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Determinants of resource specialisation and its ecological consequences for the corallivorous filefish, *Oxymonacanthus longirostris*

Thesis submitted by

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Statement on the contribution of others

This thesis includes collaborative work with my supervisors Professor Geoffrey Jones and Professor Philip Munday, as well as Ian McLeod and Professor Douglas Chivers. I led these collaborative projects and experimental design, data collection, technical analysis, and ecological interpretation were primarily conducted by me. My co-authors provided intellectual guidance, financial support, advice on experimental design, assistance with editing, and assistance during fieldwork.

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The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council (NHMRC) Australian Code of Practice for the Care and Use of Animals for Scientific Purposes, 7th Edition, 2004 and the Qld Animal Care and Protection Act, 2001. The proposed research study received animal ethics approval from the JCU Animal Ethics Committee. Approval Numbers A1920 and A1399.

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General abstract

All organisms are dependent upon their habitat for the resources necessary for survival and reproduction, but they vary immensely in the degree to which they are specialized on particular resources. Habitat specialists appear to evolve in environments where preferred resources are stable, however specialists are vulnerable to extinction should these resources become scarce. Given global declines in the quantity and quality of available habitats, it is critical to understand why species are specialised, and what resources they are specialized on, in order to determine their vulnerability to habitat loss. Coral reefs are home to a diverse assemblage of coral-associated organisms and of these, corallivorous fishes are among the most specialised. One such species, the harlequin filefish, *Oxymonacanthus longirostris*, is distributed throughout the Indo-Pacific in areas of high coral cover. This study investigated the ecology of *O. longirostris* to determine how specialised it is, the roles of prey quality and predation pressure as drivers of specialisation, and the consequences of being a coral specialist in light of increasing coral degradation.

Most animals consume a narrower range of food resources than is potentially available in the environment. **Chapter 2** examined the drivers of this prey selection by testing the consequences of prey preferences for key fitness-related parameters. While the diet of *O. longirostris* was dominated by the most abundant coral species, *Acropora nobilis*, fish appeared to preferentially feed on rarer acroporids, such as *Acropora millepora*. Choice experiments confirmed strong preferences for these rarer corals, suggesting diet is constrained by availability of different coral species. In a feeding experiment, reproductive pairs fed on non-preferred corals exhibited dramatic declines in condition and reproductive output compared with those fed preferred corals. These experiments suggest that fish distinguish between available corals based on their intrinsic value as prey, that reproductive success is dependent on the presence of particular coral species, and that differential loss of preferred corals could have significant consequences for population success.

Foraging theory predicts that preferred prey should maximise energetic reward relative to the energy expended to access, capture, and consume prey. However, the relative roles of differences in the nutritive value of prey and costs associated with differences in prey accessibility are not always clear. **Chapter 3** investigated within-colony feeding in *O. longirostris* to establish if prey accessibility determines foraging patterns. *O. longirostris* exhibited non-uniform patterns of foraging in the field, feeding midway along branches. On

simulated corals, fish replicated this pattern when food accessibility was equal along the branch. However, when food access varied, fish consistently modified their foraging behaviour, feeding where food was most accessible. When foraging patterns were compared with coral morphology, fish preferred larger polyps and less skeletal protection. Consequently, it appears that patterns of prey selectivity are influenced by coral morphology, with fish preferring corals with structural characteristics that increase prey accessibility.

A selective coral diet may further benefit *O. longirostris* by reducing predation risk. Many organisms primarily interact with their surroundings using non-visual sensory systems and may have evolved mechanisms to 'blend in' with chemical components of their habitat. One potential mechanism of camouflage is through the sequestering of dietary elements, causing a consumers odour to chemically match the odour of its prey. **Chapter 4** tested for diet-induced chemical crypsis in *O. longirostris* by using the olfactory preferences of coral-obligate crabs to determine the effect of coral diet on fish odour. Crabs strongly preferred the odour of filefish fed their normal coral host, suggesting coral-specific dietary elements that influence odour are sequestered. In behavioural trials, predatory cod were less attracted to filefish odour presented alongside the coral it had been feeding on, suggesting reduced detectability. This evidence suggests that a close coupling between diet and habitat can form an effective anti-predator strategy.

Many animals select a habitat from the range of those available, driven by factors such as food quality or shelter availability, and these preferences may have consequences for the distribution and abundance of populations. **Chapter 5** examined how the distribution and abundance of *O. longirostris* relates to coral architecture and diversity. The main drivers of distribution and abundance among reefs were coral species richness and availability of branching coral. Feeding territories had a higher percentage of *Acropora* coral than surrounding habitat. In addition, feeding territories had a higher percentage of the structurally important branching coral, *A. nobilis*, and the preferred prey species, *A. millepora*. Pair-wise choice experiments in which both structural complexity and coral tissue quality were independently manipulated showed that habitat choice was primarily based on shelter characteristics. These results suggest species-diverse coral habitats, which provide structural complexity along with nutritionally important prey, may be essential for population persistence.

While extinctions of marine species are infrequent, local extinctions are becoming common. Yet, the role of habitat degradation and resource specialisation in explaining local extinction is

still poorly understood. On coral reefs, coral bleaching is an increasingly frequent cause of coral mortality that can result in dramatic changes to coral community composition. **Chapter 6** documents the local extinction of *O. longirostris* following a mass bleaching event. Local extinction occurred on reefs that lost all colonies of the key prey species, *A. millepora*, even though overall coral cover remained high. In an experimental test, fish continued to select bleached *A. millepora* over non-preferred species, irrespective of their condition. These results suggest that behavioural inflexibility may limit the ability of specialists to cope with even subtle changes to resource availability.

This study demonstrates that *O. longirostris* is a highly specialised species that has evolved precise behavioural mechanisms to exploit the corals with which it associates. Its reliance on a relatively limited suite of corals leaves it highly vulnerable to climate change and other anthropogenic disturbances that threaten to reduce coral cover and abundance. This study also highlights how variable corals can be with regards to their value as prey and habitat. It appears that habitats that contain a specific combination of corals may be necessary for the survival and persistence of *O. longirostris*. When assessing the vulnerability of such highly specialised species, it is important to understand and evaluate the full range of their critical resources.

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Chapter 1: General introduction

All organisms depend on their habitat for the resources needed for survival and reproduction. Habitat is therefore directly linked to a range of critical ecological patterns and processes, ranging from an individual's condition and fitness (Huey 1991; Franklin et al. 2000), to species distributions and patterns of abundance (Crowe and Underwood 1998), and to the structure of communities and ecosystems (Lawton 1983; Tews et al. 2004; Hortal et al. 2009). Most species occur within a characteristic habitat, although the degree to which an organism is specialised and dependent on this habitat can vary immensely. For essential resources, such as food or shelter, an organism exists somewhere along an axis from an extreme resource specialist to a generalist (MacNally 1995). Often an organism will be highly specialised with regards to certain aspects of its ecology and highly generalised in others. However, the underlying factors that drive the evolution of specialisation or generalisation for a specific trait are often unknown. Determining the degree of specialisation, the underlying factors that drive specialisation for specific resources, and the effects of resource specialisation on key processes such as reproduction, distribution, and abundance will further our understanding of how organisms interact with their habitats, as well as their potential vulnerability to environmental change.

1.1. Determinants of resource specialisation

Resource specialists frequently appear to evolve when they have stable access to preferred resources and they typically have physical and behavioural adaptations that allow them to maximise the efficiency with which they can exploit these resources (Futuyma and Moreno 1988; Forister et al. 2011). Therefore, when access to preferred resources is not limited, a specialist could be expected to be in better condition, have a greater reproductive output, or display higher survival rates than organisms without these adaptations, giving specialists a competitive advantage over more generalist species occupying the same habitat (Caley and Munday 2003). However, these adaptations may disadvantage an organism if preferred resources become scarce and they reduce its ability to exploit alternatives. Under these conditions, specialists that can switch to less preferred resources may suffer sub-lethal effects, reducing their relative competitiveness (Berumen et al. 2005). However, those organisms that are specialised to the point that they are unable to use alternative resources may suffer population declines and are at a higher risk of extinction (Gaston and Blackburn 2000; Biesmeijer et al. 2006). By examining the determinants of specialisation in an organism, predictions can be made regarding its vulnerability to population decline and extinction under suboptimal conditions.

Habitats contain a range of potential resources that can be exploited. The underlying ecological and evolutionary mechanisms that promote specialisation for a limited suite of those available are not well understood. Adaptation to exploit resources more efficiently may act as a driving force. For instance, the koala, *Phascolarctos cinereus*, has evolved behavioural, physiological, and morphological traits that enable it to feed on eucalypt leaves, an abundant resource that is unpalatable for most other species (Higgins et al. 2011). Specialists may also evolve independently to use the narrowest range of resources necessary to maximise energy intake or reduce predation pressure, which may explain why organisms within a specific habitat will often select similar resources. This can be observed in tropical forests where many frugivorous species will target the same types of fruit despite potential competition for these resources (da Silva and de Melo 2013).

Competition for resources is often proposed as a key driving force in the evolution of specialisation in organisms (Futuyma and Moreno 1988; Bolnick et al. 2003; Johnson et al. 2009). For any organism, the optimal behavioural response to the presence of a direct competitor that lowers the abundance of a preferred resource is to either widen the breadth of resources used, or to restrict resource use to a less exploited alternative (Futuyma and Moreno 1988; Holbrook and Schmitt 1992). For this reason, organisms may specialise on different resources in order to reduce the strength of interspecific and intraspecific competition i.e. resource partitioning (Poisot et al. 2011). If access to several resources within an environment is limiting, then trade-offs in the ability to use each resource may promote coexistence between potential competitors (Miller et al. 2005). Where competitive pressure remains high, these trade-offs may propel the further evolution of behavioural or morphological adaptations to optimise the efficiency with which a specific resource can be exploited (Hulsey and Garcia De Leon 2005; Larsen et al. 2006).

However, the growing body of empirical evidence indicating the importance of interaction complexity in ecological systems (Werner and Peacor 2003; Schmitz et al. 2004; Strauss and Irwin 2004) suggests that many of the indirect and conjunctional processes inherent in complex, multispecies interactions i.e. community complexity, could act as driving forces in the evolution of specialisation (Sandoval and Nosil 2005; Lankau and Strauss 2008; Kaminski et al. 2010). Interactions resulting from specialisation along one axis may in themselves act as agents for further specialisation along multiple axes (Forister et al. 2011). For example, a predator may be generalised with regards to an abiotic gradient, but is optimised to feed on a prey that is restricted to habitats within a narrow abiotic range. If dietary specialisation thereby restricts the predator to these habitats, it may adapt to the abiotic gradient optimal for its prey, essentially becoming specialised along both resource and abiotic axes. Interaction complexity can thereby increase an organism's chances of encountering trade-offs or favourable conditions that can trigger specialisation (Singer and Stireman 2005).

For any organism, reducing mortality risk is critically important as death immediately reduces fitness potential to zero. As a key source of mortality is via predation, vulnerable species may select habitats that minimise the ability for predators to locate, capture, and consume them (Lima and Dill 1990). Many species have evolved adaptations that allow them to inhabit structurally complex or defended habitats. For example, the northern bobwhite, *Colinus virginianus*, often builds its nest in amongst the branches of cacti, relying on the sharp spines to deter potential predators (Hernández et al. 2003). Many species have also evolved camouflage mechanisms that allow them to avoid detection in specific habitats (Stevens and Merilaita 2009). Many of these mechanisms, such as crypsis, rely on context to be effective (Akino et al. 2004; Ruxton 2009), which limits organisms to specific habitats if any benefit is to be achieved, and thus reinforces patterns of specialisation. Understanding the ecological basis of specialisation and the drivers of resource selection is critical to predict responses to environmental change (Laurance 1991; Travis 2003)

1.2. Habitat degradation and extinction risk

Habitats worldwide are becoming increasingly degraded due rapid increases in direct and indirect anthropogenic disturbance, resulting in a massive global decline in both the quantity, and quality of available habitat (Western 2001; Brooks et al. 2002). This degradation is expected to have highly detrimental effects for associated fauna and flora, with even conservative estimates suggesting at least ~18% species are 'committed to extinction' globally (Thomas et al. 2004). Specialist species are expected to be the most vulnerable to habitat loss and, while these species may have once been at a competitive advantage in their preferred habitats, they may now face population declines, shifts in their distribution, and possible extinction as habitats rapidly change (Clavel et al. 2010). In contrast, generalist species may be less impacted by habitat change and degradation because of their ability to use alternative resources (Devictor et al. 2008) A decline of specialist species from a variety of disparate taxa has already been seen, with biological communities associated with disturbed or degraded habitats often now dominated by generalist species (Fisher et al. 2003; Julliard et al. 2004; Rooney et al. 2004).

