et al. 2018) compared with *D. aruanus*, which displays less impairment (select circumstances of impairing coral growth) to host corals.

6.4 Benefits of damselfishes across seascapes

6.4.1 Which colonies benefit from fish services, and why?

While damselfishes can provide significant benefits for host corals, this thesis showed that these fish-coral associations are relatively restricted, with only 32% of branching corals occupied by damselfishes, mainly by *D. aruanus* and *P. moluccensis* (70% of interactions). The highest incidence of occupations was in sheltered lagoon sand patches and slope/base environments, where up to 95% of the branching coral species were occupied (Chapter 2). These results are consistent with other studies which show that *D. aruanus*, *P. moluccensis* and other coral-inhabiting damselfishes, are most commonly found on corals located in these sheltered, low water flow habitats (Johansen et al. 2015), and reef/sand edge environments (Holbrook et al. 2000; Sambrook et al. 2016). Subsequently, the positive impacts of aggregating damselfish on coral growth are also highest in sand patches and reef slopes in areas of reduced light intensities (Chase et al. 2014). As a result, there is spatial congruency between where the damselfish with strong coral interaction natures are located, and the strength of their benefits to host corals.

For corals, the benefits of hosting damselfishes depend on both the density and species of fishes. For instance, the same biomass of *C. viridis* and *D. aruanus* will not have equal benefits to their host colonies, due to the species-specific behaviours. Of the focal damselfishes, the *Dascyllus* species engaged in behaviours and services more mutualistic in nature, especially at night, when these coral-dwelling fishes exert high levels of coral use (Chapter 3). As a result, an even smaller proportion of coral populations that host fish are actually receiving quantifiable benefits (potentially only when exposed to certain environmental stressors) from these more mutualistic species, compared to corals hosting *Pomacentrus* species, which have a more commensalistic interaction with their hosts (Figure 6.1).

Despite being restricted spatially, the major benefits from these damselfishes, including the ability to facilitate coral survival under adverse conditions, and consistent in space and time (i.e. regular, long-lasting impacts, see Meyer et al. 1983; Holbrook et al. 2008; Appledorn et al. 2009) make them integral components in the coral meta-organism. Their presence and function are anticipated to become even more essential to coral colonies under future anthropogenic stressors.

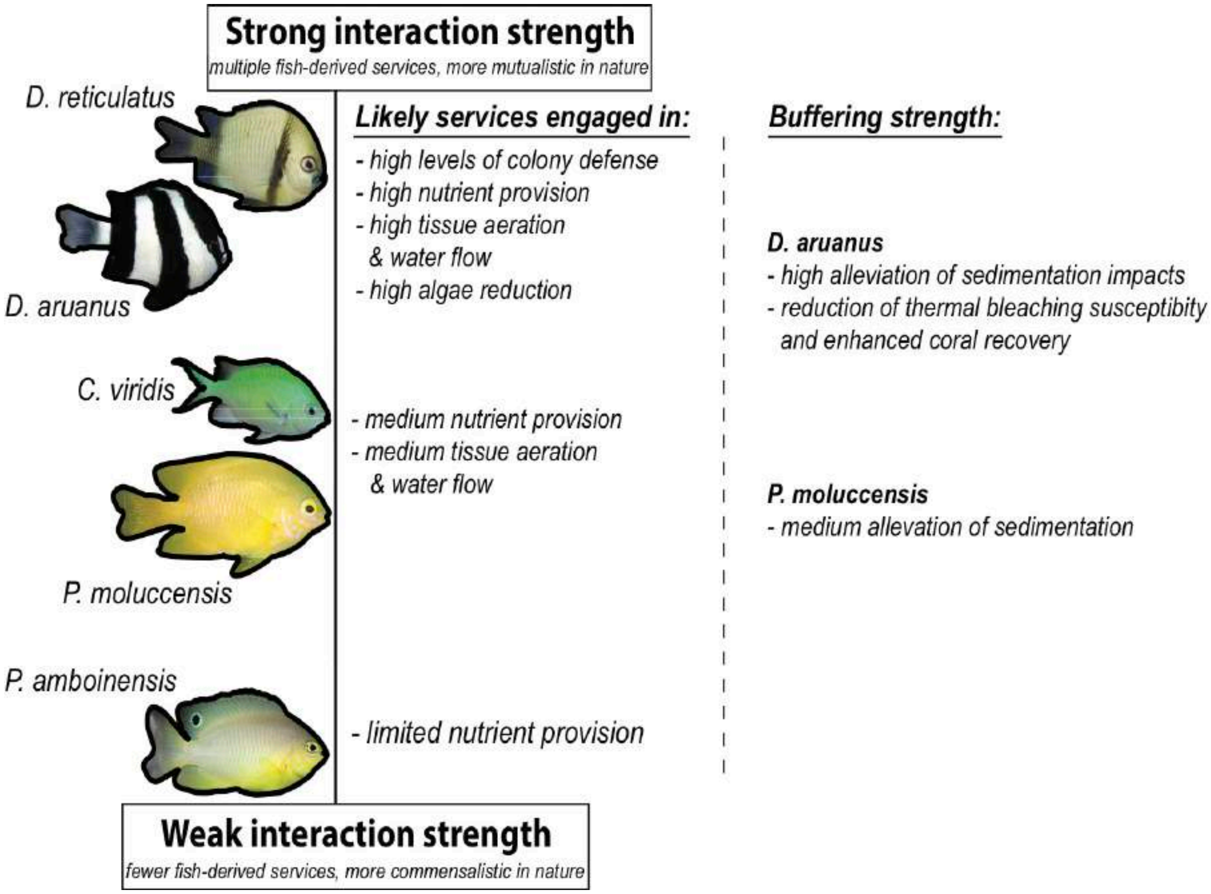


Figure 6.1 Conceptualization of the damselfish-coral interaction ranking for the five different species of Pomacentridae studied in this thesis, in regard to the major behaviours demonstrated around their host colony, and potential fish-derived services (Chapter 3) and empirically tested buffering capabilities (Chapters 4 and 5). Stronger interaction strengths translate to multiple fish-derived services that benefit corals, with an overall association more mutualistic in nature. A weak fish-coral interaction strength translates to fewer fish-derived services that benefit corals, with an overall association more commensalistic in nature.

6.4.2 Biomass context of damselfishes' benefits

There is likely a biomass threshold above which fishes become useful to host corals, suggesting that certain density-dependent services may be limited to high biomass colonies. A damselfishes' biomass of ≥ 10 g of fishes (average biomass of fish-occupied colonies *in-situ,* Chapter 1) will likely be advantageous for host corals, potentially creating fish-derived nutrient hotspots (McClaine et al. 2003; McIntyre et al. 2008). This is apparent from the experimental results from Chapters 4 and Chapter 5 (Chapter 4: 6-12 g of damselfish per coral and Chapter 5: 15 g per coral), as well as other studies with high damselfishes' biomass (Liberman et al. 1995; Holbrook et al. 2008), resulting in quantifiable benefits to coral hosts in aquaria and in the field. Chapter 1 results indicate that when present on corals, *C. viridis*, *D. aruanus*, and sometimes *P. moluccensis*, are in groups of high biomass (e.g. group biomass of < 20 – 120 g seen in 10% of colonies, Chapter 2, see Figure 2.3), especially in sand patch and slope habitats where average colony biomass is more than two-fold greater than other reef habitats (up to 2000 g per 250 m^{-2}). These high biomass colonies (often forming, localized biogeochemical hotspots, with resident biomass from 0 to 830 g m^{-2}, see Layman et al. 2013; Shantz et al. 2015) have also been documented in studies focusing on larger-bodied or more abundant fish species (fish biomass from 39 to 172 g m^{-2}, see Meyer et al. 1983; Meyer and Schultz 1985a, b). Conversely, the capacity for high fish biomass to be disadvantageous for corals hosts (i.e. removing plankton for coral heterotrophy or eutrophication of inner colony water) only exists in very limited situations (Bongiorni et al. 2003: Zikova et al. 2011; Chase et al. 2014).

Other services will also be dependent upon on the size of the host colony. Small levels of fish biomass dispersed too thinly over larger colonies will prevent perceptible benefits at the colony level. However, certain services will exist independently of biomass. For example, the presence of a single fish parabiont may be enough deter colony attackers (e.g. defence, Chase et al. 2014; Chapter 2). Additionally, results from

Chapter 2 indicate the services may be dependent upon host coral morphologies, and trade-offs exist between suitable colonies and those able to most effectively take advantage of the benefits (i.e. nutrient uptake ability, Muscatine and D'Elia 1978; Godinot et al. 2011). Although more open colonies attract resident fishes (and higher fish biomass, see Kane et al. 2009; Nadler et al. 2014), tighter branching coral species (i.e. *S. hystrix*), with stagnant water inner-regions retain nutrients more efficiently (Holbrook et al. 2008) and are more likely to absorb fish-derived nutrients when compared with larger branching colonies (i.e. *A. intermedia*).

6.4.3 Fish-derived services within the context of buffering

Some of the benefits provided to host colonies by coral-dwelling damselfishes are only valuable in certain environments, such as areas with low water flow. More specifically, supplemental nutrients and enhanced water flow can enhance coral health and enable colonies to cope with environmental stress (Nakamura and van Woesik 2001; Suefuji and van Woesik 2001; Wiedenmann et al. 2013; Gowan et al. 2014; Wong and Candolin 2015), and also affect coral metabolism, the colony immune system, and holobiont nutrient imbalance (Figure 6.2). Previously, auxiliary nutrients were thought to negatively impact corals exposed to temperature stress, (Muscatine and Porter 1977; Pollock et al. 2014; Sweet and Brown 2016), yet recent research demonstrates that nutrients in balanced ratios aid in maintaining coral metabolism and calcification during thermal stress (Wiedenmann et al. 2013; Shantz and Burkepile 2014; Ezzat et al. 2016). Furthermore, nutrients provided by fishes contain nearly the optimum concentrations, in quality and ratio (i.e. N:P of 20:3 in natural ocean plankton, Redfield 1958); hence, corals may already be adapted to these pulses of enhanced nutrients, and be well-suited to recycling and utilizing fish-derived nutrients (Redfield 1958; Shantz and Burkepile 2014; Shantz et al. 2015).

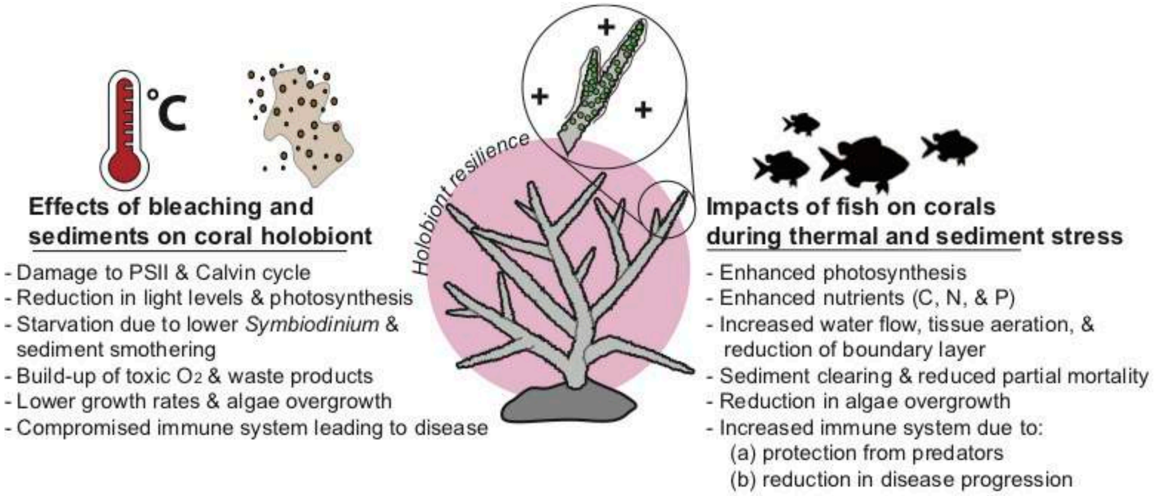


Figure 6.2 Conceptual diagram illustrating the negative impacts of increased thermal and sediment stress, resulting in coral bleaching and compromised health on the coral holobiont, as well as beneficial fish services that directly combat deteriorating coral functions. Holobiont resilience and buffering, specifically increased tolerance and recovery during coral bleaching events and increased sediment stress can be provided by select damselfish associations (see Chapters 4 and 5).

6.5 Coral-fish interactions as an ecological buffer

On the whole, the world is losing corals through natural and anthropogenic stressors, and the research presented in this thesis aids in predicting how damselfish-coral interactions will fare. Positive interactions will increase with abiotic stress, with species interactions shifting to “survival mode”, with reductions in negative interactions and greater reliance on mutualism and facilitation (i.e. stress-gradient hypothesis, He et al. 2013). With coral reefs subjected to copious abiotic stressors (Hoegh-Guldberg 2011; Hughes et al. 2017a, b; 2018a, b), mutualistic interactions can stabilize coexistence during moderate periods of stress, thus, leading to a net positive effect on both partners at the individual and population levels (Holland et al. 2002). As a result, several of the coral-dwelling fishes-coral interactions benefit coral health, and improve resilience characteristics, further promoting buffering capabilities to the coral holobiont (Chapters 4 and 5).

This thesis demonstrates, for the first time, that corals with coral-dwelling damselfishes tolerate stressors more effectively (Chapters 4 and 5); however, coral resilience via fishes only operates up to a certain threshold, under low to medium level (in intensity and duration) environmental stressors. High stress conditions, such as the recent intense bleaching events that occurred in the northern sections of the GBR (see Chapter 5, Hughes et al. 2017a; 2018b), will overwhelm natural resilience limits (McClanahan et al. 2002; Donelson et al. 2011), resulting in widespread mortality (i.e. in Chapter 5, > 90% of focal *S. hystrix* colonies bleached and died regardless of fish presence). Consequently, fish services will be rendered inadequate, coral health will be severely reduced, and collapse of the association will follow (Hughes et al. 2017a; 2018b). This is consistent with widespread bleaching events (Hughes et al. 2017a; 2018a, b), leading to high coral mortality, shattering community resilience levels, resulting in short-term changes such as loss of suitable habitat for aggregating fish, long-term changes, such as loss of complexity (Munday et al. 2008; Pratchett et al. 2012), and lowered local species richness (Graham et al. 2006).