Direct disturbances, such as land clearing or sea bed trawling, can result in the rapid loss of important environmental characteristics that promote biodiversity, such as structural complexity (Thrush et al. 2006). In many environments, the majority of habitat structure and diversity is in itself provided by living organisms, for example trees within forests or macroalgae within temperate reef ecosystems (Steneck et al. 2002; Williams et al. 2002). The decline of these habitat forming organisms can have a major impact on associated communities, especially habitat-specialists that often depend on these specific resources (McKinney and Lockwood 1999; Clavel et al. 2010). The indirect effects of climate change are also becoming increasingly apparent. Many habitat-forming species are themselves specialised to a degree, with regards to resource requirements or range of abiotic tolerance (i.e. Smale and Wernberg 2013), and so they are vulnerable to changes in environmental conditions. Predicted climate change effects, such as increasing mean temperatures and a heightened risk of extreme weather events, are expected to have dramatic and devastating impacts on both terrestrial and aquatic ecosystems, with habitat range shifts, habitat fragmentation, and increasing frequent large-scale disturbance expected (Walther et al. 2002). The net result of these impacts will be dramatic changes in the composition and abundance of biological communities.

1.3. Specialisation and habitat loss on coral reefs

One of the most biologically complex ecosystems on earth, coral reefs are home to an almost unmatched diversity of associated organisms (Reaka-Kudla 1997). Much of this diversity is directly linked to the complexity of the underlying habitat, formed by reef-building scleractinian corals (Stella et al. 2011; Jones et al. 2004). There is a high level of specialisation amongst mobile reef organisms, with many requiring corals, or even specific species of corals to provide essential resources (Stella et al. 2011; Cole et al. 2008). However, coral reefs only persist within a relatively narrow range of environmental parameters, which makes coral communities inherently vulnerable to changes to environmental conditions (Hoegh-Guldberg et al. 2007). Globally, coral reefs are in a long-standing state of decline due to a history of extensive anthropogenic exploitation and other forms of habitat degradation (Gardner et al.

2003; Hughes et al. 2003; Pandolfi et al. 2003; De'ath et al. 2012). The impacts of climate change on tropical marine systems will only exacerbate unfavourable conditions for coral growth and recovery. For instance, predicted tropical sea surface temperature increases will push corals towards their thermal tolerance thresholds (Hoegh-Guldberg 1999). Sustained thermal stress causes corals to bleach, expelling the photosynthetic zooxanthellae that provide much of their energetic requirements and leading to declines in condition, an increased susceptibility to compounding stressors such as disease, and extensive coral mortality. The ongoing decline of coral communities will have significant effects on the diversity of other organisms that depend on coral reef habitat, with coral specialists likely to be the most impacted (Jones et al. 2004; Stella et al. 2011).

While all corals are vulnerable to the predicted impacts of climate change and anthropogenic exploitation, not all coral taxa are equally susceptible to these impacts. For instance, complex branching corals from the genus *Acropora* are especially susceptible to coral bleaching (Marshall and Baird 2000), as well as ocean acidification (Albright et al. 2010), and mechanical damage during events such as storms (Madin et al. 2012). Changes in the proportional abundance of coral taxa following long term disturbance have already been reported in Moorea, where structurally complex *Acropora* communities were replaced with low complexity *Porites* dominated assemblages (Berumen and Pratchett 2006). As *Acropora* corals are a primary habitat forming species on reefs, the loss of these coral species, even if overall coral cover remains high, may have a considerable effect on biodiversity. In an experimental manipulation of coral diversity, Messmer et al. (2012) showed that high coral species richness corresponds with high fish species richness, with some coral species disproportionately important in promoting high fish diversity. For these reasons there in a need to define the relationships that exist between corals and associated organisms and how the underlying coral habitat affects the ecology and biology of these species.

Coral reefs are home to a great diversity of fish species that are dependent on coral habitat for food, shelter and living space (Pratchett et al. 2008a). Access to live corals is of critical importance with approximately 10% of fishes relying on corals directly as food or shelter (Jones et al. 2004; Coker et al. 2014) and an estimated 65% using live corals during settlement (Jones et al. 2004; Garpe and Öhman 2007). Corals can also play an important role in behavioural processes, including habitat selection (Gardiner and Jones 2010; Bonin 2012) and mediating processes such as competitive and predator-prey interactions (Schmitt and Holbrook 2000; Kane et al. 2009; Johnson et al. 2011). The vital importance of live coral for reef-associated fishes becomes fully apparent with the loss of coral cover. For instance, a 90% decline in coral cover in Kimbe Bay, Papua New Guinea corresponded with declines in abundance in 75% of reef-associated fish species (Jones et al. 2004). The more specialised a species is, the more vulnerable it is to extinction following coral declines. For example, Munday (2004) found that declines in the abundance of several coral-dwelling goby species, following coral loss, reflected the extent to which they were specialised. These findings suggest there is a strong link between the level of coral specialisation and extinction risk.

1.4. Corallivorous fishes; specialisation and vulnerability

Some of the most specialised fishes on coral reefs are those species that feed on corals. While the majority of these species are facultative corallivores, with coral representing only a portion of the diet, many are obligate corallivores for which coral represents the primary food (Cole et al. 2008). Scleractinian corals represent a unique food source; they remain stationary, are often abundant, and are non-cryptic, and corallivorous fishes have developed a wide range of specialised strategies to exploit this resource. Many corallivorous species are selective between corals, to the genus or even species level (Cole et al. 2008). Foraging theory predicts that these preferred corals should represent superior food resources (Futuyma and Moreno 1988). While there is some evidence that feeding on preferred corals can increase growth and condition (Berumen et al. 2005; Berumen and Pratchett 2008), the relationship between coral diet and fitness potential is not known.

While many species selectively target specific corals, suggesting they are more valuable as prey (Pratchett 2007), strong correlations between prey selection and nutritional value have proven elusive (Pratchett 2013). Although these studies have generally assumed fishes feed on corals uniformly, there is evidence that significant biochemical and morphological variation can exist within a single coral colony (Fang et al. 1989). If fishes exhibit consistent patterns of within-colony selectivity, determining the driving factors could reveal the underlying basis for prey selection. Most studies have assumed that preferences will reflect variations in the biochemical composition of the prey i.e. energetic content (Pisapia et al. 2012). However, morphological characteristics, that increase the efficiency with which coral tissue can be located and consumed relative to effort, could also increase a coral's relative value. Coral tissue is generally assumed to be a relatively low quality prey (Tricas 1989a), so the need to forage as efficiently as possible may drive dietary selectivity.

For any organism, the need to feed must be balanced with the need to reduce mortality risk. For many small-bodied species, predation is a major cause of mortality and so the evolution of mechanisms that can reduce predation risk may be critical for persistence. Crypsis mechanisms that allow organisms to 'blend in' with their surroundings can be effective at reducing a predator's ability to detect, locate, and capture individuals (Stevens and Merilaita 2009). One mechanism that has been observed in systems where there is a close coupling between diet and habitat is diet-induced chemical crypsis (Ruxton 2009). This is where diet-specific compounds are sequestered, causing a consumer's odour to chemically match the odour of its prey (Akino et al. 2004). If coral-specific compounds are able to be sequestered, a specialised coral diet may benefit corallivorous fishes that also remain closely associated with corals as habitat. This may influence prey selectivity as, for any benefit to occur, the chemical signatures of the fish and habitat would have to be close enough to reduce a fish's detectability.

For organisms vulnerable to predation, habitats that provide direct shelter from potential predators are essential. With regards to corallivorous fishes, the majority of studies that have investigated distribution and abundance have only considered the presence and abundance of prey resources as driving factors. However, if the need to reduce mortality risk outweighs the need to maximise energy intake, the presence or absence of resources that provide shelter could also influence the distribution and abundance of these species. Scleractinian coral colonies exist along a wide axis of morphological complexity, from simple massive forms through to complex branching structures, and corals that represent the best food resource may not necessarily also represent the best shelter. Investigating the habitat preferences of corallivorous fishes, and the relative importance of shelter and prey resources, will further our understanding of the critical factors underlying the presence and persistence of these species within these environments.

For corallivores, their dependency on live corals means that their survival is directly linked to the presence of suitable corals for feeding, and that they may be highly sensitive to changes to coral communities (Coker et al. 2014). There are now numerous reports of corallivore declines following decreases in coral abundance caused by anthropogenic disturbance (i.e. Kokita and Nakazono 2001; Pratchett et al. 2006; Graham 2007). However, the underlying mechanisms responsible for these declines are less clear. As the specific composition of corals on reefs is expected to change, the ability of specialised corallivores to persist through the potential loss of preferred corals depends on their ability to recognise and exploit alternatives.

Understanding behavioural flexibility in specialised species, or lack of flexibility, will provide insights into their potential vulnerability to predicted changes. If fishes are unable to recognise alternative sources of prey this puts them at high risk of population declines and, potentially, extinction.

Corallivory is exhibited in a taxonomically diverse range of fishes. This feeding mode has been identified in at least 11 different reef fish families (Cole et al. 2008). Despite this diversity, the vast majority of literature (~75%) on the ecology of corallivory by fishes has focused on just one family, the butterflyfishes (Cole et al. 2008). Consequently, it is important to examine other species within this feeding guild to determine if predictions drawn from studies on butterflyfishes are relevant for taxonomically distinct but functionally similar species. This will also increase knowledge of the degree of resource specialisation among corallivores and improve our understanding of how these potentially highly vulnerable species will respond to predicted environmental changes. One such species is the harlequin filefish, *Oxymonacanthus longirostris*, which is found in areas of high coral cover throughout the Indo-Pacific (Barlow 1987; Kokita and Nakazono 2001). This small, brightly coloured species generally forms a monogamous breeding pair that will defend an area of reef from conspecifics (Kokita and Nakazono 1999). An obligate corallivore, this species represents an excellent model for testing hypotheses regarding ecological specialisation and their relevance to corallivorous fishes.

1.5. Aims and thesis outline

The overall aim of this study is to investigate the ecology of *O. longirostris* to determine its level of specialisation, the roles of prey quality and predation pressure as drivers of specialisation, and the consequences of being a coral specialist in an era of increasing degradation to coral reefs.

The different components of this study are addressed in a series of five data chapters;

In **chapter 2** I examine prey use by *O. longirostris* to determine if it selectively feeds on certain corals in the field and if this selectivity reflects underlying prey preferences. The underlying drivers of prey preferences are not well understood, but are thought to reflect prey quality. To test this I then examine whether consuming preferred corals has significant positive effects on key fitness-related parameters.

When attempting to determine the underlying factors behind prey preferences, it is critical to understand the benefits and trade-offs associated with feeding on a particular resource. In **chapter 3** I examine whether coral colonies represent a uniform resource for *O. longirostris* or, alternatively, this species exhibits within-colony prey selectivity. While prey preferences are often thought to reflect relative nutritional or energetic content, morphological characteristics that increase foraging efficiency may also drive feeding preferences. To test this I examine how observed patterns of interspecific and intraspecific selectivity reflect morphological characteristics of the coral polyps consumed by *O. longirostris*.

O. longirostris uses corals almost exclusively for both food and shelter. Where a close coupling between diet and habitat occurs there is the potential for dietary selection to have an anti-predator benefit if diet-specific compounds are sequestered leading to an olfactory similarity between both predator and prey. In **chapter 4**, I examine whether coral-specific dietary elements are sequestered by *O. longirostris,* causing the odour of the fish to match that of its coral prey. I then test if this diet-induced chemical crypsis is able to reduce a fish's detectability to predators.