Prior to disrupting many interactions, climate change can strengthen direct and indirect interaction (i.e. multi-level symbioses) up to a point, resulting in enhanced holobiont responses. It is evident that moderate levels of abiotic stressors, such as increases in sea surface temperatures and sedimentation may actually enhance the damselfish-coral association up to a threshold; this has been demonstrated in terrestrial ecosystems between plants and insects (e.g. grassland field food webs, see Barton et al. 2009; Zhou et al. 2017). It is possible that slight increases in ambient seawater temperature below a critical thermal maximum, could enhance fish movement (Eme and Bennett 2009; Johansen and Jones 2011; Chase et al. 2018a), and by extension, coral benefits. As increased sediments and turbidity reduce fishes foraging distance (a common event as damselfishes such as *P. moluccensis* encounters sub-optimal turbidity conditions between 8 - 53% of the time, see Wegner and McCormick 2013; Wegner et al. 2013) and boost colony visits and average distance, fish-rendered services to their host colony may also increase.

Several of the mutually beneficial interactions between coral-dwelling fishes and coral colonies foster resilience, further promoting the buffering capabilities to the coral holobiont (Chapters 4 and 5). By enhancing coral tissue components, reducing susceptibility to stressors and increasing survival through small scale acts (i.e. deterring corallivory or sediment removal), coral-dwelling fishes may help reduce destabilizing interactions such as predation or the build-up of toxic chemicals within coral tissues, thereby, promoting growth and regulating sub-food webs that are dependent upon the host holobiont (McCann 2000; Halpern et al. 2007). In fact, there is evidence that many exosymbioses act as ecological buffers across many biological systems (Barton et al. 2009; Kiers et al. 2010; Traveset et al. 2013; Marquis et al. 2014; Wong and Candolin 2015). Again, on coral reefs, coral-dwelling crabs reduce colony mortality up to 60% more than corals with no crabs (Stewart et al. 2006). In terrestrial ecosystems, insect mutualisms buffer warming temperature effects on multiple trophic levels through the presence of third-party partners; plant stress decreased, and performance increased only when aphids were present on cottonwood trees under rising temperatures (Marquis et al. 2014).

The concept that damselfishes can act as buffers and insurance for corals under perturbation is further supported by the resilience characteristics exhibited in the partnership. Damselfish-coral interactions often display broad and novel niches; some services are provided by multiple fish species, flexibility exists between partners (Coker et al. 2014) during pre-disturbance and in times of change, and the partnership exhibits protection from environmental variation, (see Kiers et al. 2010), thereby increasing persistence (McCann 2000), at both colony and local community levels (Mellin et al. 2016). Damselfishes are resilient to stages of declining coral health (Feary et al. 2007), suggesting robustness to the association and temporary continuation of services despite abiotic stressors. The complex nature of coral reef symbioses, often with multiple suitable partners, (i.e. the presence of a third-party present in defence and nutrient subsidy reef mutualisms, see Rothans and Miller 1991; Stier and Leray 2014; Marquis et al. 2014) may be to their benefit when exposed to unfavourable environmental conditions. Relative to terrestrial and freshwater systems with fewer potential symbiotic partners, coral reef mutualisms may exhibit higher resilience via functional redundancies and high levels of connectivity, especially under severely varying abiotic conditions (Kiers et al. 2010; Chamberlain et al. 2014; Hock et al. 2017).

6.6 Future directions for coral-fish interactions at the holobiont and population scales

Whether finite fish-derived benefits extend to the entire holobiont and surrounding organisms, or even provide benefits at the coral population level, is a crucial knowledge gap within coral reef research. To fully determine the impacts of fish at the population level, information regarding: a) the degree to which fish impact coral calcification, and thereby the structure of the reef and processes, and b) the extent fish impact coral lifetime reproductive output (i.e. egg production, colony fecundity, and size-dependent growth), is needed in models to scale up colony-level impacts. This advantageous partnership between aggregating damselfishes (e.g. habitat and shelter) and coral colonies (i.e. metabolism) may impact coral demographic rates and confer evolutionary advantages at the colony or population levels (Chase et al. 2014; Garcia-Herrera et al. 2017). It is possible that small branching colonies have coevolved with fishes and develop a specific morphology that fosters damselfishes' presence, thereby benefiting from enhanced water motion or nutrients inside the colony. Conversely, areas of natural mechanisms that augment coral health, such as exposed high flow habitats of the crest, will not receive the same degree of fish-derived services due to the presence of other abiotic factors, potentially explaining why these corals have low fish occupancy. The eco-evolutionary dynamics between coral-dwelling damselfishes and branching corals are likely driven by growth feedback loops and the cost-benefit ratios present in damselfishes' behaviours. While more fish may lead to more colony benefits, from the perspective of the damselfishes, larger social groups can have drawbacks governed by social trade-offs (e.g. competition vs predation risk, Coker et al. 2009, 2012b, Boström-

Einarsson 2018). Many damselfish species exhibit negative density dependence, spreading out among colonies, as local fish density increases (Kent et al. 2006; Chase et al. 2014), further diminishing high biomass colonies. The link between damselfishes' behaviours with both the local physical and social conditions is key in determining degree and type of these coral holobiont mutualisms. This, in turn, will further elucidate the evolutionary connections of these interspecific interactions.

Although the present research only investigates the effects of sediment stress and thermal bleaching on this damselfish-coral interaction, it is feasible that coral-fish feedbacks help to alleviate stress caused by other environmental factors, such as the suite of stressors associated with climate change, that will certainly impact the coral holobiont additively or synergistically (e.g. increased sea surface temperatures are associated with turbidity levels and sedimentation). Stressors such as intense solar radiation, elevated pCO_2, and eutrophication, may also be combatted by fish services due to the capability to mimic natural mitigations. Novel services and interaction forms could arise under different conditions, involving additional fish families that closely associate with or live in coral colonies. Prevalence of fish-coral interactions and subsequent benefits to corals may potentially be utilised in coral restoration efforts (Halpern et al. 2017; Shaver and Silliman 2017; Ladd et al. 2018), although further research is required to confirm the stability of fish groups after capture and movement among coral colonies. Local factors and positive fish-coral interactions that are key in maintaining the function and health of current reef dynamics, (especially coral growth and nutrient supply) should be emphasized in marine conservation criteria (Maynard et al. 2010; Mellin et al. 2016).

6.7 Concluding Remarks

This thesis highlights the prevalence and importance of species-specific fish-coral associations in the context of coral health under varying environmental conditions. By linking fish services and associations with metrics of coral health, my research reveals that while biotic interactions (between coral-dwelling damselfishes and host corals) are variable across reefs and corals, they deliver significant consequences for individual colony survival and health under environmental stressors. However, these relationships are constrained to confined habitats and coral morphologies, with damselfish species fluctuating and disparate in their association and service strength.

Climate change and coastal sedimentation are among the foremost threats to corals and reef fishes (GBRMPA 2014), contributing to widespread degradation of coral reef ecosystems. However, coral-fish associations can better resist these abiotic stressors than corals alone, and this may represent a critical feedback, enabling the persistence of coral assemblages during times of stress (Callaway et al. 2002; He et al. 2013). This information is paramount, considering recent (2016/2017) bleaching events (Hughes 2017a, b; 2018a, b), and increased sediments on inshore GBR reefs due to land use practices (Bainbridge et al. 2018). By addressing critical knowledge gaps regarding the functions of coral-dwelling damselfishes in promoting the health and survival of corals, this thesis contributes important information that can help investigation of potential trajectories of multiple species interactions that account for the current state of the systems. This in turn allows for more realistic predictions of future reef stressor events, coral health and coral mortality, thereby aiding conservation efforts (Schoepf et al. 2015). Finally, identifying and quantifying new aspects of the coral-fish symbiosis suggests that fish symbionts should be included in the coral ‘metaorganism’, especially when evaluating coral growth. This PhD thesis not only supports the presence of quantifiable fish-derived services, but also identifies the factors that impact the overall magnitude of the services and benefits to host coral (i.e. partnership abundance, species-specific behaviours and services, and extent of coral benefits under abiotic stressors), thereby significantly advancing the current understanding of the scope of benefits that fishes can provide to corals at the individual colony level.

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APPENDIX S2 – Extended results for spatial prevalence of damselfishes

Table S2.1 Binomial generalized linear model (GLM) output for fishes (species pooled) occupation by coral species. Significant p-values are in bold.

Factor	**z-value**	**p-value**
Intercept (*A. intermedia*)	-7.921	**< 0.001**
A. spathulata	1.547	0.122
P. damicornis	3.419	**0.001**
S. hystrix	0.207	0.836
S. pistillata	3.137	**0.002**

Null deviance: 3788 on 3096 d.f.
Residual deviance: 3750 on 3092 d.f.

Table S2.2 Descriptive statistics of reef seascape level biomass estimated (mean grams ± SE) for each damselfish species (*C. viridis, D. aruanus, D. reticulatus, P. amboinensis,* and *P. moluccensis*) and total biomass pooled for all coral species (per occupied colony of *A. intermedia*, *A. spathulata P. damicornis, S. hystrix,* and *S. pistillata*) by habitat zone (lagoon sandy patches, flat, crest, wall, or slope/base). The number of occupied colonies per habitat zone (n) is displayed and the total average biomass of all damselfish species (pooled) per occupied colony per habitat zone are displayed.

		Average damselfish biomass (g) per colony per habitat zone					**Total avg. biomass**
Habitat zone	***n***	*C. viridis*	*D. aruanus*	*D. reticulatus*	*P. amboinensis*	*P. moluccensis*	
Lagoon and patch	54	1.59 ± 0.54	9.12 ± 0.81	0.19 ± 0.12	0.66 ± 0.04	2.64 ± 0.22	**13.87 ± 1.02**
Flat	36	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	3.04 ± 0.47	**3.04 ± 0.47**
Crest	319	1.15 ± 0.43	0.00 ± 0.00	0.00 ± 0.00	0.14 ± 0.06	6.74 ± 0.57	**8.03 ± 0.43**
Wall	189	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.03	5.09 ± 0.76	**5.13 ± 0.76**
Slope/base	300	0.04 ± 0.02	1.43 ± 0.21	0.73 ± 0.26	0.99 ± 0.10	5.18 ± 0.33	**8.34 ± 0.41**
Total / Average	898	0.79 ± 0.6	3.76 ± 0.10	0.36 ± 0.03	0.66 ± 0.02	4.45 ± 0.05	

Table S2.3 Descriptive statistics of reef seascape biomass estimates (mean ± SE) for each damselfish species (*C. viridis, D. aruanus, D. reticulatus, P. amboinensis,* and *P. moluccensis*) on each coral species (*A. intermedia*, *A. spathulata P. damicornis, S. hystrix,* and *S. pistillata*) and total biomass per coral colony (fish pooled).

		Average damselfish biomass (g) per coral species					**Total avg. biomass**
Coral species	***n***	*C. viridis*	*D. aruanus*	*D. reticulatus*	*P. amboinensis*	*P. moluccensis*	
A. intermedia	54	0.70 ± 0.55	1.55 ± 0.68	0.66 ± 0.63	0.82 ± 0.22	3.12 ± 0.50	**6.87 ± 1.33**
A. spathulata	36	3.88 ± 1.71	0.50 ± 0.40	0.14 ± 0.14	0.07 ± 0.05	6.28 ± 0.97	**10.83 ± 1.83**
P. damicornis	348	0.45 ± 0.17	3.66 ± 0.59	0.61 ± 0.29	0.75 ± 0.10	4.58 ± 0.37	**10.03 ± 0.73**
S. hystrix	189	2.05 ± 0.86	6.60 ± 0.92	0.01 ± 0.01	0.67 ± 0.10	3.11 ± 0.34	**12.45 ± 1.33**
S. pistillata	306	0.01 ± 0.01	2.89 ± 0.41	0.31 ± 0.09	0.50 ± 0.09	5.22 ± 0.36	**8.98 ± 0.46**

Table S2.4 Multiple comparisons of coral-species, with p-values, (Tukey's HSD *post-hoc*) based on a linear model of total damselfishes' biomass (damselfish species pooled), for only occupied colonies (reef seascape dataset): linear model: total damselfishes' biomass (dependent) and colony species (independent variable). Significant p-values are in bold.

Comparison	**p-value**
A. intermedia – A. spathulata	0.5487
A. intermedia – P. damicornis	0.4508
A. intermedia – S. hystrix	**0.0292**
A. intermedia – S. pistillata	0.7792
A. spathulata – P. damicornis	0.9899
A. spathulata – S. hystrix	0.9553
A. spathulata – S. pistillata	0.8977
P. damicornis – S. hystrix	0.1420
P. damicornis - S. pistillata	0.8712
S. hystrix – S. pistillata	**0.0196**

Table S2.5 Multiple coral species comparisons with p-values (*post-hoc* Dunn Test for Benjamini-Hochberg method based off a Kruskal-Wallis rank sum test) for each damselfish species (damselfish-species specific biomass) for only occupied colonies (n = 932, reef seascape dataset). Significant p-values are in bold.