Reducing predation risk may be a primary determinant of habitat selection in small, vulnerable reef fishes such as *O. longirostris*. However, structurally complex corals that offer the best shelter may not necessarily be the same as those that represent the most nutritious prey thereby forcing fish to trade-off maximising energetic intake with minimising predation risk. In **chapter 5** I examine whether the distribution and abundance of *O. longirostris* reflects the presence or absence of specific habitat characteristics, namely preferred food and shelter. As corals that provide the best food and the best shelter may not necessarily be the same, I then test which characteristic drives habitat selection in *O. longirostris*.

Coral specialists such as *O. longirostris* are predicted to be highly vulnerable to population declines or even extinction following disturbance that removes essential coral resources. In **chapter 6** I document the local extinction of *O. longirostris* from reefs that lost a key prey coral, *Acropora millepora*. I then conduct a behaviour experiment to determine if behavioural inflexibility could limit the ability of this species to persist following disturbances that alter the composition of coral communities.

Chapter 2: Prey selectivity affects reproductive success of a corallivorous reef fish

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2.1. Summary

Most animals consume a narrower range of food resources than is potentially available in the environment, but the underlying basis for these preferences is often poorly understood. Foraging theory predicts that prey selection should represent a trade-off between prey preferences based on nutritional value and prey availability. That is, species should consume preferred prey when available, but select less preferred prey when preferred prey is rare. We employed both field observation and laboratory experiments to examine the relationship between prey selection and preferences in the obligate coral-feeding filefish, *Oxymonacanthus longirostris*. To determine the drivers of prey selection, we experimentally established prey preferences in choice arenas and tested the consequences of prey preferences for key fitness-related parameters. Field studies showed that individuals fed almost exclusively on live corals from the genus *Acropora*. While diet was dominated by the most abundant species, *Acropora nobilis*, fish appeared to preferentially select rarer acroporids, such as *A. millepora* and *A. hyacinthus*. Prey choice experiments confirmed strong preferences for these corals, suggesting that field consumption is constrained by availability. In a longer-term feeding experiment, reproductive pairs fed on non-preferred corals exhibited dramatic reductions to body weight, and in hepatic and gonad condition, compared with those fed preferred corals. The majority of pairs fed preferred corals spawned frequently, while no spawning was observed for any pairs fed a non-preferred species of coral. These experiments suggest that fish distinguish between available corals based on their intrinsic value as prey, that reproductive success is dependent on the presence of particular coral species, and that differential loss of preferred corals could have serious consequences for the population success of these dietary specialists.

2.2. Introduction

Most animals consume a narrower range of prey than is potentially available in the environment (Colwell and Futuyma 1971). Patterns of prey selection, or the amounts of the various prey consumed, can depend on innate preferences that may be linked to the nutritional quality or abundance of different prey (Pyke et al. 1977; Johnson 1980; Morris 1989). Prey consumption may also be modified by interactions with competitors, the risk of harm in consumption, or risk of predation while foraging (Lima and Dill 1990). All else being equal, foraging theory predicts that species should consume a narrow range of preferred prey when they are abundant, but use a much wider range of less preferred prey when preferred prey become scarce (Charnov 1976). To test this prediction, it is critical to not only describe patterns of prey use in the field but also test for preferences under conditions of equal resource availability (Chesson 1983). Furthermore, it is important to quantify the nutritional benefits associated with consuming different prey (McNett and Rypstra 2000; Heithaus and Dill 2002). In theory, species should prefer prey that ultimately lead to better condition or a higher reproductive success (Pyke et al. 1977; Lemine and Himmelman 1996; Wanless et al. 2005; Naya et al. 2007), but this has seldom been tested. An understanding of the basis of prey preferences and the benefits they convey is critical to predicting responses to environmental changes in light of global declines in habitat quality (Laurence 1991; McCarty 2001; Travis 2003).

Coral reefs are highly complex habitats that support an unparalleled diversity of fish species (Reaka-Kudla 1997), many of which are dependent on corals for food (Cole et al. 2008). Corallivores are often highly selective, consuming a small subset of available genera or species (Pratchett 2007; Graham 2007; Cole et al. 2010). However, the underlying basis for this apparent selectivity is not well understood. While the overall dietary scope for corallivorous fishes is limited, individuals may still be flexible depending on the availability of preferred corals. For example, on the Great Barrier Reef, the obligate coral-feeding butterflyfish, *Chaetodon baronessa*, consumes mainly *Acropora hyacinthus* when it is abundant (Berumen et al. 2005). However, when this coral is scarce, the butterflyfish selects alternative, presumably lower quality, corals (Berumen et al. 2005). Assessing the ability of corallivores to consume different corals is important for predicting the future effects of coral reef degradation. Significant changes in the relative abundance of corals due to climate change and other anthropogenic stresses (Marshall and Baird 2000; Loya et al. 2001) could have significant effects on populations of dietary specialists if these events remove corals critical for their persistence.

To determine the underlying basis of patterns of prey selection by corallivores, it is important to identify prey preferences, which can be tested in aquarium choice arenas. In addition, the consequences of feeding on preferred, or less preferred, prey can be evaluated by long-term, controlled feeding experiments. To date, the innate preferences of corallivores have rarely been tested and the consequences of feeding on either preferred or non-preferred prey is seldom known. The positive effects of preferred coral on condition have been experimentally shown in juveniles of the butterflyfish, *Chaetodon trifacialis*, with individuals fed preferred coral experiencing higher growth rates (Berumen and Pratchett 2008). However, while selectivity appears to relate to prey quality, it is not yet known if this selectivity affects reproductive success, and thus individual fitness.

The objective of this study was to investigate resource use, prey preferences, and the relationship between these preferences and reproductive success for the corallivorous filefish, *Oxymonacanthus longirostris*. Specifically we: (1) compared patterns of prey use and availability in the field to determine patterns of coral selection and avoidance, (2) experimentally tested whether prey preferences are exhibited between corals under conditions of equal availability to determine whether levels of consumption in the field relate to intrinsic preferences, and (3) determined if there is a positive relationship between consumption of preferred prey, and body condition or reproductive success in the filefish.

2.3. Methods

Study sites and species

The field components of this study were conducted at Big Peninsular Reef, Great Keppel Island on the southern Great Barrier Reef (GBR), Australia, during September 2009. Great Keppel Island (23°10.7’S, 150°57.6’E) is a large continental island located approximately 18 km from the mainland, surrounded by *Acropora*-dominated fringing reefs. Aquarium experiments were conducted at Reef HQ Aquarium, Townsville, Australia, in June 2010 and at Lizard Island on the northern GBR (14°40’S, 145°27’E) during November and December 2010. The harlequin filefish, *O. longirostris* (Monacanthidae), is widely distributed on shallow coral reefs throughout the Indo-Pacific. It is an obligate corallivore, known to feed almost exclusively on corals from the genus *Acropora* (Kokita and Nakazono 2001). It is generally monogamous, with fish forming exclusive heterosexual pairs which share a feeding territory (Kokita and Nakazono 1999).

Prey use, prey availability, and apparent selectivity

A field study was conducted to determine if *O. longirostris* selectively feeds on certain corals as prey by comparing the proportional consumption of particular coral species with their availability. As this species is diurnally active, feeding observations were conducted between 0900 and 1600 hours over 3 weeks in September 2009. Twenty haphazardly chosen individuals were followed for 10 min periods with all bites on coral or alternative substrate recorded. All *Acropora* corals were recorded to species level while all other scleractinian corals were categorized to genera. Observations began when fish commenced feeding, taken as an indication of acclimation of the fish to the diver's presence. Fish were followed at 2–3 m distance and showed no signs of disturbance. As *O. longirostris* may exhibit restricted movement across reefs (Kokita and Nakazono 1999), the relative abundance of corals available as prey was measured within 10 replicate pair feeding ranges. A randomly selected pair was followed on scuba for a period of 20 min with the outer points of their feeding range marked. Pairs were followed at a distance of 2–3 m and showed no sign of disturbance due to diver's presence. Ten replicate 1 × 1 m quadrates were placed within each feeding range and the coral or other substrate directly beneath 10 random points within each quadrat was recorded.

The log-likelihood statistic (Manly et al. 1993) was used to test for selectivity among all the resources consumed by the fish. The statistic was calculated using the following formula:

$$X_{L2}^{2} = 2\sum_{j=1}^{n}\sum_{i=1}^{l} u_{ij} In\{u_{ij} / E(u_{ij})\}$$

where *uij* is the proportional use of each food type (*i*) by each individual (*j*) and *E*(*uij*) is the number of bites expected on food type *i* by individual *j* if use of feeding resources is proportional to availability. To examine which resources were being used disproportionately to availability, resource selection ratios (*wi*) were then calculated for each fish.

Experimental evaluation of feeding preferences

A cafeteria-style choice experiment was used to determine if prey selectivity on reefs is primarily driven by feeding preferences. Fish from two spatially disparate areas, northern GBR and southern GBR, were tested independently to determine if prey selection patterns are consistent between populations. Northern GBR fish were collected from mid-shelf reefs off Cairns, Australia, while southern GBR fish were collected from reefs surrounding Great Keppel Island. Prior to commencement of experiments, fish were fed ad libitum with equal proportions of the *Acropora* species used in experiment, supplemented with a standard conditioning diet of prawn meal. This ensured fish maintained good physical condition and preserved feeding responses during experimentation while preventing a bias in feeding preference due to learned foraging behaviour for certain coral species while in captivity.

Experiments were conducted in a circular enclosure (80 cm diameter) located within a larger flow through tank (1.2 × 1.2 × 0.5 m) lined with coral sand. Individuals were presented with fragments from four widely distributed *Acropora* species present during field surveys: *Acropora nobilis*, *A. hyacinthus*, *A. millepora* and *A. valida*. Fragments 2 cm in length of each coral species were used to standardise for interspecific differences in coral colony morphology. Fragments were removed from whole colonies collected from Pioneer Bay, Orpheus Island, Australia (18°36’S, 146°29’E) housed at Reef HQ Aquarium. To account for intraspecific variation in tissue condition or biochemical profiles, three colonies of each species were haphazardly collected from varying locations along the reef on SCUBA. To account for any within-colony variation that may affect preferences, fragments used in the experiment were randomly selected from within these colonies. Fragments were removed using needle-nose pliers which minimised physical damage to tissue surrounding the break point. Following removal, fragments were kept in flow through aquaria for 24 h to allow for initial recovery from mechanical stress. Fragments were placed within the experimental enclosure at four points, each 15 cm from the enclosure edge. Fragments were positioned at equal distance from each other and the fish release point. The position and orientation of fragments within the enclosure was randomised among all replicates. Each fragment was held upright within a plastic cap using a small amount of synthetic rubber compound, reducing any handling or direct contact with coral prior to trials. Following placement, fragments were left to acclimate for 20 min.

Fish were not fed for 12 h prior to experimentation. Each fish was released into a 20 cm diameter mesh cylinder at the centre of the experimental enclosure and left to acclimate for a 10 min period. This cylinder’s mesh construction allowed the fish to observe each coral fragment and did not restrict visual and olfactory cues. The cylinder was then removed and foraging behaviour was recorded for a 10 min period after the first bite was taken. During trials, fish were not able to see the observer. Each coral fragment was only used in one trial as any prior foraging may affect the attractiveness of a fragment to subsequent consumers. The number of total bites per fragment was converted into the percentage of the total bites taken during trial. Due to non-independence of coral fragments, data for each population was analysed using a non-parametric Kruskal–Wallis test.

Prey preferences and fitness

A month-long, controlled feeding experiment was conducted at Lizard Island during the summer breeding season (November and December 2010) to test the effect of prey selectivity on reproductive success. Naturally associated breeding pairs of *O. longirostris* were collected from the Lizard Island Lagoon using hand nets and clove oil. Following collection, fish were starved for 24 h to allow gut contents to be evacuated after which body weight, total, and standard lengths were recorded. Each pair was housed in a 68 L tank (internal dimensions 597 × 362 × 381 cm) constantly supplied with fresh sea water and aeration to maintain high water quality. Tanks were dark blue, nonreflective, and lined with coral sand to minimise stress to fish while in captivity. Habitat structure was created using pieces of coral rubble, each approximately 30 cm in length.