	Fish Species				
Comparison	*C. viridis*	*D. aruanus*	*D. reticulatus*	*P. amboinensis*	*P. moluccensis*
A. intermedia – A. spathulata	**0.0027**	0.6937	1.0000	**0.0258**	**0.0047**
A. intermedia – P. damicornis	0.6187	0.2328	0.8967	0.4866	0.5573
A. intermedia – S. hystrix	0.5100	**< 0.0001**	1.0000	0.7315	0.5809
A. intermedia – S. pistillata	0.0988	0.4570	1.0000	0.3089	0.3801
A. spathulata – P. damicornis	**< 0.0001**	**0.0371**	1.0000	0.1634	0.1557
A. spathulata – S. hystrix	**< 0.0001**	**< 0.0001**	1.0000	**0.0461**	**0.0004**
A. spathulata – S. pistillata	**< 0.0001**	0.0944	1.0000	0.2828	0.2783
P. damicornis – S. hystrix	0.7141	**< 0.0001**	0.3689	0.7639	**0.0006**
P. damicornis – S. pistillata	0.1737	**0.4012**	1.0000	0.5676	0.5009
S. hystrix – S. pistillata	0.0537	**< 0.0001**	**0.0279**	0.4397	**< 0.001**

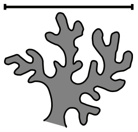
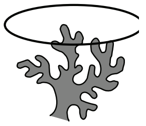
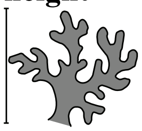
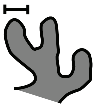
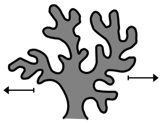
Table S2.6 Tukey's HSD *post-hoc* test for multiple comparisons of position of coral on benthos (colony level dataset), with p-values, based on a binomial generalized linear model of damselfish presence with damselfish species pooled: damselfish presence (dependent) and position on benthos (independent variable). Significant p-values are in bold.

Comparison	**p-value**
open – crevice	0.102
sand – crevice	**< 0.001**
underhang – crevice	0.748
sand – open	**0.002**
underhang – open	0.467
underhang – sand	**< 0.001**

Table S2.7 Tukey's HSD *post-hoc* test for multiple comparisons of position of coral on benthos, with p-values, based on a lognormal linear model of total biomass with damselfish species pooled for only occupied colonies (colony level dataset): total damselfishes' biomass (dependent) and colony position (independent variable). Significant p-values are in bold.

Comparison	**p-value**
open – crevice	0.273
sand – crevice	**0.032**
underhang – crevice	0.984
sand – open	0.980
underhang – open	0.182
underhang – sand	**0.005**

Table S2.8 Series of linear models illustrating variation in damselfishes' occupancy of small branching coral colonies (*A. intermedia*, *A. spathulata P. damicornis, S. hystrix, and S. pistillata*), by damselfishes (*C. viridis*, *D. aruanus*, *D. reticulatus*, *P. amboinensis and P. moluccensis)* for six fine scale measures of colony attributes (colony level dataset). Significant p-values are in bold.

Coral species	**n**	**Colony diameter** 	**Planar area** 	**Colony height** 	**Branch spacing** 	**Branch width** 	**Isolation** 
Proportion of colonies occupies							
A. intermedia	22	0.066	0.176	0.257	0.701	0.827	0.137
A. spathulata	32	0.314	**0.135**	**0.041**	**0.002**	0.685	**0.009**
P. damicornis	66	**< 0.001**	**< 0.001**	**0.009**	**< 0.001**	0.928	**0.013**
S. hystrix	44	0.304	0.433	0.189	**< 0.001**	**< 0.001**	**0.019**
S. pistillata	62	0.669	**0.007**	**0.003**	**< 0.001**	**< 0.001**	0.144
All colonies	224	**0.021**	**0.026**	**0.001**	**< 0.001**	**0.001**	**< 0.001**

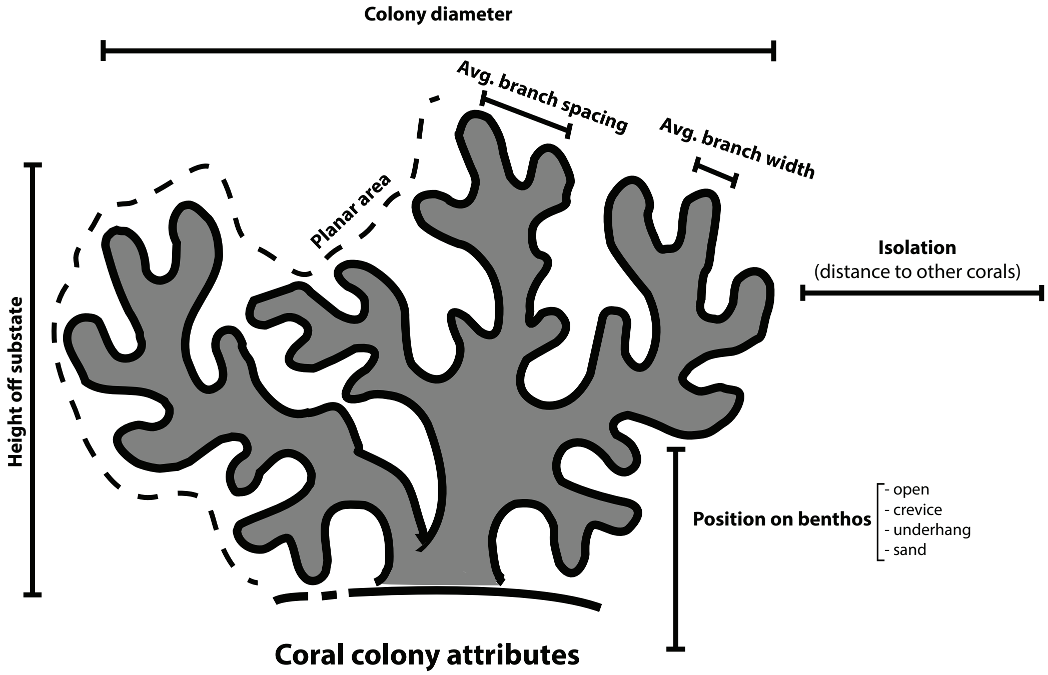


Figure S2.1 Illustration of 7 coral colony microstructure attributes for five species of branching colonies (15-100 cm diameter) for 226 colonies over 15 sites on 11 reefs (colony level dataset). For full descriptions of coral microstructure attributes refer to Table 2.1.

APPENDIX S3 – Extended results for damselfishes' behaviours around host coral colonies

Table S3.1 Person's Chi-squared (χ^2) test values for average modal diurnal fish position (top, side, under, in) and positions around healthy and bleached covered colonies (colony bleaching status). Significant p-values are in bold.

Fish species	Analysis	χ^2 value	d.f.	p-value
C. viridis	Colony bleaching	29.08	3	**< 0.001**
D. aruanus	Colony bleaching	41.06	3	**< 0.001**
D. reticulatus	Colony bleaching	16.50	3	**< 0.001**
P. amoboinensis	Colony bleaching	25.33	3	**< 0.001**
P. moluccensis	Colony bleaching	23.98	3	**< 0.001**

Table S3.2 Results of a zero-inflated generalized linear mixed model (GLMM) examining the *in-situ* startle shelter response of five different species of damselfish around small branching host colonies. The most parsimonious model the best model included the number of fishes in each position (dependent variable), fish species and position (independent variables), colony number as a random factor and startle number nested within colony, and total fish per species on each colony as an offset. Significant p-values are in bold.

Factor	z-value	p-value
(intercept) (*C. viridis*)	-0.635	0.5253
D. aruanus	-0.536	0.5918
D. reticulatus	-0.759	**0.4481**
P. amboinensis	-9.708	**< 0.0001**
P. moluccensis	-5.842	**< 0.0001**
Out position	-11.102	**< 0.0001**
Under position	-10.572	**< 0.0001**
D. aruanus: Out	4.174	**< 0.0001**
D. reticulatus: Out	3.754	**0.0002**
P. amboinensis: Out	10.899	**< 0.0001**
P. moluccensis: Out	8.899	**< 0.0001**
D. aruanus: Under	4.103	**< 0.0001**
D. reticulatus: Under	4.829	**< 0.0001**
P. amboinensis: Under	11.030	**< 0.0001**
P. moluccensis: Under	8.293	**< 0.0001**

Table S3.3 *Post-hoc* test ('emmean') for multiple comparisons of startle shelter response (position) of five different species of damselfish around small branching host colonies. Values are based off the zero-inflated generalized linear mixed model (GLMM) that included the number of fishes in each position (dependent variable), fish species and position (independent variables), colony number as a random factor and startle number nested within colony, and total fish per species on each colony as an offset. Significant p-values are in bold.

Contrast	**t. ratio**	**p. value**
Position: IN		
C. viridis – D. aruanus	1.045	0.9836
C. viridis - D. reticulatus	1.203	0.9423
C. viridis – P. amboinensis	10.554	**< 0.001**
C. viridis - P. moluccensis	6.440	**< 0.001**
D. aruanus - D. reticulatus	0.487	0.9957
D. aruanus - P. amboinensis	9.841	**< 0.001**
D. aruanus – P. moluccensis	5.025	**< 0.001**
D. reticulatus - P. amboinensis	8.767	**< 0.001**
D. reticulatus - P. moluccensis	3.157	0.0035
P. amboinensis - P. moluccensis	-6.778	**< 0.001**
Position: OUT		
C. viridis – D. aruanus	-3.525	**0.0004**
C. viridis - D. reticulatus	-3.383	**0.0022**
C. viridis – P. amboinensis	-13.228	**< 0.0001**
C. viridis - P. moluccensis	-11.001	**< 0.0001**
D. aruanus - D. reticulatus	-0.802	1.000
D. aruanus - P. amboinensis	-10.029	**< 0.0001**
D. aruanus – P. moluccensis	-7.459	**< 0.0001**
D. reticulatus - P. amboinensis	-5.391	**< 0.0001**
D. reticulatus - P. moluccensis	-3.816	**0.0010**
P. amboinensis - P. moluccensis	-3.822	**0.0013**
Position: IN		
C. viridis – D. aruanus	-4.070	**0.0005**
C. viridis - D. reticulatus	-4.770	**< 0.0001**
C. viridis – P. amboinensis	-9.074	**< 0.0001**
C. viridis - P. moluccensis	-7.638	**< 0.0001**
D. aruanus - D. reticulatus	-1.471	0.5817
D. aruanus - P. amboinensis	10.269	**< 0.0001**
D. aruanus – P. moluccensis	-7.020	**< 0.0001**
D. reticulatus - P. amboinensis	-6.421	**< 0.0001**
D. reticulatus - P. moluccensis	-3.900	**0.0010**
P. amboinensis - P. moluccensis	4.953	**< 0.0001**

Table S3.4 Results of a Poisson Generalized Linear Model (GLM) examining the *in-situ* colony visits of five different species of damselfish around small branching host colonies. Values are based off of model selection practice using degrees of freedom and Akaike information criteria (AIC) scores; the best model included colony visits (dependent variable), fish species (independent variable), coral colony (random factor), and fish number per each species as an offset.

Factor	**z-value**	**p-value**
(intercept) (*C. viridis*)	11.87	2×10^{-16}
D. aruanus	11.86	**< 0.001**
D. reticulatus	7.46	**< 0.001**
P. amboinensis	-16.43	**< 0.001**
P. moluccensis	-16.04	**< 0.001**

Table S3.5 Results of a generalized linear model examining the *in-situ* average distance (log + 1) of five different species of damselfish around small branching host colonies.

Factor	**t-value**	**p-value**
(intercept) (*C. viridis*)	13.807	$< 2 \times 10^{-16}$
D. aruanus	-0.099	0.9209
D. reticulatus	-1.042	0.2992
P. amboinensis	-3.148	**0.0021**
P. moluccensis	-3.526	**0.0006**

Table S3.6 Results of a generalized linear model (GLM) examining the *in-situ* maximum distance above (log + 1) the host coral colony of five different species of damselfish around small branching host colonies.

Factor	**t-value**	**p-value**
(intercept) (*C. viridis*)	15.355	$< 2 \times 10^{-16}$
D. aruanus	-0.060	0.9520
D. reticulatus	-0.216	0.8290
P. amboinensis	-9.104	**< 0.0001**
P. moluccensis	-4.633	**< 0.0001**

Table S3.7 Results of a generalized linear model (GLM) examining the *in-situ* maximum distance to the side (log + 1) the host coral colony of five different species of damselfish around small branching host colonies.

Factor	**t-value**	**p-value**
(intercept) (*C. viridis*)	9.188	6.22×10^{-16}
D. aruanus	2.175	**0.0315**
D. reticulatus	1.250	0.2138
P. amboinensis	-0.419	0.6761
P. moluccensis	-0.331	0.7411

Table S3.8 Results of a Generalized Linear Model (GLM) examining the *in-situ* conspecific aggressions of five different species of damselfish around small branching host colonies. Values are based off of model selection practice using degrees of freedom and Akaike information criteria (AIC) scores; the best model included conspecific aggressions (dependent variable), fish species (independent variable), coral colony (random factor), and fish number per each species as an offset.

Factor	**t-value**	**p-value**
(intercept) (*C. viridis*)	0.8994	0.3731
D. aruanus	6.164	**< 0.001**
D. reticulatus	2.749	**0.0077**
P. amboinensis	-0.209	**0.8346**
P. moluccensis	1.320	**0.1913**

Table S3.9 Results of a negative binomial Generalized Linear Model (GLM) examining the *in-situ* heterospecific aggressions (log + 1) of five different species of damselfish around small branching host colonies. Values are based off of model selection practice using degrees of freedom and Akaike information criteria (AIC) scores; the best model included heterospecific aggressions (dependent variable), fish species (independent variable), coral colony (random factor), and fish number per each species and other fish on the colony as offsets. Significant p-values are in bold.

Factor	**t-value**	**p-value**
(intercept) (*C. viridis*)	-0.0182	0.9855
D. aruanus	3.7775	**0.003**
D. reticulatus	2.5950	**0.0117**
P. amboinensis	0.8552	0.8552
P. moluccensis	0.5318	0.5967

APPENDIX S4 – Extended field sediment analysis

Supplemental Text S4.1: Field sediment quantification

Introduction

An assessment of natural sedimentation rates around the Palm Islands was conducted to put the experiment into context and assess relevant sedimentation rates for use in the experiment.

Methods

Field sediment methods

Field sampling was conducted between April – June 2017 around the Palm Islands, an inner-shelf, island group of the Great Barrier Reef (GBR). Orpheus Island is located ~20 km from the Queensland coast and close to the Herbert (20 km) and Burdekin rivers (150 km). Sediments were collected at six locations around the Palm Islands to quantify and identify natural levels of sedimentation in the area pertinent to the aquaria experiment (Figure S1). Sediment traps and SedPods were deployed from three exposed sites (SE Pelorus, East Orpheus, Snapper Point), and three sheltered sites (SW Pelorus, Cattle Bay, Hazard Bay), over the course of 34 days, roughly 3 months post-wet season.

Quantification of sediment dynamics

Sediment accumulation was measured using simple tube traps constructed from PVC. Sediment trap design and placement followed the recommendations of Storlazzi et al. (2011). Specifically, the dimensions of traps were as follows: trap diameter (D): 54 mm; trap height (H): 30 mm, with a 5 cm diameter mesh placed in the top of the trap to limit resuspension, or organisms getting inside the trap. Traps were affixed to a picket on the reef ensuring they were vertical. The cylindrical traps had a diameter greater than 50mm and a trap Reynolds number

(R_t) of ~6:1. Twenty-four traps, four per site, deployed at depths between 2-5.5 m, lowest astronomical tide (LAT), and were positioned with the sediment trap mouth at ~70 cm above the reef substrate. Traps were deployed three times per site, each deployment lasting 7-13 days.

In addition to traps, twenty-four SedPods (diameter: 5.5 cm, area: 23.76 cm, see Field et al. 2013 for design and application) were deployed in the same vicinity as the traps but were positioned directly on the substratum. SedPods were deployed three times per site, each deployment lasting 7-13 days. At a sub-sample of 4 sites, sediment samples from the epilithic algal matrix (EAM) were collected as a third measure of sedimentation/accumulation. Using an underwater sediment vacuum apparatus (submersible 12 V electron vacuum sampler, design described in Purcell 1996; Kramer et al. 2012), all sediment was removed from a defined area of 78.5 cm^2 (circular pipe with a 10 cm diameter) of EAM. Suitable EAM covered areas were approximately horizontal, flat (i.e. free of holes or sediment retaining pits), free of macroalgae and encrusting organisms, and covered by algal turfs (following Tebbett et al. 2018). Subsequently, 12 - 24 days later the areas were vacuumed again, and the sediments were retained to assess accumulation rate during this time period.

Sample processing

All collected sediments from traps, SedPods and vacuum samples were frozen and transported to James Cook University for further processing. Sediment samples were then rinsed with fresh water three times to remove salts, transferred into labelled sample containers, dried at 60°C (Axyos Microdigital Incubator) for > 4 days, weighed for constant weight (g), sieved into three factions (Wentworth 1922): < 125 µm (very fine sand and silt), 125-500 µm (fine to medium sand), 500-4000 µm (coarse sand to gravel) and weighed (using Kern PCB, John Morris

Scientific balance, precision 0.001 g). All sediment samples were converted to grams m^{-2} day^{-1} for consistency.

Statistical analysis

Sediment trapping rates (measured with sediment traps) were compared among sites (fixed factor) using a lognormal generalized least squares (gls) model. The gls model was necessary to account for heteroscedasticity, which was still present after a log transformation. A variance structure was fitted allowing for unequal variances among individual sites. Differences between individual sites were examined using Least Square Means (lsmeans) multiple comparisons with Tukey's adjustment *post-hoc*. Sedimentation rates assessed using the SedPods were compared among sites using a lognormal linear model with site as a fixed factor. In all cases, model fits were assessed using residual plots, all of which were satisfactory. Statistical modelling was performed in the software R (R Development Core Team 2018) using the *nlme* (Pinheiro et al. 2018) and *lsmeans* (Lenth 2016) packages.

Differences in sediment grain size composition in traps were examined among sites using a permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA was based on a Euclidean distance matrix of standardised data and included site as a fixed factor. Following the PERMANOVA, pair-wise tests were performed to determine where between site differences occurred. Homogeneity of dispersions was assessed using a permutational analysis of multivariate dispersions (PERMDISP). A canonical analysis of principle components (CAP) was employed following the PERMANOVA to visualise significant groupings. Multivariate analysis was performed using PRIMER 7.0 PERMANOVA+. No formal analysis was conducted on vacuum samples due to low samples sizes.

Results

Sediment around the Palm Islands results

Sedimentation rates varied markedly between exposed and sheltered regions and by sediment capture method (Figures S4.3, S4.4, S4.5 and Tables S4.1, S4.2, S4.3, S4.4, S4.5, S4.6 in Appendix S4). Exposed sites experienced ~30x more daily sediment loads (29 ± 10 g day^{-1}) than sheltered sites (0.68 ± 0.3g m^{-2} day^{-1}), as measured by sediment traps (Table S4.3 and Figure S3 in Appendix S4). Total daily sediment load around the Palm Islands (all sites pooled) was ~137 mg cm^{-2} day^{-1}.

In terms of sediment load rates as quantified using the traps, rates were consistently higher for all three exposed sites (SEP: 106.35 ± 29.57 g day^{-1}, EOIRS: 9.17 ± 3.39 g day^{-1}, and SP: 3.23 ± 0.69 g day^{-1}), compared to all three sheltered sites (SWP: 0.34 ± 0.04 g day^{-1}, CB: 0.35 ± 0.35 g day^{-1}, and HB: 1.37 ± 0.98 g day^{-1}). Indeed, all exposed-sheltered site pairwise comparisons of sediment trapping rates were significantly different (Tables S4.1, S4.2, S4.3, S4.4 and Figures S4.3 in Appendix S4). Furthermore, significant differences among individual sheltered and exposed sites were also noted (Table S4.1 and Figure S4.3 in Appendix S4). In terms of sediment grain size distributions, 93% of sediment collected in traps on exposed sites consisted of medium or coarse sediments, while medium- and coarse-grained sediments only accounted for 60% of sediment mass in traps on sheltered sites. The PERMANOVA suggested that grain size distributions differed significantly among individual sites (PERMANOVA: Pseudo-$F_{5,71}$ = 17.643, $p_{[perm]} < 0.001$; Table S4.2 and Figure S4.4 in Appendix S4). However, the homogeneity of dispersions also differed significantly among sites (Table S4.3 in Appendix S4), which may have influenced the significance of the PERMANOVA, especially in-terms of comparisons among sheltered and exposed sites due to the homogenous nature of sediment collected from sheltered locations (Figure S4.4).

Only fine sediments (0 – 125 µm) were collected by the SedPods and these exhibited contrasting trends to the sediment traps. Specifically, sheltered sites experienced a two-fold higher sedimentation rate (1.02 ± 0.29 g m^{-2} day^{-1}) compared to exposed sites (0.45 ± 0.13 g m^{-2} day^{-1}). Again, sedimentation rates differed significantly among sites (Tables S4.5, S4.6 Figure S4.5), with Hazard Bay and SW Pelorus experiencing particularly high levels of sediment deposition on SedPods (1.6 ± 0.8 and 1.1 ± 0.4 g m^{-2} day^{-1}, respectively). Exposed sites SE Pelorus and East Orpheus displayed the lowest sediment accumulation on SedPods (0.0 ± 0.0 and 0.1 ± 0.4 g m^{-2} day^{-1}, respectively), however the third exposed site, Snapper Point, had an average of 0.88 ± 0.2 g m^{-2} day^{-1}).

Sediment accumulation rates in the algal turfs of three sheltered and one exposed site (Snapper Point) showed similar trends with SedPods. Again, lower average sediment deposition than sediment traps (Table S4.7) were recorded, except for Snapper Point, which displayed ten-fold more vacuumed sediments (2.8 ± 1.3 g m^{-2} day^{-1}) than sheltered sites.

Discussion

The sedimentation rates and grain size distributions quantified around the Palm Islands, varied markedly among habitats and the methods used. This supports a number of previous studies that have noted differences in sediment dynamics among habitats (e.g. Purcell 2000; Browne et al. 2013; Tebbett et al. 2018) and quantification methods (e.g. Storlazzi et al. 2011; Whinney et al. 2017). The hydrodynamic activity that suspended medium and coarse sediments on exposed sites (Yahel et al. 2002; Weber et al. 2006) may lead to higher coral abrasion rates in these habitats (Loya 1976; Rogers 1990; PIANC 2010). By contrast, lower-energy hydrodynamic activity in sheltered locations can lead to coral smothering, characteristic of inshore GBR reefs (Fabricius 2005).

While sediment traps have been criticised for measuring a trapping rate as they limit resuspension activity (Storlazzi et al. 2011) and SedPods were developed to mimic sediment dynamics on a coral surface (Field et al. 2013), the most accurate representation of sediment deposition on the focal branching corals is probably achieved by using a combination of both techniques. This is because SedPods represent exposed flat coral surfaces (e.g. massive *Porites* or exposed areas of branching corals), while within the branches of corals hydrodynamic activity is reduced, thus facilitating sedimentation and limiting resuspension (as in traps). Therefore, any one measure is likely to either underestimate or overestimate sediment accumulation on coral surfaces. However, in terms of this study, the key appears to be the removal of trapped sediments from within the branches of coral colonies.

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TABLES AND FIGURES ASSOCIATED WITH FIELD SEDIMENT SAMPLING

Table S4.1 Results of lsmeans pairwise comparisons with a Tukey's adjustment based on a lognormal generalized least squares (gls) model examining differences in sedimentation rates (g m^{-2} day^{-1}) among sites using sediment traps. Sites were sheltered (HB, CB, and SWP) and exposed (SP, EOIRS, and SEP) around the Palm Islands.

Site comparison	**P-adjusted**
CB – EOIRS	< **0.0001**
CB – HB	0.9444
CB – SEP	**< 0.0001**
CB – SP	**< 0.0001**
CB – SWP	<0.9991
EOIRS - HB	**0.0010**
EOIRS – SEP	**0.0015**
EOIRS – SP	0.8225
EOIRS –SWP	**< 0.0001**
HB – SEP	**< 0.0001**
HB – SP	0.0001
HB – SWP	0.9052
SEP – SP	**< 0.0001**
SEP – SWP	**< 0.0001**
SP –SWP	**< 0.0001**

Table S4.2 Permutational multivariate analysis of variance (PERMANOVA) the effect of site for grain size of sediment collected (g m^{-2} day^{-1}) in sediment traps at sheltered (3 sites: HB, CB, and SWP) and exposed (3 sites: SP, EOIRS, and SEP) locations around the Palm Islands.

Source	**DF**	**SS**	**MS**	**Pseudo-F**	**P (perm)**	**Unique Perms**
Site	5	1.106×10^5	22121	17.643	**0.0001**	99523
Residual	66	82752	1253.8			
Totals	71	1.9336×10^5				

Table S4.3 Results from pairwise tests following a PERMANOVA, which examined the variation in grain size distributions among sites. The PERMANOVA was based on a Euclidian distance matrix of standardised data. Sites were sheltered (HB, CB, and SWP) and exposed (SP, EOIRS, and SEP) around the Palm Islands.

Site comparison	**P adjusted**
CB – EOIRS	**0.001**
CB – HB	1.0000
CB – SEP	**0.0001**
CB – SP	**0.0024**
CB – SWP	1.0000
EOIRS - HB	**0.0031**
EOIRS – SEP	**0.0011**
EOIRS – SP	0.2938
EOIRS –SWP	**0.0002**
HB – SEP	**0.0001**
HB – SP	**0.0123**
HB – SWP	0.4755
SEP – SP	**0.0001**
SEP – SWP	**0.0001**
SP –SWP	**0.0001**

Table S4.4 Results from PERMDISP pairwise tests, which examined the variation in grain size distribution homogeneity among sites. Sites were sheltered (HB, CB, and SWP) and exposed (SP, EOIRS, and SEP) around the Palm Islands.

Site comparison	**P-adjusted**
CB – EOIRS	0.2485
CB – HB	0.7447
CB – SEP	0.0886
CB – SP	0.8921
CB – SWP	**0.0001**
EOIRS - HB	0.6827
EOIRS – SEP	0.4345
EOIRS – SP	0.3505
EOIRS –SWP	**0.0001**
HB – SEP	0.4091
HB – SP	0.6632
HB – SWP	**0.0001**
SEP – SP	**0.0258**
SEP – SWP	**0.0001**
SP –SWP	**0.0001**

Table S4.5 Linear model of the effect of exposure and site on sediment collected (g m^{-2} day^{-1}) in SedPods at sheltered (HB, CB, and SWP) and exposed (SP, EOIRS, and SEP) locations around the Palm Islands. SE Pelorus SedPod data was removed from the figures and analysis due to low replicates.

Source	DF	SS	MS	F-value	P
Exposure	1	0.800	0.7998	4.562	**0.0375**
Site	3	2.342	0.7807	4.453	**0.0075**
Residuals	51	8.941	0.1753		

Table S4.6 Tukey's HSD *post-hoc* multiple comparisons table (including confidence intervals) for total sediment, log (x+1) transformed, collected in SedPods at sheltered (HB, CB, and SWP) and exposed (SP, EOIRS, and SEP) locations around the Palm Islands. SE Pelorus SedPod data was removed from the figures and analysis due to low replicates.

Site comparison	Lower	Upper	P adjusted
CB – EOIRS	-0.7741	0.1959	0.4519
CB – HB	-0.1573	0.8545	0.3065
CB – SP	-0.2677	0.7420	0.6751
CB – SWP	-0.2802	0.7545	0.6946
EOIRS - HB	0.1516	1.1217	**0.0045**
EOIRS – SP	0.0412	1.0113	**0.0272**
EOIRS –SWP	0.0282	1.0243	**0.0335**
HB – SP	-0.6153	0.3944	0.9715
HB – SWP	-0.6278	0.4069	0.9739
SP –SWP	-0.5173	0.5173	1.0000

Table S4.7 Average sediments (g m^{-2} day^{-1}) ± S.E at four locations around the Palm Islands, collected by a submersible vacuum.