For the duration of the experiment, pairs were fed exclusively one of two *Acropora* species; *A. nobilis* or *A. millepora*. *O. longirostris* feeds on each, although under controlled conditions fish exhibit a strong preference for *A. millepora* over *A. nobilis*. To account for intraspecific variability in the condition of corals, coral fragments were collected from randomly selected colonies throughout the lagoon. Care was taken to ensure minimal physical damage or stress to fragments during collection and transport. Coral fragments were placed on stands consisting of acrylic pipe (50 mm height, 120 mm diameter) with galvanised wire hoops around the outside parameter. The base of the fragments was placed on this hoop, extending each fragment vertically into the water column separated from those surrounding it. This allowed maximum access by fish to fragments and prevented tissue necrosis due to contact with the substratum. A minimum 250 cm^2 of coral was provided, with this coral completely exchanged every 2 days. Coral tissue was actively consumed throughout this time suggesting satiation. Following use, coral fragments were returned to their original collection site.

A variety of fitness-related parameters were recorded. Reproductive output was monitored throughout the experimental period. *O. longirostris* spawns regularly during the reproductive season, generally several hours prior to sunset. Pairs create a nest in a tuft of filamentous algae into which they release a clutch of adhesive eggs (Barlow 1987). An artificial spawning site was placed in each tank consisting of a plastic clasp tied to a 30 cm piece of coral rubble onto which a fresh tuft of algae (*Sargassum* spp.) could be attached. Following sunset, algal tufts were removed and checked for the presence of eggs. At the conclusion of the experiment all coral was removed for 24 h to allow gut contents to be expelled. Fish were euthanised using clove oil and body weight, total, and standard lengths were recorded. Livers were then removed and weighed. Gonads were removed, weighed and fixed in 4 % formaldehyde, 5 % acetic acid, and 1.3 % calcium chloride (FAACC). Once fixed, gonads were embedded in histoparaffin and 5 lm sections were taken at 3 points along the widest axis, mounted on glass micro-slides and stained with Mayer's alum haematoxylin and Young's eosin-erythrosine. To determine the reproductive status of individuals, a transect was run along each representative section with the type of sex cell under each 10 graticule mark on an eyepiece micrometer recorded at x200 magnification. In ovaries, cells were divided into oogonia, perinucleolus, cortical alveolus, early vitellogenic oocytes, and late vitellogenic oocytes with the relative abundance of each recorded. In testis, cells were divided into spermatogonia, primary spermatocysts, secondary spermatocysts, spermatids and spermatozoa (Kroon et al. 2003) (Table 2.1).

MANOVA followed by ANOVA was used to compare body condition (length–weight change, hepatosomatic index) between feeding treatments. For females, proportion of total weight contributed by ovary was used as the gonadosomatic index (GSI). One-way ANOVA was used to compare GSI between treatments. Two-way ANOVA was used to compare the mean proportion of gamete stages between each feeding treatment group.

2.4. Results

Prey use, prey availability, and apparent selectivity

In the field, *O. longirostris* did not consume coral species in proportion to their availability (Fig. 2.1a, b). Only five prey types were used and of the scleractinian coral genera present, only *Acropora* was consumed. Log-likelihood analysis indicated that there was selective feeding among these prey types ($X^2_{L2} = 9 \times 10^2$; $p < 0.01$). Between the *Acropora* species used, *A. millepora* had the highest mean selection function followed by *A. hyacinthus*, suggesting that these species are exploited more than expected given availability (Fig. 2.1c). While the majority of feeding was on a single species, *A. nobilis*, this coral was highly abundant resulting in a relatively low selection function (Fig. 2.1c). Six other *Acropora* species, *A. valida*, *A. nana*, *A. latistella*, *A. clathrata*, *A. subulata* and *A. glauca*, were present on transects in very low abundance but were not consumed during observations. A small number of bites were also observed on sections of dead *Acropora* branches within live colonies.

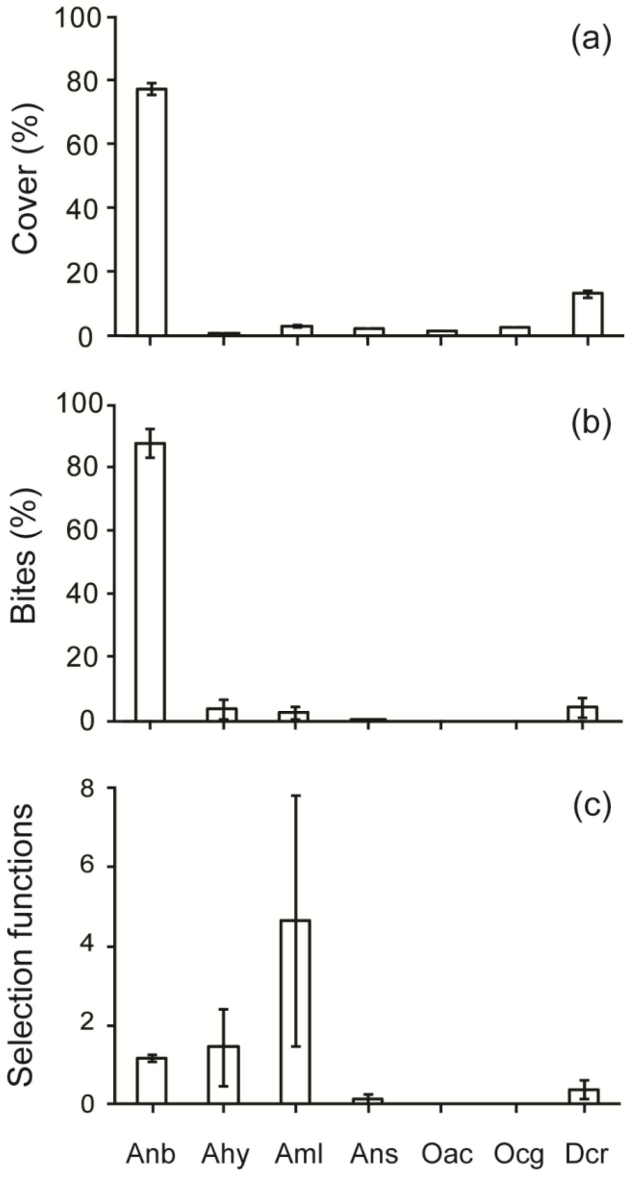

Figure 2.1. Prey use and selectivity by *Oxymonacanthus longirostris* at Great Keppel Island, Australia. For each food resource: a abundance (percent cover), b consumption (percent of total bites) and c selection functions (see ''Materials and methods''), mean ± SE, n = 20. Food resources are: Anb, *Acropora* nobilis; Ahy, *A. hyacinthus*; Aml, *A. millepora*; Ans, *A. nasuta*; Oac, other *Acropora* species; Ocg, other coral genera; Dcr, dead coral. Oac group includes all *A. valida*, *A. nana*, *A. latistella*, *A. clathrata*, *A. subulata* and *A. glauca* observed. Ocg group includes all *Pocillopora*, *Porites*, *Echinopora*, *Platygyra*, *Fungia*, *Montipora*, *Favia*, and *Lobophyllia* observed

Experimental evaluation of feeding preferences

Laboratory choice experiments indicated significant preferences for certain *Acropora* species, with consistent choices made by individuals collected from both northern (Kruskal–Wallis test: $H_c = 32.5$, $p < 0.01$) and southern (Kruskal–Wallis test: $H_c = 9.17$, $p = 0.03$) locations (Fig. 2.2). In both cases *A. millepora* was preferred over *A. hyacinthus* with *A. valida* and *A. nobilis* avoided.

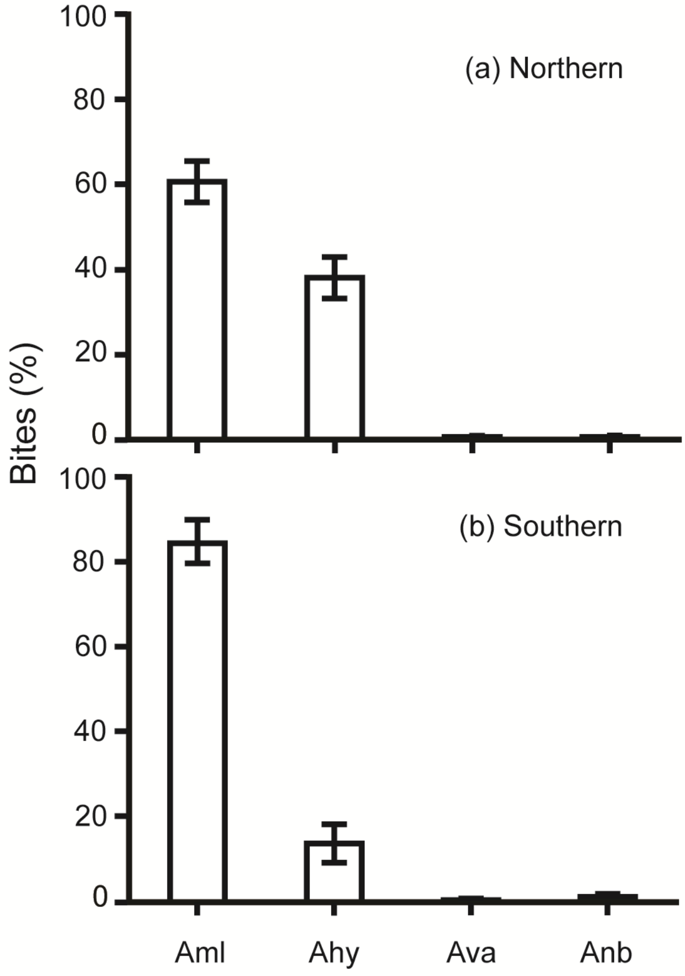

Figure 2.2. Percentage of total bites (mean ± SE) on each *Acropora* sp. fragment by individuals from (a) northern and (b) southern Great Barrier Reef populations during cafeteria-style experiment. Acropora spp. are: Anb, *A. nobilis*; Ahy, *A. hyacinthus*; Am Aml, *A. millepora*; Ava, *A. valida*. Sample sizes are: northern $n = 21$, southern $n = 7$

Prey preferences and reproduction

Body condition

Weight and liver condition varied significantly between coral diets (MANOVA, Pillai's trace = 0.79, *df* = 2, $p < 0.01$) (Fig. 2.3). Fish fed *A. nobilis* exhibited a greater proportional weight loss compared with fish fed *A. millepora* (ANOVA, $F = 18.05$, *df* = 1.20, $p < 0.01$). Similarly, the hepatosomatic index on *A. millepora* was significantly greater than on *A. nobilis* (ANOVA, $F = 66.41$, *df* = 1.20, $p < 0.01$). There was no significant interaction with sex, indicating that the condition of both males and females were similarly affected. However, proportional weight loss did appear higher in females compared to males fed *A. millepora* (Fig. 2.3a).

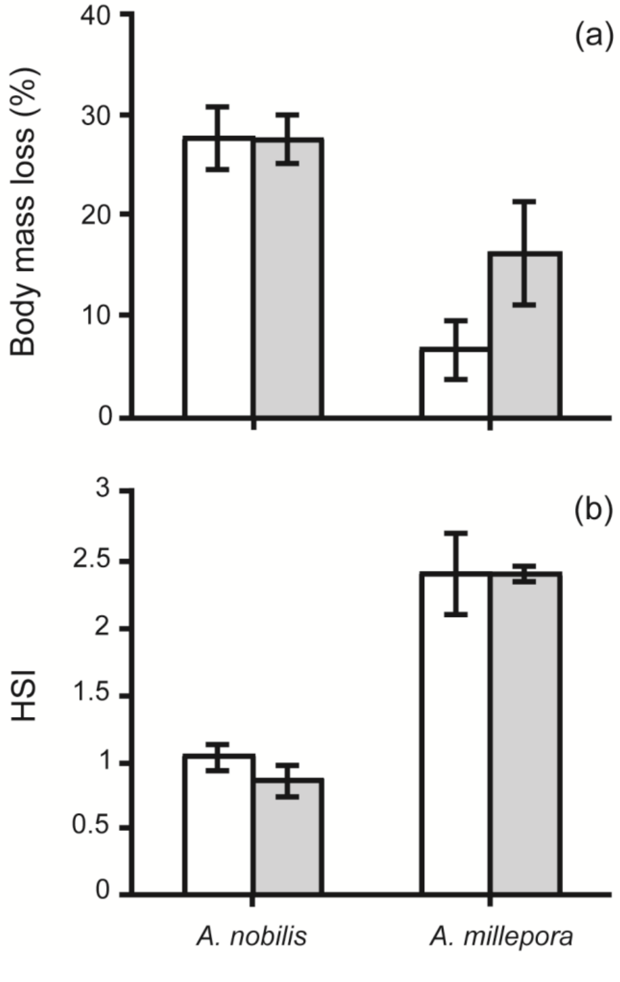

Figure 2.3. Differences in body condition of male (white bars) and female (shaded bars) *O. longirostris* fed exclusively on one of two coral species, *A. nobilis* or *A. millepora*, for 30 days. (a) Percent of total body mass lost and (b) hepatosomatic index (HSI). Values shown are mean ± SE; sample sizes *n* are five male, five female *A. nobilis* and six male, six female *A. millepora*

Reproduction

Reproductive output and gonad condition differed significantly between diet treatments. Pairs fed *A. millepora* spawned on 49 % of nights. In contrast, no pairs fed *A. nobilis* spawned during the experimental period (Fig. 2.4a). The gonadosomatic index of females fed *A. millepora* was significantly higher than females fed *A. nobilis* (ANOVA, *F* = 10.97, *df* = 1.9, *p* < 0.01) (Fig. 2.4b). The condition of gonads (i.e. the relative number of cells in each stage of gamete development) varied significantly between groups for both males (ANOVA, *F* = 27.1, *df* = 1.3, *p* < 0.01) and females (ANOVA, *F* = 45.58, *df* = 1.4, *p* < 0.01) (Fig. 2.5).