Site	Exposure	Collections	Average sediment (g m^{-2} day^{-1}) ± S.E
SW Pelorus	*sheltered*	4	0.20 ± 0.05
Cattle Bay	*sheltered*	4	0.185 ± 0.05
Hazard Bay	*sheltered*	4	0.65 ± 0.21
Snapper Point	*exposed*	4	2.79 ± 1.26

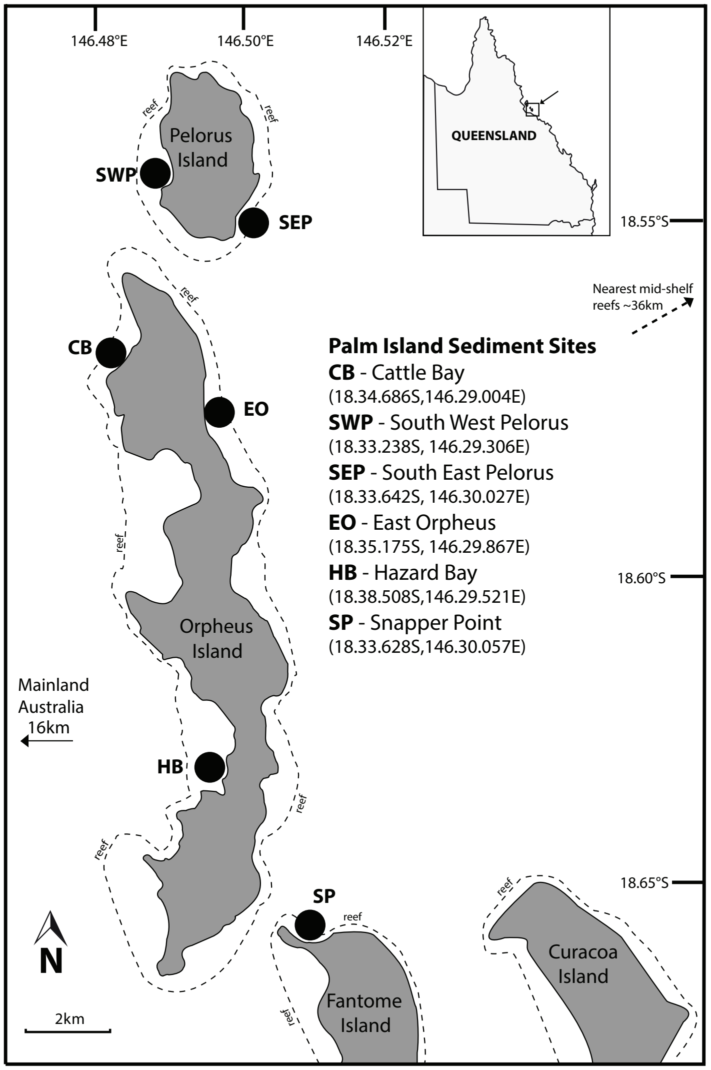

Figure S4.1 Sampling locations around the Palm Island reefs, located ~12 km from the Queensland coast. SWP, CB, and HB sites are sheltered locations, on the leeward side of Pelorus and Orpheus Island, and SEP, EO, and SP are exposed locations on the windward side of Pelorus, Orpheus, and Fantome Islands. Two sediment traps and SedPods were deployed three times per site, at depths of 2-5.5 m (LAT), from May to June 2017.

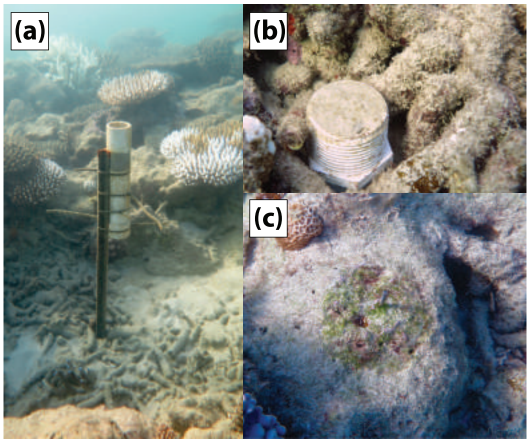

Figure S4.2 Example methods and deployment of sediment capture in the field: **(a)** sediment trap, **(b)** SedPod, and **(c)** sediment vacuum collection area. Refer to the methods section in Appendix S4 for sediment sample specifications.

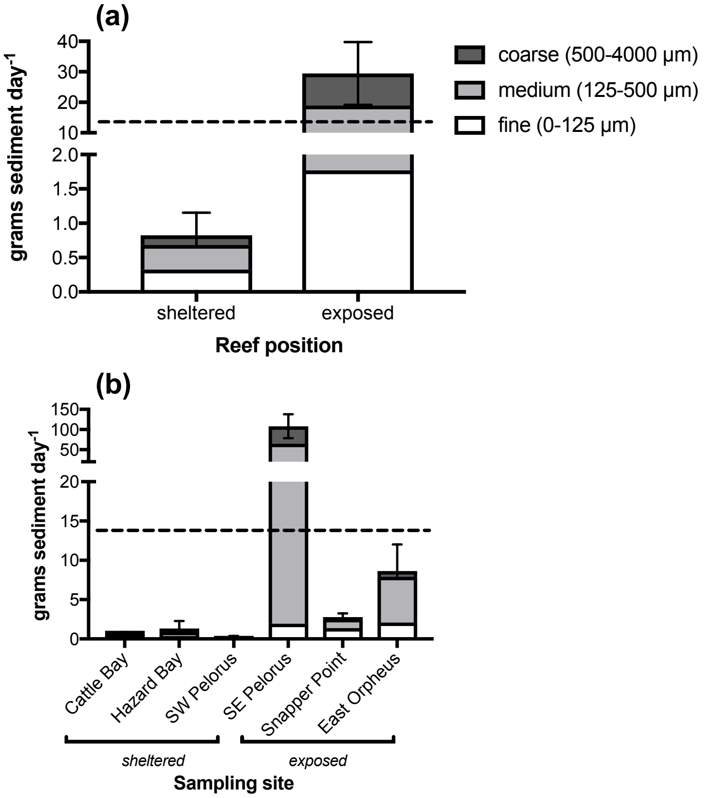

Figure S4.3 Comparison of sedimentation rates measured using traps on **(a)** sheltered (n = 36) and exposed sites (n = 30) and **(b)** at each of the individual sites around the Palm Islands. Dashed lines represent the maximum quantities (14 g = 100 mg cm^{-2} day^{-1}) added to coral colonies in the manipulative sediment aquaria experiment. Sediment traps deployed per site were as follows: Cattle Bay (n = 12), Hazard Bay (n = 12), SW Pelorus (n = 12), SE Pelorus (n = 7), Snapper Point (n = 12), East Orpheus (n = 11).

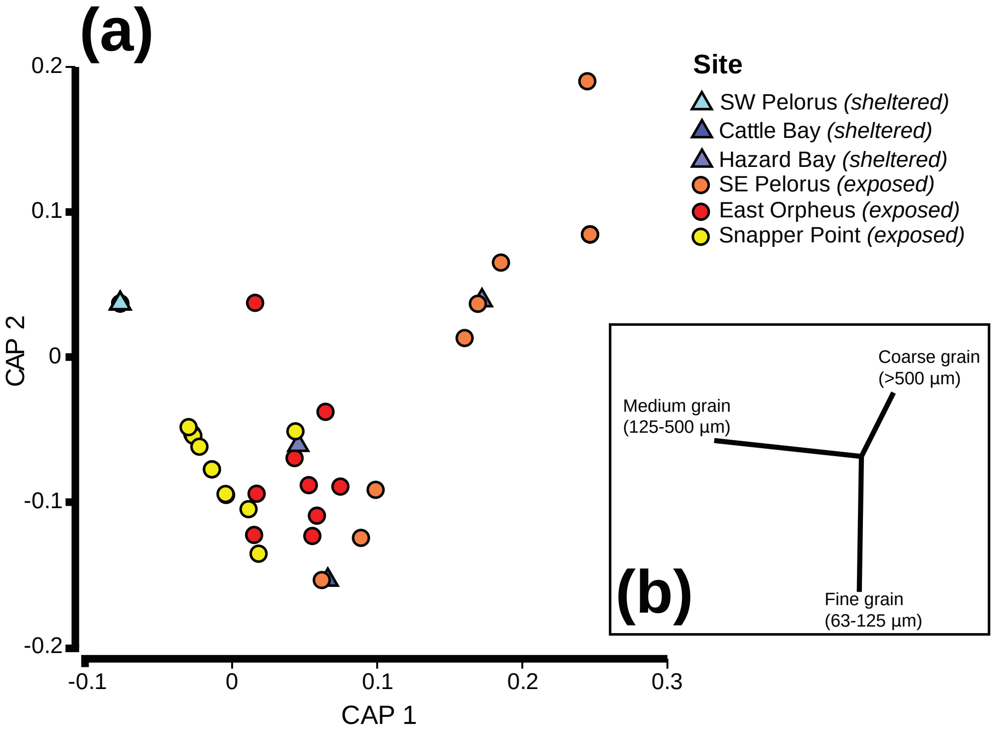

Figure S4.4 (a) Canonical analysis of principal (CAP) coordinates ordination based on a Euclidean distance matrix of standardised grain size distribution from sediments collected in sediment traps at sheltered (3 sites: HB, CB, and SWP) and exposed (3 sites: SP, EOIRS, and SEP) locations around the Palm Islands. **(b)** Vectors show the relationship among sediment grain size fractions (µm) and how they influence the position of data points in the CAP. Vectors were calculated using a multiple correlation model. Several of the sheltered sites (SWP, CB, and HB) are overlaid due to similar grain size compositions.

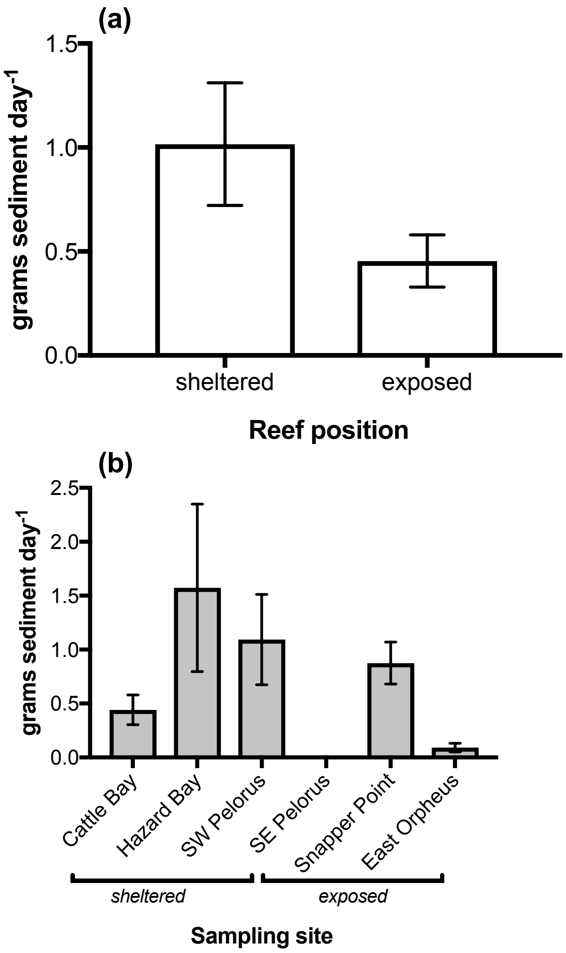

Figure S4.5 Comparison of average sedimentation rates measured using Sedpods in (a) sheltered (n = 33) and exposed sites (n = 23) and (b) at each of the individual sites around the Palm Islands. Sediment grain size was pooled into a single category as it was all fine grain in nature. SedPods deployed per site were as follows: Cattle Bay (n = 12), Hazard Bay (n = 11), SW Pelorus (n = 10), SE Pelorus (n = 0), Snapper Point (n = 11), East Orpheus (n = 9).

Supplemental Text S4.2 – Extended methods and results for experimental study

Methods

Suspended sediment samples were collected 1 h after sediment was added, using a syringe placed 5 cm above the coral colony. This sampling was conducted to determine if fish re-suspended sediment. Suspension samples were filtered using Whatman glass fibre filter paper (MicroScience, MSGA grade, 47 mm) and vacuum (John Morris Air Admiral), dried and weighed (using a Sartorius Entris 124I-1S, precision 0.0001 g). Suspended sediment in aquaria was analysed with a two-way ANOVA with sediment and fish as fixed factors. Again, model residuals were assessed with QQ normal plots and frequency distributions.

Results

Suspended sediment concentrations were negligible in aquaria ($< 6.2 \times 10^{-5}$ mg ml^{-1}, see Table S4.9 and Figure S4.6) one hour after sediment dosage. Indeed, water in the aquaria appeared clear and comparable with non-sediment treatments. Suspended sediments did not differ significantly between sediment treatments ($F_{1,46} = 0.193$, $p = 0.662$) nor with fish treatment ($F_{2,48} = 2.634$, $p=0.082$).

TABLES AND FIGURES ASSOCIATED WITH AQUARIA SEDIMENT SAMPLING

Table S4.8 Descriptions and mineral compositions of sorted sediment fractions All sediments had zero microbial content. See Esslemont 2000 and Ricardo et al. 2016 for further details regarding sediment composition.

Location	Size class	Mineral description and XRD analysis
Middle Reef, inshore GBR	< 53µm	Grey-brown silt
Davie's Reef, mid-shelf GBR	< 53 µm	Carbonate sediments white silt, carbonate: 80% aragonite, 20% calcite, Total Organic Carbon: 0.27%
Orpheus Island, inshore island GBR	90-4000 µm	Coarse beach sediments tan-brown subangular to rounded to bioclastics sand: 45% quartz, 19% kaolinite, 7% albite, carbonate: 30% Calcite Total organic Carbon: 2.76%

Esselmont G (2000) Heavy metals in seawaters, marine sediments and corals from the Townsville section, Great Barrier Reef Marine Park, Queensland. Marine Chemistry 71:215-231

Ricardo GR, Jones RJ, Clode PL, Negri AP (2016) Mucous secretion and cilia beating defend developing coral larvae from suspended sediments. PLoS ONE 11:e0162743. doi:10.1371/journal.pone.0162743

Table S4.9 Two-way analysis of variance (ANOVA) results table for average suspended sediments (mg ml^{-1}) under different fish and sediment treatments in the manipulated sediment experiment.

Source	**DF**	**SS**	**MS**	**F-value**	**P**
Sediment	1	2.2×10^{-10}	2.16×10^{-10}	0.193	0.663
Fish	2	5.7×10^{-9}	2.89×10^{-9}	2.581	0.087
Sediment*Fish	2	1.15×10^{-9}	5.78×10^{-10}	0.515	0.601
Residuals	46	5.14×10^{-8}	1.12×10^{-9}		

Table S4.10 Results of pairwise tests following the permutational analysis of multivariate dispersions (PERMDISP), which assessed the homogeneity of sediment grain size distributions remaining on coral colonies under different fish treatments (*D. aruanus*, *P. moluccensis*, and No fish) in the manipulated sediment experiment. Only data from coral colonies with sediment added were included.

PERMDISP: $F_{2,33} = 15.699$, $p =$ **0.002**

Site comparison	**P-adjusted**
D. aruanus – *P. moluccensis*	**0.0022**
D. aruanus – No Fish	**0.0002**
P. moluccensis – No Fish	0.4277

Table S4.11 Results of a betaregression model examining the proportion of partial colony mortality for *P. damicornis* colonies under different sediment and fish treatments in the manipulated sediment experiment.

Factor	**z-value**	**p-value**
(intercept)	-13.427	$< 2 \times 10^{-16}$
Fish *P. moluccensis*	0.000	1.0000
Fish No Fish	0.000	1.0000
Sediment Sediment	0.893	0.3317
Fish *P. moluccensis* : Sediment Sediment	2.468	**0.0149**
Fish No Fish : Sediment Sediment	3.498	**0.0002**

Table S4.12 Results of lsmeans pairwise comparisons with a Tukey's adjustment based on a betaregression model comparing the interacting effects of sediment exposure and fish treatment on partial colony mortality rates of *P. damicornis* colonies in the experiment.

Treatment comparison	**z ratio**	**P adjusted**
Clean *D. aruanus* – Clean *P. moluccensis*	0.000	1.0000
Clean *D. aruanus* – Clean No fish	0.000	1.0000
Clean *D. aruanus* – Sediment *D. aruanus*	-0.881	0.9210
Clean *D. aruanus* – Sediment *P. moluccensis*	**-3.880**	**0.0007**
Clean *D. aruanus* – Sediment No Fish	**-5.082**	**< 0.0001**
Clean *P. moluccensis* – Clean No Fish	0.000	1.0000
Clean *P. moluccensis* – Sediment *D. aruanus*	-0.894	0.9210
Clean *P. moluccensis* – Sediment *P. moluccensis*	-3.892	**0.0007**
Clean *P. moluccensis* – Sediment No Fish	**-5.090**	**< 0.0001**
Clean No Fish – Sediment *D. aruanus*	**-0.894**	0.9210
Clean No Fish – Sediment *P. moluccensis*	-3.892	**0.0007**
Clean No Fish – Sediment No Fish	**-5.090**	**< 0.0001**
Sediment *D. aruanus* – Sediment *P. moluccensis*	**-3.404**	**0.0060**
Sediment *D. aruanus* – Sediment No Fish	**-4.734**	**< 0.001**
Sediment *P. moluccensis* – Sediment No Fish	**-1.880**	**0.0461**

Table S4.13 Results of multiple selected comparisons as a *post hoc* test of the two-way analyses of variance (ANOVAs) analysing the effects of sediment and fish presence on *P. damicornis* colonies. Separate ANOVAs were completed for the two phases of the experiment: Start and End. Samples sizes for each treatment are displayed in brackets.

Coral tissue	Phase	Comparison	Lower	Upper	P-value
Total Chlorophyll	Start	Clean *D. aruanus* (n = 12) – Clean *P. moluccensis* (n = 12)	-0.9533	0.9082	0.9999
		Clean *D. aruanus* (n = 12) – Clean No fish (n = 12)	-0.9373	0.7861	0.9998
		Clean *D. aruanus* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.9141	0.9935	0.9997
		Clean *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	0.5867	1.2208	0.9047
		Clean *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.6782	1.0452	0.9885
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	-0.9383	0.8777	0.9999
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.8575	1.0821	0.9994
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.6302	1.3094	0.9905
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	0.7247	1.1368	0.9864
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 12)	0.7384	1.0691	0.9943
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.5110	1.2965	0.7947
		Clean No Fish (n = 12)– Sediment No Fish (n = 12)	-0.6026	1.1208	0.9485
		Sediment *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.7166	1.1713	0.9801
		Sediment *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.8100	0.9975	0.9996
		Sediment *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-1.0374	0.7701	0.9979
	End	Clean *D. aruanus* (n = 11) – Clean *P. moluccensis* (n = 12)	-4.4159	2.6053	0.9734
		Clean *D. aruanus* (n = 11) – Clean No fish (n = 12)	-5.1124	1.9089	0.7607
		Clean *D. aruanus* (n = 11) – Sediment *D. aruanus* (n = 10)	-2.8080	4.5414	0.9820
		Clean *D. aruanus* (n = 11) – Sediment *P. moluccensis* (n = 11)	-4.8683	2.3039	0.8983
		Clean *D. aruanus* (n = 11) – Sediment No Fish (n = 12)	-6.7723	0.2489	0.0832
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	-4.1299	2.7371	0.9909
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 10)	-1.8290	5.3731	0.6984
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 11)	-3.8875	3.1338	0.9996
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-5.8875	1.0771	0.3441
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 10)	-1.1326	6.0695	0.3454
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 11)	-3.1911	3.3802	0.9998
		Clean No Fish (n = 12) – Sediment No Fish (n = 12)	-5.0934	1.7735	0.7138

		Sediment *D. aruanus* (n = 10) – Sediment *P. moluccensis* (n = 11)	-5.8236	1.5258	0.5244
		Sediment *D. aruanus* (n = 10) – Sediment No Fish (n = 12)	-7.7294	0.5273	**0.0156**
		Sediment *P. moluccensis* (n = 11) – Sediment No Fish (n = 12)	-5.4901	1.5312	0.5641
Total Proteins	Start	Clean *D. aruanus* (n = 12) – Clean *P. moluccensis* (n = 12)	-0.6457	1.0649	0.9789
		Clean *D. aruanus* (n = 12) – Clean No fish (n = 12)	-0.7991	0.9115	0.9999
		Clean *D. aruanus* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.6507	1.0599	0.9811
		Clean *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-1.1199	0.5907	0.9431
		Clean *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.7522	0.9584	0.9992
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	-1.0087	0.7019	0.9949
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.8603	0.8503	1.0000
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 12)	-1.3295	0.3811	0.5838
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.9618	0.7488	0.9991
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 12)	-0.7069	1.0037	0.9957
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 12)	-1.1762	0.5344	0.8792
		Clean No Fish (n = 12) – Sediment No Fish (n = 12)	-0.8085	0.9021	0.9999
		Sediment *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-1.3245	0.3861	0.5948
		Sediment *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.9568	0.7538	0.9993
		Sediment *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.4876	1.2229	0.8044
	End	Clean *D. aruanus* (n = 12) – Clean *P. moluccensis* (n = 12)	-0.1868	0.0177	0.1622
		Clean *D. aruanus* (n = 12) – Clean No fish (n = 12)	0.1656	0.0288	0.4607
		Clean *D. aruanus* (n = 12) – Sediment *D. aruanus* (n = 11)	-0.1467	0.0623	0.8423
		Clean *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.1518	0.0537	0.7129
		Clean *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.2421	0.0376	**0.0021**
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	0.0811	0.1234	0.9901
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 11)	-0.0622	0.1469	0.8406
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.0673	0.1372	0.9149
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.1575	0.0469	0.6092
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 11)	-0.0834	0.1257	0.9911
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.0884	0.1160	0.9987
		Clean No Fish (n = 12) – Sediment No Fish (n = 12)	-0.1787	0.0258	0.2538
		Sediment *D. aruanus* (n = 11) – Sediment *P. moluccensis* (n = 12)	-0.1119	0.0972	0.9999
		Sediment *D. aruanus* (n = 11) – Sediment No Fish (n = 12)	-0.2022	0.0069	0.0807

		Sediment *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.1925	0.1199	0.1139
Tissue Biomass	Start	Clean *D. aruanus* (n = 12) – Clean *P. moluccensis* (n = 12)	-0.4099	0.7798	0.9419
		Clean *D. aruanus* (n = 12) – Clean No fish (n = 12)	-0.5717	0.6189	0.9999
		Clean *D. aruanus* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.5245	0.6652	0.9993
		Clean *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.7046	0.4851	0.9942
		Clean *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.4528	0.7368	0.9812
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	-0.7667	0.4430	0.9668
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 12)	-0.7095	0.4803	0.9929
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.8896	0.3002	0.6941
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.6378	0.5519	0.9999
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 12)	-0.5476	0.6421	0.9999
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.7277	0.4620	0.9861
		Clean No Fish (n = 12) – Sediment No Fish (n = 12)	-0.4760	0.7137	0.9916
		Sediment *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.7750	0.4148	0.9479
		Sediment *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.5232	0.6665	0.9992
		Sediment *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.3431	0.8466	0.8145
	End	Clean *D. aruanus* (n = 12) – Clean *P. moluccensis* (n = 12)	-0.0108	0.0038	0.7184
		Clean *D. aruanus* (n = 12) – Clean No fish (n = 12)	-0.0076	0.0070	0.9999
		Clean *D. aruanus* (n = 12) – Sediment *D. aruanus* (n = 11)	-0.0066	0.0083	0.9995
		Clean *D. aruanus* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.0076	0.0071	0.9999
		Clean *D. aruanus* (n = 12) – Sediment No Fish (n = 12)	-0.0122	0.0024	0.3661
		Clean *P. moluccensis* (n = 12) – Clean No Fish (n = 12)	-0.0041	0.0105	0.7881
		Clean *P. moluccensis* (n = 12) – Sediment *D. aruanus* (n = 11)	-0.0031	0.0118	0.5307
		Clean *P. moluccensis* (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.0040	0.0106	0.7763
		Clean *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.0087	0.0059	0.9930
		Clean No Fish (n = 12) – Sediment *D. aruanus* (n = 11)	-0.0063	0.0086	0.9977
		Clean No Fish (n = 12) – Sediment *P. moluccensis* (n = 12)	-0.0073	0.0074	1.0000
		Clean No Fish (n = 12) – Sediment No Fish (n = 12)	-0.0119	0.0027	0.4381
		Sediment *D. aruanus* (n = 11) – Sediment *P. moluccensis* (n = 12)	-0.0085	0.0064	0.9982
		Sediment *D. aruanus* (n = 11) – Sediment No Fish (n = 12)	-0.0132	0.0017	0.2252
		Sediment *P. moluccensis* (n = 12) – Sediment No Fish (n = 12)	-0.0119	0.0026	0.4249

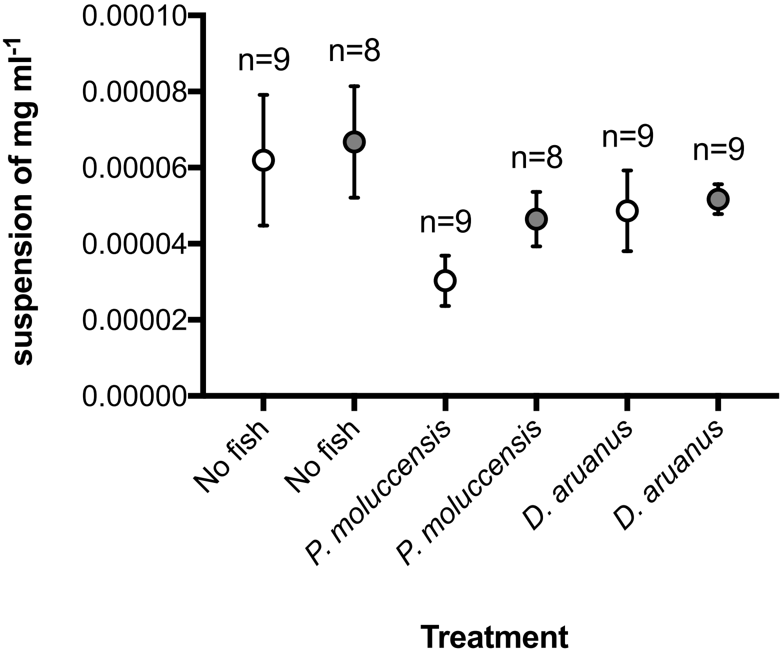

Figure S4.6 Average suspended sediments (mg ml^{-1}) per treatment in the manipulative sediment experiment. No sediment treatments are displayed with white dots and with sediment added are displayed with grey dots. Half of the total coral colonies were exposed to sediment treatments and treatment sample sizes analysed (n) are displayed above points.