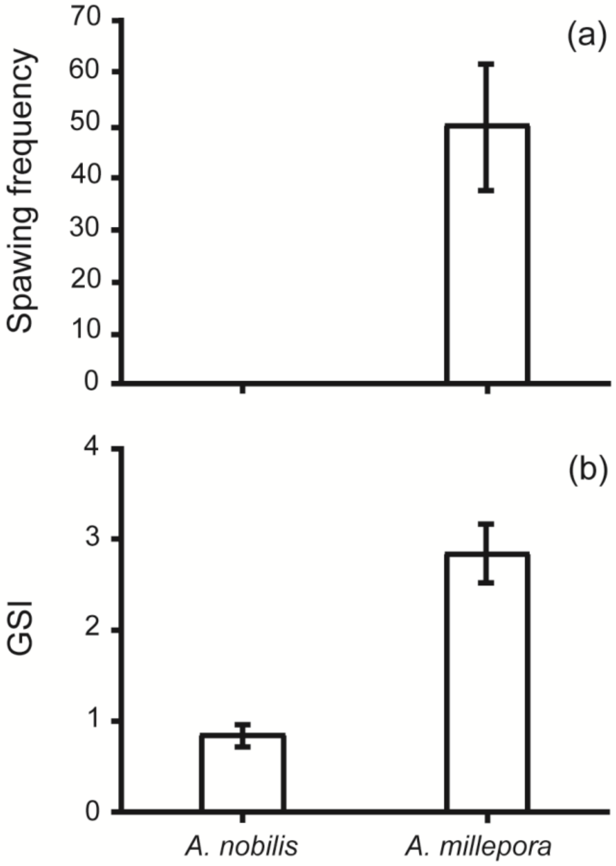

Figure 2. 4. Reproductive output and condition of *O. longirostris* fed exclusively on one of two coral species, *A. nobilis* or *A. millepora*, for 30 days. (a) Spawning frequency in days of monogamous pairs and (b) gonadosomatic index (GSI) value of females. No spawning was observed in pairs fed *A. nobilis*. Values shown are mean ± SE; sample sizes *n* are five male, five female *A. nobilis* and six male, six female *A. millepora*

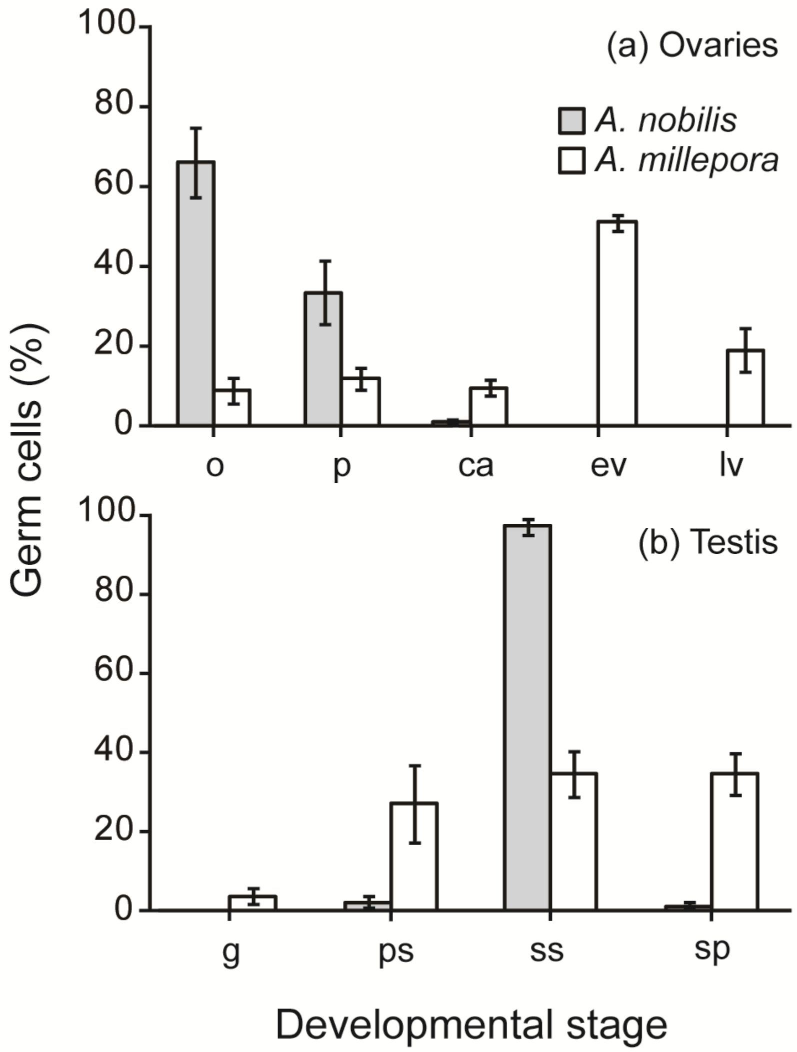

Figure 2.5. Percent of germ cells at each stage of development in a ovaries and b testis of *O. longirostris* fed *A. nobilis* (shaded) or *A. millepora* (white) coral. Developmental stages for ovaries are oogonia (o), perinucleolus (p), cortical alveolus (ca), early vitellogenic oocytes (ev), and late vitellogenic oocytes (lv). Developmental stages for testis are gonia (g), primary spermatocytes (ps), secondary spermatocytes (ss), spermatids and spermatozoa (sp). Values shown are mean ± SE; sample sizes *n* = 6

2.5. Discussion

We have shown that the filefish *O. longirostris* is a highly specialised corallivore, consuming a restricted range of *Acropora* coral species. In the field, the majority of foraging was on the branching species, A. *nobilis*, which was the dominant coral on fringing reefs. However, the comparison of consumption and availability indicated greater selectivity for two less abundant coral species, *A. millepora* and *A. hyacinthus*. This selectivity was confirmed in the choice experiment that demonstrated a feeding preference for *A. millepora* and *A. hyacinthus* over *A. nobilis*, suggesting that coral consumption in the field is constrained by the low abundance of these preferred species. The longer term performance experiments show that access to preferred corals can have a dramatic impact on an individual's condition and ability to breed. Thus, while there is a heavy reliance on abundant corals such as *A. nobilis* for survival, it seems that access to the rarer coral species may be critical for reproductive success.

Coral tissue is a relatively low quality food (Tricas 1989a). Consequently, corallivores often need to spend large parts of their active periods feeding to meet energy requirements and foraging efficiently should be critical. Given the relative scarcity of preferred species, individuals would need to invest energy into searching, reducing the relative value of preferred prey when encountered. For this reason it may be most efficient for *O. longirostris* to trade-off prey quality and mostly consume a highly abundant prey, at least to maintain basic metabolic processes. Animals may also attempt to maximise their potential fitness by reducing mortality risk or the threat of predation (Gilliam and Fraser 1987). Hence, the high consumption of *A. nobilis* may reflect not only abundance but also habitat preferences due to superior shelter characteristics. The complex branching morphology of *A. nobilis* may reduce mortality risk by restricting movement or visual acuity of predators as well as providing shelter or refuge sites (Brooker et al. 2011). Nevertheless, it appears that rarer acroporids such as *A. millepora* are also essential for reproductive success and that *O. longirostris* populations may require environments rich in a variety of both *Acropora* species and morphologies to persist.

Under conditions of equal availability, strong preferences were exhibited between the *Acropora* species provided. It is likely that the preferences relate in some way to the nutritional qualities of the corals. A general preference was exhibited for *A. millepora* and *A. hyacinthus*, two species which have comparatively large, fleshy polyps, diurnal tentacle extension and an open corallite structure. These factors may increase the amount of material removed per feeding strike, reducing the energetic cost of foraging when encountered. Similarly, polyp structure that increased calorific intake per bite explained selection for *Porites meandra* by the butterflyfish, *Chaetodon multicinctus* (Hourigan et al. 1988; Tricas 1989a), which suggests that small variations which affect efficiency could potentially drive prey preferences.

The results of the controlled feeding experiment suggest that *Acropora* species can vary substantially in their value as prey in terms of maintaining body condition and reproduction, and that preferences correspond to these performance measures. Limited weight loss along with preservation of hepatic tissue while in captivity indicate that the preferred *A. millepora* provided sufficient nutrition, either through prey quality or limited foraging costs, to require only limited dependence on stored energy. This positive relationship between apparent preferences and body condition is consistent with studies of obligate corallivorous butterflyfish, which have reported correlation between selected prey abundance and condition of associated adults (Berumen et al. 2005), and direct increases in juvenile growth when fed a selected coral (Berumen and Pratchett 2008). In our study, parental condition directly affected the reproductive output of pairs. Advanced gonad development in both males and females fed preferred coral indicated continuing investment into reproductive processes. In females, advanced gamete development in ovaries was matched by high GSI values, suggesting that this is an adequate measure of reproductive status.

The direct relationship between prey consumed and fitness measures in the laboratory suggests that coral species composition may have a critical role in the reproductive output of associated populations. While *A. nobilis* composed the majority of foraging in the field, pairs fed exclusively on this species did not reproduce in captivity. When low quality prey is abundant within a system, consumers may compensate by increasing feeding rates so as to meet energy requirements (Cruz-Rivera and Hay 2000). However, some access to rarer, preferred prey may be required for reproductive success.

A small number of individuals were observed foraging on sections of dead coral amongst live branches. The epilithic algal turfs on these surfaces are home to complex communities of associated organisms (Wilson and Bellwood 1997), including various macroinvertebrates consumed by other coral-feeding monacanthids (Hobson 1974). While primarily corallivorous, it is probable that *O. longirostris* will opportunistically feed on these other suitable prey when encountered.

Further work is required to understand the nutritional basis of coral preferences in *O. longirostris* and other corallivores. Corallivores may derive energy and essential nutrients from both coral tissue and associated by-products such as mucus (Cole et al. 2008). Interspecific biochemical variation, which affects a coral's nutritional quality, may therefore drive specific preferences. Recent comparisons have failed to find strong correlations between overall biochemistry and preferences (Tricas 1989a; Keesing 1990). However, the specific biochemical components of coral most important to fish condition are not known (Cole et al. 2008).

Coral reef ecosystems are becoming increasingly degraded due to anthropogenic disturbance (Hughes et al. 2003). Losses of coral cover will have the most immediate effects on resident specialists such as *O. longirostris* that have a critical dependence on specific corals (Munday 2004; Wilson et al. 2006; Bonin et al. 2009). Our results suggest that the loss of rare, less abundant, but highly preferred, coral species would have a dramatic negative effect on the ability of *O. longirostris* to breed. *Acropora* corals are especially vulnerable to major sources of disturbance, especially coral bleaching (Marshall and Baird 2000). If corals essential for reproductive success of *O. longirostris* decline in abundance then the ability of populations to be replenished may be compromised.