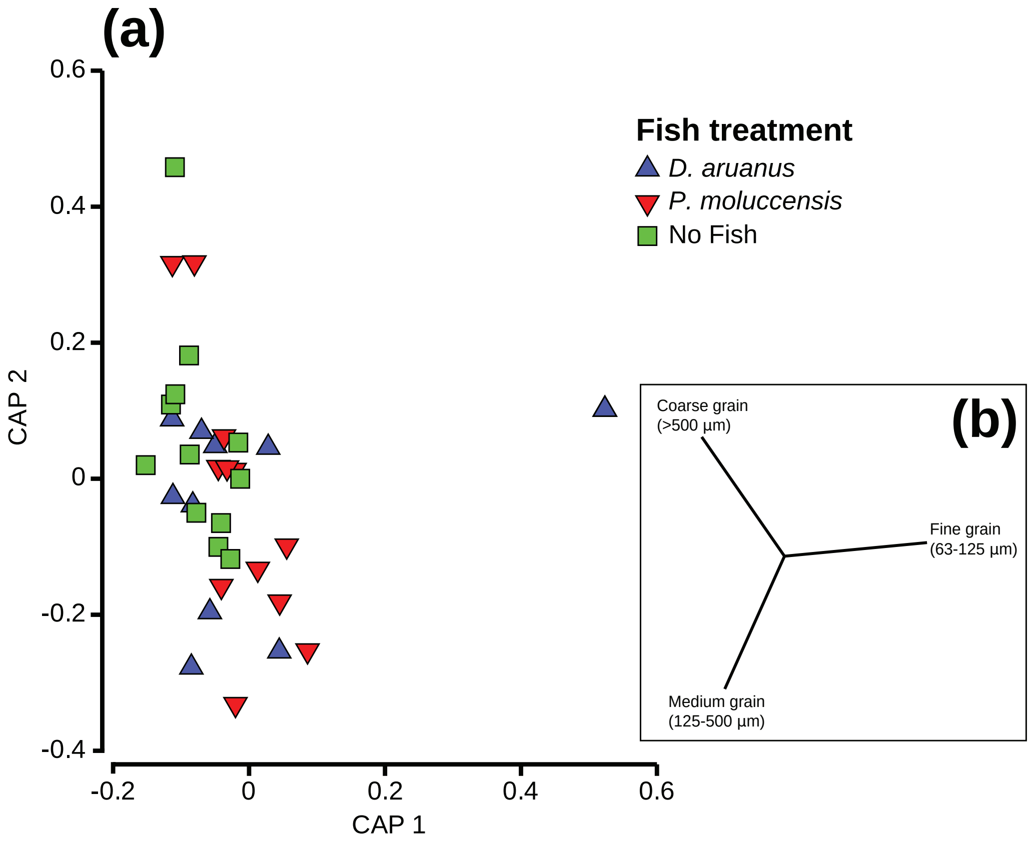

Figure S4.7 (a) Canonical analysis of principal (CAP) coordinates ordination based on a Euclidean distance matrix of standardised grain size distribution data from sediments remaining on coral colonies under different fish treatments (No fish, *D. aruanus*, and *P. moluccensis*). **(b)** Vectors show the relationship among sediment grain size fractions (µm) and how they influence the position of data points in the CAP. Vectors were calculated using a multiple correlation model.

APPENDIX S5 – Extended laboratory and field analysis

Supplemental Text S5.1: Aquaria experimental bleaching field recovery

Fish and colonies were monitored for 1 week upon being returned to the field and again at six-months post-experiment. There was a rapid decline of fish on experimentally occupied colonies that were placed 1-2 m off the surrounding patch-reefs, due to predation (via *P. leopardus*, personal observation) and movement to adjacent healthy corals. Rapid decline of fish density on these manipulated coral patches following fish relocation is common due to short-term processes and adjustment to novel habitat features (Lassig (1976). At six months post experiment 45% of corals 'experimentally occupied corals' were still occupied with *D. aruanus* (including newly settled recruits). Of all the experimental colonies, irrespective of bleaching status or previous fish treatment, over 72% were occupied by *D. aruanus* or additional damselfishes from the surrounding area (mainly, *P. amboinensis* and *P. moluccensis*). At six-months post experiment, February 2016, experimental *P. damicornis* corals were already subject to bleaching conditions in the field. As significant resident fish shuffling, displacement, and recruitment had occurred over six months, original fish treatment categories were confounded. Of the original experimental colonies, 40% exhibited mortality, covered in filamenous algae in February 2016; this could be due to delayed effects of experimental treatment, increases in mortality commonly observed in dislodged corals (Ward S 1993), or onset of the field beaching. Of these dead colonies, half contained small resident damselfish. 84% of still alive experimental colonies were inhabited by fishes, 43% of which had *D. aruanus* present. Using new fish treatment categories based on fish position in February 2016, alive *P. damicornis* colonies with fish present displayed higher mean F_V/F_M values (based on 6 replicates over two non-sequential nights) than colonies without fish, (ANOVA: $F_{1,154} = 0.0686$, $p = 0.0079$). When regrouping the colonies into, with only *D. aruanus* present, and no *D. aruanus* present (irrespective of other fish present), colonies with *D. aruanus* also displayed higher mean F_V/F_M values (ANOVA: $F_{1,154} = 0.05175$, $p = 0.0215$,

Figure S5.2 in Appendix S5). Here, the difference in photosynthetic efficiency, cannot be solely attributed to fish presence, as previous occupation, experimental temperature treatments, and current bleaching onset could potentially confound results.

Literature cited

Lassig B (1976) Filed observations on the reproductive behavior of Paragobiodon spp. (Osteichtyes: Gobiidae) at Heron Island, Great Barrier Reef. Marine Behavioral Physiology 3:283-293

Ward S (1993) The effect of damage on the growth, reproduction, and storage of lipids in the scleractinian coral, *Pocillopora damicornis* (Linnaeus) Journal of Experimental Marine Biology and Ecology 187:193-206

Supplemental Text S5.2: Coral tissue analysis

One coral fragment per colony, approximately 6cm in length was collected from each experimental colony at the end of the acclimation, stress, and recovery phases. Fragments (n = 114 in total) were subsequently frozen with liquid nitrogen and transported to James Cook University for analysis. Tissue was removed from the skeleton using compressed air and 0.45 µm filtered seawater, collected, and homogenized. The resulting tissue 'slurries" were divided into aliquots for protein assays (1 ml), symbiont counts (0.9 ml of 'slurry' and 0.1 ml of formaldehyde, to preserve samples), total chlorophyll (5 ml), and tissue biomass (8 mL). Coral skeletons were retained to quantify fragment surface area using a wax coating technique (Stimson and Kinzie 1991; Vytopil and Willis 2001) as:

$$Surface\ area\ (cm^2) = Z\ x\ W \qquad (1)$$

Where Z is the regression equation for the standard calibration curve (cm^2 x mg^{-1}) and W is the difference in weight between wax coating (mg). *Symbiodinium* density was determined by 6 replicate counts of each homogenized (IKA T10 basic, Ultra Turrax Homogenizer) sample (1ml) using an improved Neubauer Haemocytometer (for 1 minute, Hirschmann EM, 0.100mm). Symbiodinium (zooxanthellae) density was calculated as follows:

$$\#\ symbiodinium\ cc^{-3} = N\ x\ 16^4\ x\ dilution\ factor \qquad (2)$$

with N as the mean number of zooxanthellae counted in 25-medium-squares of the Hemocytometer. Chlorophyll was extracted by adding 4mL acetone to each sample and vortexing it for 30s to mix. Total chlorophyll (chl *a* + chl *c*, µg/ml^{-1}) content was measured using spectrophotometry on a SpectraMex Plus^{384} Microplate reader (Molecular Devices). Total chlorophyll (chl *a* + chl *c*, µg/ml) was calculated (Jeffrey and Humphrey 1975) as:

$$Chl\ a\ (ug/ml) = 11.43\ (A_{663} - A_{750}) - 0.64\ (A_{630} - A_{750}) +$$

$$Chl\ c\ (ug/ml) = -3.63\ (A_{663} - A_{750}) + 27.09\ (A_{630} - A_{750})$$

(3)

where A_{630}, A_{663}, and A_{750} are the absorbance at 630, 663, and 750nm. As coral fragments were not the sample size, measurements of *Symbiodinum* density and total chlorophyll were normalized by surface area and are reported per cm^2. Total protein content (mg cm^{-2}) was extracted using spectrophotometry from fragments in a buffered solution and quantified using the Red 660 protein assay and using bovine serum albumen protein (BAS) as a standard curve (Palmer et al. 2009)). The tissue biomass of the coral tissue was determined using the ash-free dry weight (AFDW) method by placing 8ml of the coral tissue 'slurry' into a freeze dryer (Christ, Alpaa 1-1 LO plus)) for 48 hours and then incinerated in a muffle furnace (Yokogawa model UP150 muffle furnace) at 550°C. The AFDW was calculated by subtracting the ash-weigh (AW) from dry weight (DF) and normalized per fragment surface area (Leuven et al. 1985). All samples were allowed sufficient time to cool (~7 days) prior to measuring AW.

Literature cited

Jeffrey SW, Humphrey GF (1975) New spectrophotometric equations for determining chlorophylls *a*, *b*, c_1, and c_2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie de Pflanzen 167:191-194

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Palmer CV, Modi CK, Mydlarz LD (2009) Coral fluorescent proteins as antioxidants. PLoS ONE 4: e7298.v doi:10.1371/journal.pone.0007298

Stimson J, Kinzie RA (1991) The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. Journal of Experimental Marine Biology 15:63-74

Vytopil E, Willis BL (2001) Epifaunal community structure in *Acropora* spp. (Scleractinian) on the Great Barrier Reef: implications of coral morphology and habitat complexity. Coral Reefs 20:281-288

Table S5.1 Mini pulse-amplitude modulator (MINI-PAM, Heinz Walz GmbH Germany), settings used for all F_V/F_M and rapid light curve (RLCs) measurements.

PAM setting	**Value**
Measurement intensity (MI)	8
Saturation intensity (SI)	8
Saturation width (SW)	0.8
Actinic intensity (AI)	5
Actinic width (AW)	0:30
Actinic light factor (AF)	1
Gain (G)	8
Damp (D)	2
ETR factor (EF)	0:84
F_o	0
Clock width (CW)	0:30
Clock item (CI)	1
Light curve width (LW)	0:10
Light curve intensity (LI)	3
Induction curve delay (ID)	0:40
Induction curve width (IW)	0:20
Temp offs (DO)	0:00
Temp gain (DG)	1.00
Light offs (LO)	0:00
Light Gain (LG)	1.00
Auto-Zero (FO	*60

*Auto-zero value was determined using the auto-zero setting along the side of the aquaria bucket in which the coral samples were kept, a non-photosynthetic surface, at the beginning of the sampling period.

Table S5.2 Results of multiple selected comparisons (n=12) as a post hoc test for the linear mixed effects model of the effects of phase, temperature, and fish presence (*D. aruanus*) on *P. damicornis* colonies. Each of the 12 comparisons are completed for four coral tissue parameters: *Symbiodinium*, total chlorophyll, total proteins, and tissue biomass. For each comparison the upper and lower confidence intervals and adjusted p-value is listed.

Coral Tissue	Phase	Comparison	CI lower	CI upper	Adjusted p-value
Symbiodinium	*Acclimation*	AAF vs. AHF	-0.17585	0.59946	0.699
		AAF vs. AAN	-0.24763	0.54783	0.877
		AHF vs AHN	-0.21795	0.57750	0.998
		AHF vs AAN	-0.44937	0.32595	0.989
		AAF vs AHN	-0.41969	0.35563	0.806
		AAN vs AHN	-0.36806	0.42740	0.999
	Stress	SHF vs. SHN	-0.05449	0.72083	0.265
		SAF vs SHF	0.30737	1.08268	**0.001**
		SAF vs SAN	-0.12215	0.67331	0.450
		SAN vs SHN	0.35488	1.15034	**< 0.001**
	Recovery	RHF vs RHN	0.11205	0.88737	**0.021**
		RAF vs RAN	0.49213	1.28759	**< 0.001**
Total chlorophyll	*Acclimation*	AAF vs. AHF	-0.48496	1.08269	0.874
		AAF vs. AAN	-0.34512	1.26297	0.669
		AHF vs AHN	-0.32092	1.28904	0.966
		AHF vs AAN	-0.62108	0.94118	0.977
		AAF vs AHN	-0.59863	0.96901	0.631
		AAN vs AHN	-0.77891	0.82918	1.000
	Stress	SHF vs. SHN	-0.11038	1.46360	0.262
		SAF vs SHF	0.42775	2.00174	**0.008**
		SAF vs SAN	-0.17445	1.42768	0.342
		SAN vs SHN	0.46366	2.06580	**0.007**
	Recovery	RHF vs RHN	0.40809	1.97573	**0.005**
		RAF vs RAN	0.55955	2.16765	**< 0.002**
Total proteins	*Acclimation*	AAF vs. AHF	-0.16955	0.363537	0.888

		AAF vs. AAN	-0.25686	0.290069	0.999
		AHF vs AHN	-0.36542	0.181513	0.945
		AHF vs AAN	-0.34694	0.186149	0.932
		AAF vs AHN	-0.45549	0.077594	0.909
		AAN vs AHN	-0.38202	0.164911	0.860
	Stress	SHF vs. SHN	-0.19569	0.337395	0.939
		SAF vs SHF	0.00117	0.534255	**0.046**
		SAF vs SAN	-0.15045	0.396483	0.765
		SAN vs SHN	-0.05792	0.489016	0.337
	Recovery	RHF vs RHN	-0.00015	0.386359	0.596
		RAF vs RAN	-0.00019	0.361128	0.774
Tissue biomass	*Acclimation*	AAF vs. AHF	-0.00036	0.00020	0.941
		AAF vs. AAN	-0.00046	0.00017	0.678
		AHF vs AHN	-0.00054	0.00001	0.652
		AHF vs AAN	-0.00037	0.00020	0.938
		AAF vs AHN	-0.00045	0.00012	0.331
		AAN vs AHN	-0.00037	0.00021	0.942
	Stress	SHF vs. SHN	-0.00022	0.00035	0.955
		SAF vs SHF	-0.00025	0.00032	0.992
		SAF vs SAN	-0.00038	0.00020	0.904
		SAN vs SHN	-0.00009	0.00049	0.478
	Recovery	RHF vs RHN	0.00039	0.00015	**0.012**
		RAF vs RAN	-0.00034	0.00025	0.941

Table S5.3 Comparison of linear (mx, b) and non-linear (mx, x0, w, a) regression equation and coefficients for photosynthetic efficiency (F_V/F_M) during Acclimation/Stress phase and Recovery phase for coral colonies under ambient and heated temperatures, and with and without fish treatments.