Table 2.1. Diagnostic characteristics used to determine cell types within the gonads of male and female *O. longirostris*

Sex	*Cell developmental stage*	*Diagnostic characteristics*
Female	Oogonia	Spherical. Highest nuclear/cytoplasmic ratio.
	Perinucleolus	Oocytes small and stained dark. Large nucleus with single nucleolus.
	Cortical alveolus	Large nucleus with multiple nucleoli. Uniformly stained cytoplasm.
	Early vitellogenic oocytes	Cytoplasm contains yolk vesicles. Chorion may be present.
	Late vitellogenic oocytes	Abundant yolk globules. Well developed chorion.
Male	Gonia	Large, spherical.
	Primary spermatocytes	Dark staining crypts of primary spermatocytes.
	Secondary spermatocytes	Crypts of spermatocytes that have undergone division.
	Spermatids and spermatozoa	Dark stained spermatids much smaller than secondary spermatocytes. Nucleolus absent. Mature spermatozoa free in lumina.

Chapter 3: Within-colony feeding selectivity by a corallivorous reef fish: foraging to maximize reward?

This chapter was published in Ecology and Evolution (2013) 3: 4109-4118. Authors: RM Brooker, GP Jones, PL Munday

3.1. Summary

Foraging theory predicts that individuals should choose a prey that maximizes energy rewards relative to the energy expended to access, capture, and consume the prey. However, the relative roles of differences in the nutritive value of foods and costs associated with differences in prey accessibility are not always clear. Coral-feeding fishes are known to be highly selective feeders on particular coral genera or species and even different parts of individual coral colonies. The absence of strong correlations between the nutritional value of corals and prey preferences suggests other factors such as polyp accessibility may be important. Here, we investigated within-colony feeding selectivity by the corallivorous filefish, *Oxymonacanthus longirostris*, and if prey accessibility determines foraging patterns. After confirming that this fish primarily feeds on coral polyps, we examined whether fish show a preference for different parts of a common branching coral, *Acropora nobilis*, both in the field and in the laboratory experiments with simulated corals. We then experimentally tested whether non-uniform patterns of feeding on preferred coral species reflect structural differences between polyps. We found that *O. longirostris* exhibits non-uniform patterns of foraging in the field, selectively feeding midway along branches. On simulated corals, fish replicated this pattern when food accessibility was equal along the branch. However, when food access varied, fish consistently modified their foraging behaviour, preferring to feed where food was most accessible. When foraging patterns were compared with coral morphology, fish preferred larger polyps and less skeletal protection. Our results highlight that patterns of interspecific and intraspecific selectivity can reflect coral morphology, with fish preferring corals or parts of coral colonies with structural characteristics that increase prey accessibility.

3.2. Introduction

Animals seldom exist within a nutritionally homogeneous environment, and as a result of variable nutritional composition and prey accessibility, they can experience a range of dietary options (Rapport 1980). Optimal foraging theory predicts that an individual should prefer prey species of high nutritional value relative to the energy spent to locate, capture, and consume the prey (Charnov 1976; Pyke et al. 1977). Differences in the nutrient composition of prey can play a key role in determining species-specific preferences (Jensen et al. 2012). However, the nutritional value of a given prey species may vary in response to differences in the condition or reproductive status of individuals, making optimum prey choice difficult (Fitzgibbon 1990; Gende et al. 2001; Lane et al. 2011). The relative accessibility, or vulnerability, of different prey species may also be important (Harder 1983; Hoogland et al. 2006; Plath et al. 2011). The presence of antipredator defences or morphological features that constrain feeding can increase the time required to locate, manipulate, and consume food (Werner and Hall 1974; Temeles et al. 2009), reducing their value. Relative nutritional value may also vary within an individual, with consumers selectively targeting specific parts that provide the greatest nutritional benefit (Andrew and Jones 1990; Gende et al. 2001; Pekar et al. 2010; Pitman and Durban 2012) or the least protected parts of a prey organism.

On coral reefs, many of the associated fishes are dependent on live corals; as food, for shelter, or during recruitment (Munday et al. 2008). Coral-feeding fishes are among the most specialized species found on coral reefs, selectively consuming corals from particular genera or species (Berumen et al. 2005; Pratchett 2007; Cole et al. 2008, 2010; Rotjan and Lewis 2008; Chapter 2). The underlying basis of this selectivity is not well understood but could relate to a variety of factors such as biochemical composition, morphology, or antipredator defences. It has often been assumed that selectivity relates to variation in the nutritional value between corals (Pisapia et al. 2012), and recent studies have shown that consuming a preferred coral can have positive effects on corallivorous fishes, improving relative growth rates (Berumen and Pratchett 2008), body condition (Berumen et al. 2005; Chapter 2), and reproductive output (Chapter 2). However, the few studies that have attempted to relate the biochemical profiles of coral tissue, in particular the levels of energetic macronutrients, to corallivore preferences have failed to find strong correlations with fitness-related benefits (Tricas 1989a; Keesing 1990; Rotjan and Lewis 2005; Pisapia et al. 2012). Furthermore, patterns of coral-feeding within different coral species have received little attention, and it is not known if coral-feeding fishes target specific parts of the coral colony, either due to nutritional variation or differences in prey accessibility.

Scleractinian corals are generally composed of colonies of individual polyps, all extending from an aragonite exoskeleton. The basic anatomy of a coral polyp is relatively simple, consisting of a gastrointestinal chamber enclosed by a tentacle-ringed mouth. Each polyp produces an individual exoskeletal cup, the corallite, that provides protection for the polyp (Klaus et al. 2007). Polyps are connected by gastrovascular canals that run through the thin layer of interpolyp tissue, the coenosarc. Exoskeletal structure and polyp morphology vary extensively both between- and within-coral taxa (Klaus et al. 2007; Todd 2008), and this variation could affect how efficiently coral tissue can be consumed. For example, by selectively foraging on the coral *Pocillopora meandrina*, a species with clustered polyps, the butterflyfish*, Chaetodon multicinctus* increased its calorific intake per bite relative to when foraging on other corals (Tricas 1989a). If corallivores attempt to maximize their efficiency when foraging, then preferences for specific corals may therefore reflect their morphological traits. To date, studies of corallivory and corallivore foraging preferences have generally considered each coral species to be an independent prey type (Cole et al. 2008) and have not tested whether corallivores use these corals uniformly or are influenced by factors, such as biochemical or morphological variation, that may occur within a single coral (but see Rotjan and Lewis 2009). Investigating prey selection at this finer scale may help define the processes driving prey selection in corallivorous fishes.

The objective of this study was to investigate, for the first time, the relative roles of nutrition and polyp accessibility in determining within-colony feeding selectivity by the corallivorous filefish, *Oxymonacanthus longirostris* (Bloch & Schneider, 1801; Fig. 3.1). This filefish is an obligate corallivore that feeds almost exclusively on corals from the genus *Acropora* (Kokita and Nakazono 2001). On the southern Great Barrier Reef (GBR), it primarily feeds on *Acropora nobilis* (Dana, 1846), which is an abundant branching coral in that region (Veron 2000). However, it also exhibits a strong dietary preference for *Acropora millepora* (Ehrenberg, 1834) and other less abundant coral species (Chapter 2). Patterns of feeding within these coral species are unknown. Here, we specifically set out to (1) confirm that *O. longirostris* primarily feeds on coral polyps; (2) determine whether or not *O. longirostris* shows a preference for different parts of *A. nobilis* coral colonies in the field and whether this is related to polyp density or corallite structure; (3) compare feeding patterns to determine whether food accessibility determines foraging location and whether fish are able to modify feeding patterns in response to food accessibility; and finally, (4) experimentally test whether non-uniform patterns of feeding on preferred coral species (*A. millepora* and *Acropora tenuis* [Dana, 1846]) reflect structural differences between polyps that may affect foraging efficiency.

Figure 3.1. The harlequin filefish, *Oxymonacanthus longirostris*, feeding on Acropora coral. Photo: RM Brooker.

3.3. Methods

Study species and sites

The harlequin filefish, *Oxymonacanthus longirostris* (Monacanthidae), is distributed on shallow coral reefs throughout the Indo-Pacific and can be found in low numbers in sheltered areas of the GBR with high coral cover. A preliminary aquarium observational study was conducted at Lizard Island, northern GBR (14°40’S; 145°27’E), to establish that *O. longirostris* feeds on coral polyps. The field components of this study were conducted at Big Peninsula Reef, Great Keppel Island (GKI) on the southern GBR, Australia, during September 2009. GKI (23°10.7'S; 150°57.6'E) is a large continental island surrounded by reefs dominated by branching *Acropora nobilis*. Two aquarium choice experiments were conducted: one at Reef HQ Aquarium, Townsville, Australia in July 2010 and the other at the James Cook University Research Aquarium, Townsville, Australia in October 2011.

What coral structures are targeted by O. longirostris?

Although it is generally assumed that *O. longirostris* is a coral polyp predator, this has not been quantified. To determine whether *O. longirostris* do target coral polyps, or alternatively feed on interpolyp tissue (coenosarc), or feed indiscriminately across the coral surface, an observational study of foraging activity was conducted. Trials took place within a circular tank (1.5 m diameter) constantly supplied with fresh sea water and aeration to maintain water quality. Twelve *O. longirostris* were kept in the tank. Coral skeleton was placed along the perimeter to provide structural complexity and reduce stress to the fish but the centre of the tank was kept clear. An underwater video camera (GoPro, Woodman Labs Ltd.) was placed at one end of the tank. For each foraging trial, a fragment of *A. millepora* composed of approximately 3 branches was placed 20 cm in front of the camera, held upright at a natural angle. All foraging was recorded for a period of 5 min, with fish generally beginning to forage within several seconds of the fragment being introduced. Footage from each trial was then analysed frame by frame with the location of the first 30 bites recorded. Only bites where both a fish's mouth and the coral surface were clearly visible were included. Bite locations were recorded as either directly on a polyp or on the coenosarc. Differences between bite locations were determined using an independent t-test.

Field study of selectivity within A. nobilis colonies

A field study was conducted to determine whether *O. longirostris* feeds on prey coral colonies uniformly. As this species is diurnally active, foraging observations were conducted between 09:00 and 16:00. Twenty haphazardly chosen individuals were followed for 10 min periods with the location of all bites on the coral *A. nobilis* recorded. This coral has an open branching morphology allowing for accurate recording of bite locations and is highly abundant at the study site where it forms the bulk of *O. longirostris* diet (Chapter 2). Each branch that an individual was observed foraging on was divided into three equal sections by the observer, recorded as top, central, and base. Observations were conducted on SCUBA with fish followed at 2–3 m distance. At this distance, fish exhibited no signs of disturbance. Observations began when fish commenced foraging, taken as indication of acclimation of the fish to the diver's presence. Data were analysed using univariate analyses of variance (ANOVA) with post hoc pairwise comparisons conducted using the Tukey HSD test.

Experimental test of preferences using simulated A. nobilis branches

A series of aquarium experiments were conducted using simulated *A. nobilis* branches to further determine the role that food accessibility plays in foraging decisions. Each simulated coral branch consisted of three separate 4 x 1.5 cm cylindrical segments, constructed of an inert polymer, threaded onto a central stand. Thus, when assembled, each simulated coral branch formed a 12 x 1.5 cm cylinder extending vertically into the water column with a base, middle, and tip. A series of 28 artificial corallites, constructed of 1.5 mm diameter plastic tubing, were fixed on to each cylindrical segment. Three distinct artificial corallite lengths were constructed; shallow 1.0 mm, medium 1.5 mm, and deep 2.0 mm, corresponding to three levels of food accessibility analogous to thecal wall extension. Each section had only one length of artificial corallite. In this arrangement, all combinations of position and accessibility could be tested. Food used in these experiments consisted of a homogenous mix of finely pureed prawn meat bound with gelatine. The fine consistency of this mix allowed the biochemical composition and amounts of food used in each trial to be standardized while gelatine component prevented dissipation during trials. Fish used in this experiment were acclimated to this food in addition to live coral tissue and were actively accepting it by the start of experimentation. Prior to each trial, 0.1 mL of food was injected into the base of each corallite using a hypodermic needle. In this way, while fish were able to access food at all depths, food was closer to the surface of shorter artificial corallites and therefore assumed to require less effort to search for and acquire. During the experimental period, fish were kept in individual 100 L circular plastic tanks supplied with constant fresh water and oxygenation. Tanks had black, nonreflective interiors to reduce stress to the fish. For each trial, the appropriately arranged simulated coral was placed at the centre of the tank. All bites, along with their location, were then recorded for a 10 min period following the first bite. Fish were not able to see the observer during the trials. Experiment one examined the relationship between foraging selectivity and branch location. During this experiment, all three segments of the simulated coral branch had the same artificial corallite depth. All fish were run through each of the three corallite depths in a randomized order with one trial per day. Experiment two examined the relationship between foraging selectivity and food accessibility. During this experiment, each simulated coral branch had one segment of each artificial corallite depth. Each fish was run through each potential combination of these three depths in a randomized order with one trial per day. Due to non independence between segments, data for each simulated coral branch experiment were analysed using a nonparametric Kruskal–Wallis test. Post hoc pairwise comparisons were conducted using Dunn's procedure (Dunn 1964) with a Bonferroni correction for multiple comparisons.

Aquarium study of within-colony selectivity

An aquarium choice experiment was conducted to further examine how foraging varies within corals and whether selectivity relates to position of structural characteristics. This experiment consisted of a series of pairwise trials where fish were offered a choice between two coral fragments from two different *Acropora* species and two points of origin (top or bottom sections of branches). The two *Acropora* species used, *A. millepora* and *A. tenuis*, have similar digitate colony morphologies along with similar individual branch sizes; however, they appear to vary with regard to corallite morphology depending on location along a branch. An initial pairwise choice experiment was conducted to determine whether fish exhibited a general foraging preference between these species. For this experiment, relatively large (15 cm diameter) fragments were chosen as they included a number of individual branches removing any branch effect. Once the presence or absence of a foraging preference was established, fish were run through six randomly ordered trials using smaller fragments representing all combinations of both *Acropora* species and points of origin (top or bottom sections of branches). For each fish, one trial was conducted per day over 6 days. *Oxymonacanthus longirostris* were collected from midshelf reefs off Cairns, Australia and held at Reef HQ aquarium, Townsville, Australia. Prior to the commencement of experiments fish were fed ad libitum with pieces of the *Acropora* species used in trials supplied in equal abundance supplemented with a standard conditioning diet consisting of prawn meal. This diet maintained fish condition and foraging responses while preventing any learned foraging behaviour for specific coral species. During the experimental period, fish were not fed outside of trials and were each kept in independent enclosures to ensure all fish were run through all treatments. Experiments were conducted in a circular enclosure (80 cm diameter) placed within a larger flow through tank (1.2 x 1.2 x 0.5 m) that was supplied with natural light and lined with coral sand. Coral fragments were removed from colonies collected from Pioneer Bay, Orpheus Island, Australia (18°36′ S; 146°29′E), and housed at Reef HQ aquarium. As intraspecific variation between corals may affect preferences, randomly selected fragments were taken from three separate colonies of both species. Fragments were removed using needle nose pliers that caused minimal physical damage to tissue and then kept in constantly flowing seawater for 24 h prior to trials to allow for initial recovery from mechanical stress.

Fragments where any tissue necrosis occurred were not used. Fragments were placed within the experimental enclosure at two, haphazardly selected, opposing points 15 cm from the enclosures edge. Fragments were held upright within a plastic cap using a synthetic rubber compound, minimizing any handling or direct contact with fragments prior to the start of trials. Once placed, fragments were left to acclimate for 20 min. Individual fish were introduced into a 20 cm diameter mesh cylinder in the centre of the experimental enclosure and allowed to acclimate for 10 min. The enclosure allowed fish to observe each fragment and did not restrict sensory cues. At the end of the acclimation period, at which time fish were not displaying stress coloration and were actively swimming, the cylinder was slowly removed allowing fish access to the coral fragments. Foraging behaviour was recorded for 10 min after the first bite was taken. Fish were not able to see the observer during trials. Each fragment was used only once as prior foraging may influence how attractive a fragment is to subsequent fishes. The number of bites on each fragment was converted into a percentage of the total taken during a trial. Due to non-independence between fragments, intraspecific selectivity pairwise trials were analysed using the nonparametric Wilcoxon signed-rank test.

Evaluation of intraspecific morphological variation in corals

The relative importance of structural variation within and between corals species was assessed by comparing fragments that varied in skeletal morphological variables that affect the underlying surface complexity, namely polyp size and density. These were corallite cup diameter across the widest axis of the theca, thecal extension from highest point of the theca to base of the septa, and intercorallite distance between the focal corallite and its nearest neighbour. Morphological variation was assessed between top, middle, and base sections of *A. nobilis* and top and base sections of *A. millepora* and *A. tenuis* to correspond with observational and experimental data. Morphological variance was determined by taking physical measurements of 10 randomly selected corallites on each section of five coral fragments of each species. Morphological variation for each species was then analysed using multivariate analysis of variance (MANOVA).

3.4. Results

What coral structures are targeted by O. longirostris?

Experimental observations showed that *O. longirostris* primarily feed on coral polyps with more bites taken directly on polyps (mean = 90.9 ± 1.3) than on coenosarcs (mean = 9.1 ± 1.3), a significant difference of 81.8 (95% CI, 78–85.5), ($t_{28} = 45.2$, $p \leq 0.01$). It is likely that *O. longirostris* consumes the tissue of corals and not mucus or other by-products as polyps were visibly removed following bites.

Field study of within A. nobilis colony selectivity

During field observations, fishes did not forage on *A. nobilis* uniformly (ANOVA, $F_{2, 57} = 164.2$, $p < 0.01$). Tukey HSD post hoc comparisons showed that fish took a significantly higher percentage of bites on the central section of branches than either the top and base sections. There were no differences in the percentage of bites taken from top or base sections (Fig. 3.2).

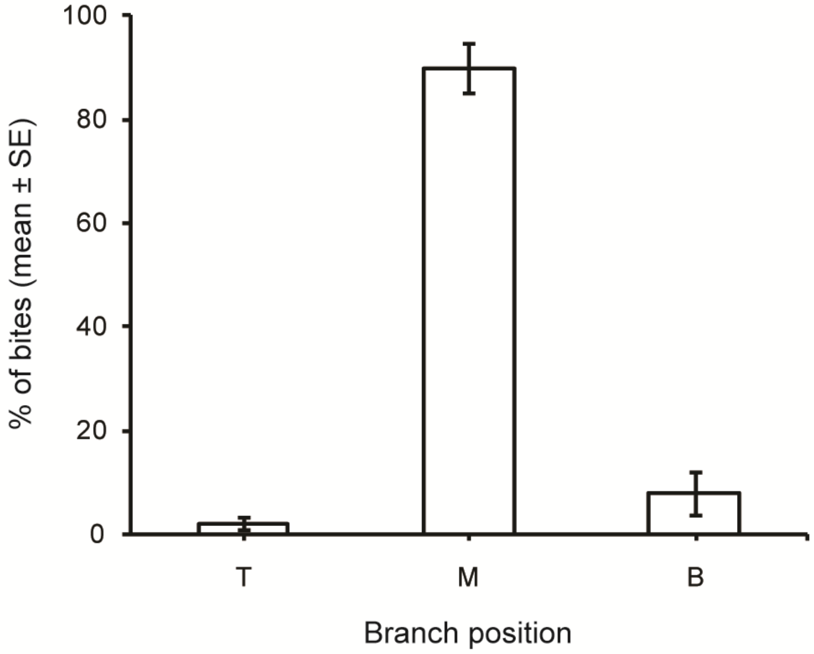

Figure 3.2. Percentage of total bites (mean ± SE) taken by *Oxymonacanthus longirostris* at different points along branches of *Acropora nobilis* during 10 min feeding observations. Individual branches were divided equally into three sections defined as top (T), middle (M), and base (B). Number of observations $n = 20$.

Experimental test of preferences using simulated A. nobilis branches

When artificial corallite extension was kept consistent, the percentage of bites was significantly greater in the central segments regardless of the corallite extension length used (all combinations, $p \leq 0.01$; Fig. 3.3). No significant difference in percentage of bites was observed between top and base segments under any of the three treatments. When artificial corallite size varied between segments, the percentage of bites also varied significantly between segments (all combinations, $p < 0.01$; Fig. 3.4). However, variation was related to artificial corallite extension, not to a particular position of a segment. The percentage of bites was significantly higher on the segment with shallow corallites than on either of the other available segments in all six trial combinations. No difference in the percentage of bites was identified between medium or deep segments in any combination.

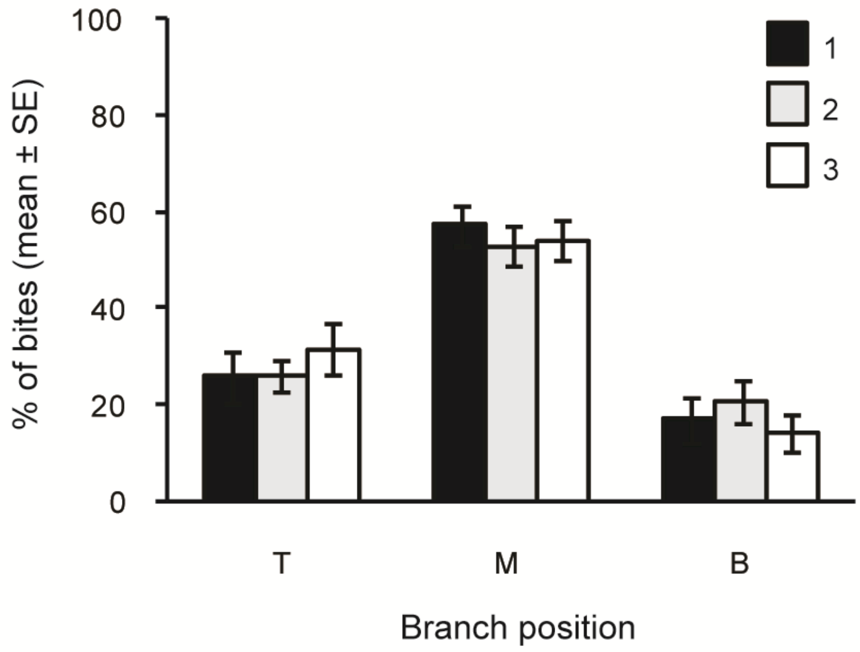

Figure 3.3. Percentage of total bites (mean ± SE) taken by *Oxymonacanthus longirostris* on each segment of a simulated *Acropora nobilis* branch when artificial corallite extension was consistent along branch. Branch segments are as follows: top (T), middle (M), and base (B). Artificial corallite extensions are as follows: shallow (1), mid depth (2), and deep (3). Sample size = 8.