Phase	Temperature	Fish Treatment	Equation
Acclimation & Stress	Ambient	Fish	$F_V/F_M = 0.0002x + 0.6929 \mid R = 0.0302$
Acclimation & Stress	Ambient	No fish	$F_V/F_M = -7E-5x + 0.6851 \mid R = 0.0053$
Acclimation & Stress	Hot	Fish	$F_V/F_M = (0.13019x + 0.54820) - (0.13019/1+\exp(-(\text{time}-27.86174)/2.52201))$
Acclimation & Stress	Hot	No fish	$F_V/F_M = (0.35775x + 0.30696) - (0.35775/1+\exp(-(\text{time}-31.91131)/2.73373))$
Recovery	Ambient	Fish	$F_V/F_M = 0.0016x+0.6234 \mid R=0.67068$
Recovery	Ambient	No fish	$F_V/F_M = 9E-6x + 0.6809 \mid R = 9.8E-5$
Recovery	Hot	Fish	$F_V/F_M = -0.0013x + 0.6169 \mid R = 0.34805$
Recovery	Hot	No Fish	$F_V/F_M = -0.0123x + 0.9074 \mid R = 0.86893$

Table S5.4 Comparison of regression models testing the effects of temperature (ambient: 25°C or hot: 32°C) and fish presence (fish or no fish) on *P. damicornis* photosynthetic efficiency (F_V/F_M) through fitting the data points for each individual colony within treatments for F_V/F_M associated with Acclimation and Stress experimental periods. Akaike's information criteria (AIC) and AIC differences (ΔAIC) were calculated per model selection practice of Burnham and Anderson (2002) and Hoogenboom et al. (2011). Constructing the model with means (mean models presented in results), allows for regressions to explain a greater amount of variation in the data, compared with using all the individual points, but reduced statistical power. Data fitted through individual points yield similar results as mean models.

No.	Model	N	AIC	delta AIC	wAIC
1	All data	700	-1378.48	1011.10	0.00
2	By temperature treatment	700	-2258.90	130.67	0.00
3	By fish treatment	700	-1466.06	923.52	0.00
4	By temperature treatment by fish treatment	700	-2389.58	0.00	1.00

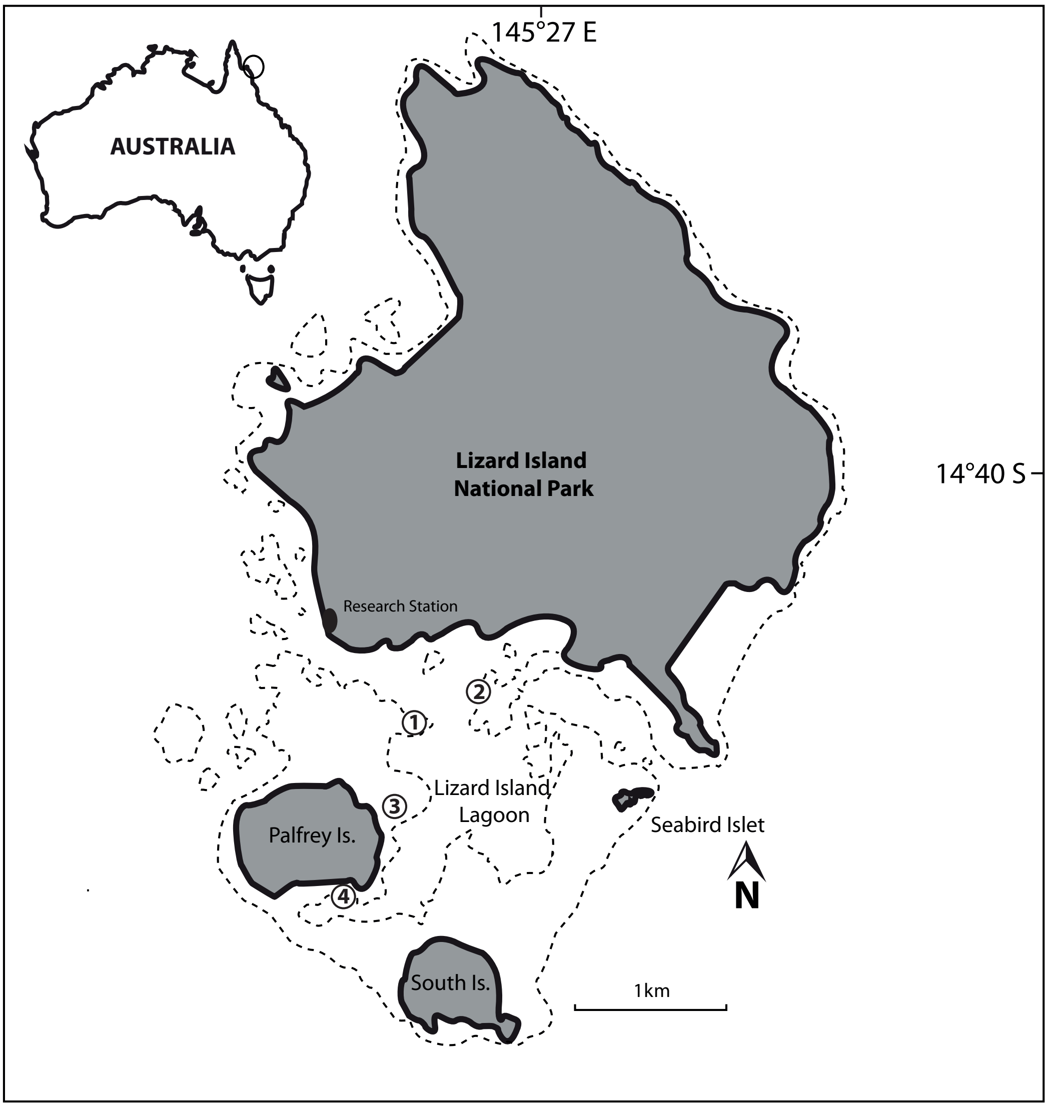

Figure S5.1 Location of four *in-situ* bleaching colonies (*S. hystrix*) within the Lizard Island Lagoon.

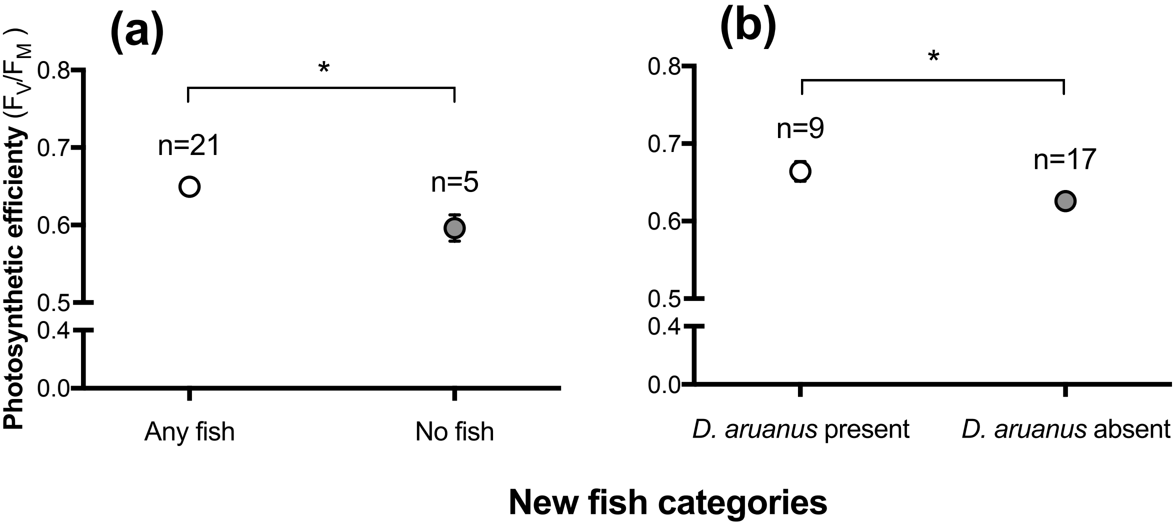

Figure S5.2 Differences in photosynthetic efficiency (F_V/F_M) of *P. damicornis* corals returned to the field, six months post aquaria bleaching experiment (February 2016, when GBR bleaching event was underway). **(a)** F_V/F_M of coral colonies under new fish categories due to movement and additional fish species present, irrespective of past experimental treatments of heat and fish presence. New fish category includes aggregating fish (*D. aruanus*, *D. reticulatus*, *P. ambionensis*, and *P. moluccensis)* present during multiple observations. No fish SE = 0.0170, and Any fish SE = 0.0087. (b) F_V/F_M of coral colonies under category of only *D. aruanus* still present. *D. aruanus* absent SE = 0.0099, and *D. aruanus* present SE = 0.0126. (*) denotes a significant difference between fish treatments and *error bars* show SE. One-way analysis of variance (ANOVA) were performed on PAM data, 6-months post-experiment test for differences in F_V/F_M levels in field samples of *P. damicornis*. Data for F_V/F_M analysis met assumptions of normality (Shapiro-Wilks test) and homogeneity of variance (Barlett's test).

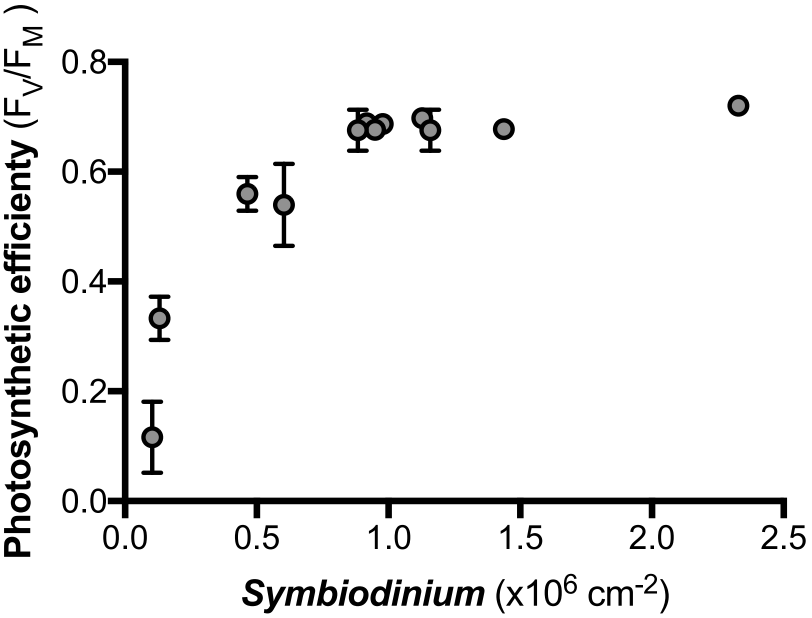

Figure S5.3 Relationship between symbionts (*Symbiodinium* density ×10^6 cm^{-2}) and photosynthetic efficiency (F_V/F_M) of *P. damicornis* colonies at three different time periods: Acclimation (day 5), Stress (day 37) and Recovery (Day 66), in aquaria experiment. Linear regression analysis (Pearson's correlation $r^2 = 0.5468$, $F_{1,10} = 12.07$, $p = 0.0060$, $y = 0.2266x + 0.378$) suggests direct correlation between *Symbiodinium* and photosynthetic efficiency in experimental corals.

APPENDIX S6: Author's publication list

Publications arising from this thesis:

***Chase TJ**, Pratchett MS, Frank GE, Hoogenboom MO **(2018)** Coral-dwelling fish moderate bleaching susceptibility of coral hosts. PLOS ONE 13:e0208545 doi: 10.1371/journal/pone.0208545*

TJC, MSP, and MOH designed experiments. TJC and GEF conducted experiments. TJC completed the data analysis, and TJC and MOH interpreted the data. TJC wrote the manuscript; MSP and MOH edited the manuscript.

***Chase TJ**, Pratchett MS, Hoogenboom MO **(in press)** Behavioural trade-offs and habitat association of coral-dwelling damselfishes (family Pomcaentridae). Marine Ecology Progress Series doi:10.3354/meps13167*

TJC and MOH designed experiments. TJC conducted experiments, completed data analysis, and wrote the manuscript. MSP and MOH edited the manuscript.

***Chase TJ**, Hoogenboom MO **(in press)** Differential occupation of available coral hosts by coral-dwelling damselfishes (Pomacentridae) on Australia's Great Barrier Reef. Diversity*

TJC and MOH designed the study. TJC, conducted the fieldwork and data collection. TJC and MOH completed the data analysis, interpreted the data, and wrote the manuscript.

Chase TJ**, Pratchett MS, McWilliam MJ, Hein MY, Tebbett SB, Hoogenboom MO (2nd revision***) Fishes alleviate the impacts of sediments on host corals. Royal Society Open Science*

TJC, MSP, and MOH designed the study. TJC, MJM, and MYH conducted the fieldwork and data collection. TJC and SBT completed the data analysis and TJC and MOH interpreted the data. TJC, MSP, and MOH, wrote the manuscript.

Additional publications arising during PhD Candidature:

Hughes TP, Kerry JT, Baird AH, Connolly SR, **Chase TJ**, Dietzel A, Hill T, Hoey AS, Hoogenboom MO, Kerswell A, Madin JS, Meog A, Paley A, Pratchett MS, Torta G, Woods RM **(2019)** Global warming impairs stock-recruitment dynamics of corals. Nature 563:387-390 doi: 10.1038/s41586-019-1081-y

McWilliam M, **Chase TJ**, Hoogenboom MO **(2018)** Neighbour diversity regulates the productivity of coral assemblages. Current Biology 28:3634-3639 doi:10.1016/j.cub.2018/09/025

Chase TJ*, Nowicki JP*, Coker DJ **(2018)** Diurnal foraging of a wild coral reef fish, *Parapercis australis*, in relation to late-summer temperatures. Journal of Fish Biology 93:158-163 doi: 10.1111/jfb.13644 *Indicates co-first authorship

Dornelas M, Antao LH, Moyes F, Bates AE, Magurran, AE and BioTIME consortium (200+ authors, including **Chase TJ**) **(2018)** Bio-Time: A data base of biodiversity time

series for the Anthropocene. Global Ecology and Biogeography 7:760-786 doi:10.1111/geb.12729

Hoogenboom MO, Frank GE**, Chase TJ**, Jurriaans S, Álvarez-Noriega M, Peterson K, Critchell K, Berry KLE, Nicolet KJ, Paley SA **(2017)** Environmental drivers of among-species variation in bleaching severity of Acropora corals during an extreme thermal anomaly. Frontiers in Marine Science 4:376 doi:10.3389/fmars.2017.00376

Hoogenboom MO, Frank GE, Blowes SA, **Chase TJ**, Zawada KJA, Dornelas M (**2015)** Disparity between projected geographic ranges of rare species: a case study of *Echinomorpha nishihirai* (Scleractinia). Marine Biodiversity Records 8; e147 doi:10.1017/S1755267215001141