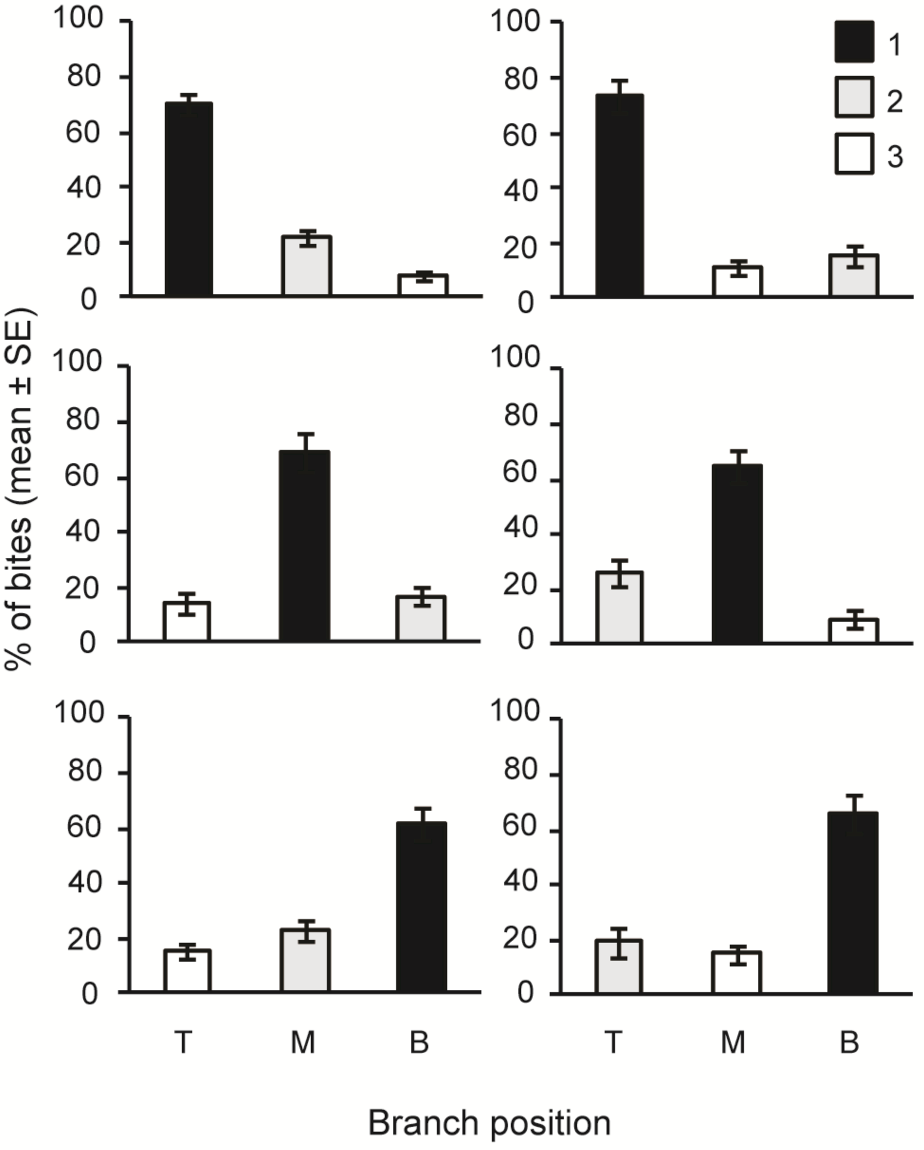

Figure 3.4. Percentage of total bites (mean ± SE) taken by *Oxymonacanthus longirostris* on each segment of a simulated *Acropora nobilis* branch when artificial corallite extension on each segment varied along branch. Branch segments are as follows: top (T), middle (M), and base (B). Artificial corallite extensions are as follows: shallow (1), mid depth (2), and deep (3). Sample size *n* = 8.

Aquarium study of within-colony selectivity

No significant preference was identified between *A. millepora* and *A. tenuis* when fish were presented with large pieces of each coral species (Z = -0.52, p = 0.61). However, during pairwise trials, feeding selectivity varied depending on the choice presented (Fig. 3.5). While no intraspecific preference was shown between top and bottom sections of *A. millepora* branches ($Z = -0.16$, $p = 0.88$), fish preferentially fed on the bottom sections of *A. tenuis* branches compared with top sections ($Z = -3.52$, $p < 0.01$). When coral species was mixed but the original location (top or bottom sections of branches) was kept the same, preferences between the two coral species depended on whether top or bottom sections were presented. Fish exhibited a preference for top sections of *A. millepora* over top sections of *A. tenuis* ($Z = -2.48$, $p = 0.01$), but preferentially consumed bottom sections of *A. tenuis* over bottom sections of *A. millepora* ($Z = -2.53$, $p = 0.01$). When both species and point of origin of fragments were mixed, fish preferentially fed on the base sections *A. millepora* over top sections of *A. tenuis* ($Z = -2.33$, $p = 0.02$) and base sections of *A. tenuis* over top sections of *A. millepora* ($Z = -2.07$, $p = 0.04$).

Evaluation of intraspecific morphological variation in corals

No significant differences were identified between sections of *A. nobilis* branches with regard to the morphometric variables recorded (corallite diameter, thecal wall extension, and intercorallite distance), $F_{3, 290} = 1.2$, $p > 0.05$; Wilk's $\lambda = 0.95$, partial $\varepsilon^2 = 0.02$. However, significant morphometric differences were detected within *A. millepora* and *A. tenuis* branches, $F_{3, 472} = 48.6$, $p > 0.05$; Wilk's $\lambda = 0.2$, partial $\varepsilon^2 = 0.4$ (Fig. 3.6). For corallite diameter, no significant difference was found within *A. millepora* or *A. tenuis*. However, *A. tenuis* corallites were significantly larger than *A. millepora* corallites regardless of location ($p < 0.05$). For thecal extension, no significant difference was found within *A. millepora*, or between bottom sections of *A. tenuis* and either *A. millepora* top or bottom sections. However, the thecal wall extension of top sections of A. tenuis was significantly higher than all other sections of both species ($p < 0.05$). For intercorallite distance, no difference was found within *A. millepora* or *A. tenuis*. However, intercorallite distance was significantly greater on *A. tenuis* than *A. millepora* regardless of location ($p < 0.05$).

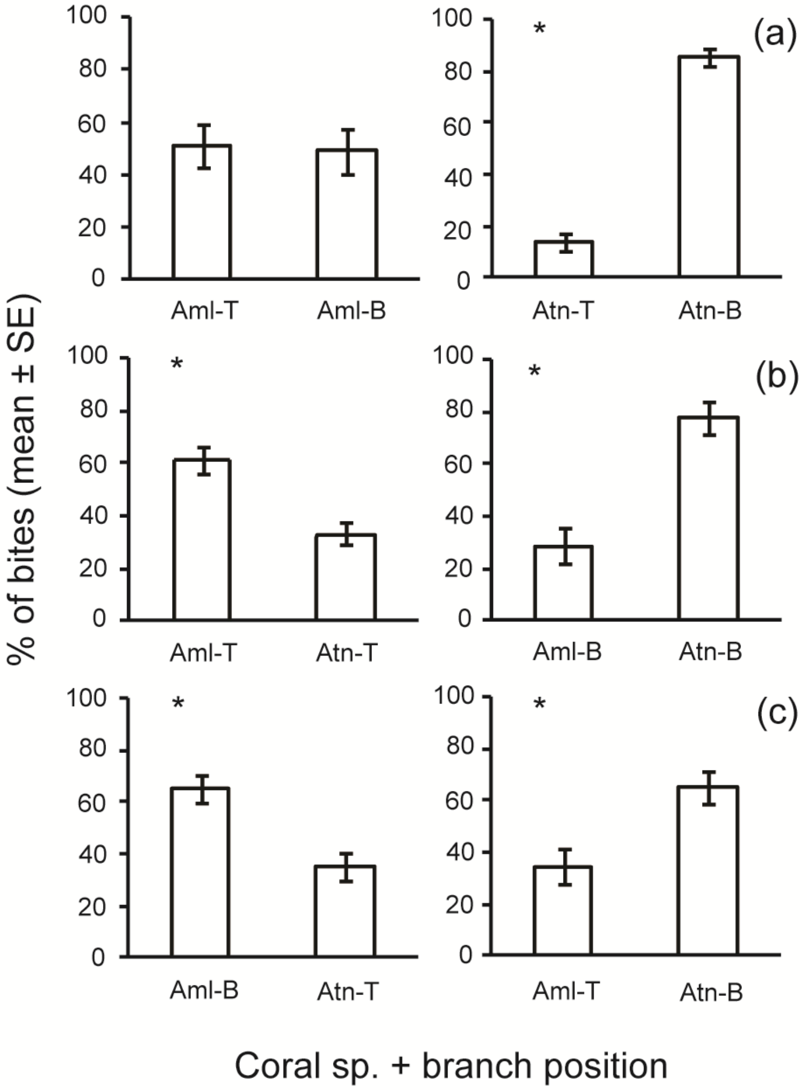

Figure 3.5. Percentage of total bites taken by *Oxymonacanthus longirostris* on different coral fragments during pairwise trials. Row (A) same coral species but different points of origin (top or base of branch), row (B) different coral species but same points of origin, and row (C) different coral species and different points of origin. Coral fragment types were *Acropora millepora* – base section (Aml-B), *A. millepora* – top section (Aml -T), *Acropora tenuis* – base section (Atn- B), and *A. tenuis* – top section (Atn- T). * indicates a significant difference between means. Number of observations *n* = 16.

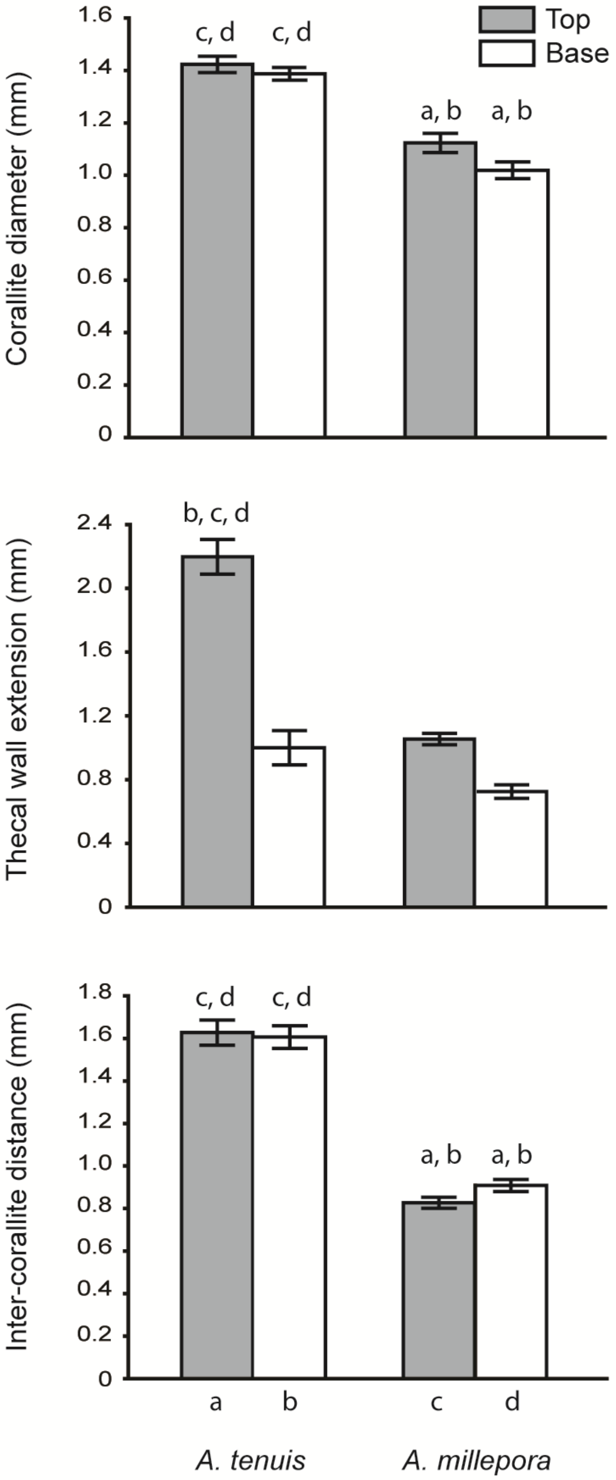

Figure 3.6. Variation in three selected measures of corallite morphology between coral fragments used in pairwise trials (see Fig. 3.3). Coral fragment types were *Acropora millepora* – base section, *A. millepora* – top section, *Acropora tenuis* – base section, and *A. tenuis* – top section. Numbers above bars denote the fragments that were significantly different from that fragment for a given measure. Number of coral fragments per type *n* = 12

3.5. Discussion

Our field studies and laboratory experiments demonstrate that *O. longirostris* does not feed uniformly from coral colonies, but is selecting feeding positions with greater polyp accessibility, rather than those that are more nutritious. In the field, *O. longirostris* fed non-uniformly on the branching coral, *A. nobilis*, a species that forms the bulk of its diet (Chapter 2). Fish mostly fed centrally on each coral branch, avoiding areas near the growing tips and bases where branches intercept. Foraging observations also confirmed that *O. longirostris* targets individual polyps. In a pairwise choice experiment, where two factors, *Acropora* species and the point of origin of fragments (top or bottom sections of branches), fish selected fragments with comparatively larger, or numerous polyps. Fish appear to modify their foraging to select the most efficient prey available. When food accessibility was standardized along a branch, fish fed mostly on the central sections of the branch, irrespective of the level of accessibility. However, when food accessibility was manipulated so that it varied along the branch, fish consistently fed on the section of branch with the shallowest corallites regardless of its location. Together, these results suggest that patterns of within-coral selectivity by *O. longirostris* may reflect active choices made to increase foraging efficiency.

The actual tissue consumed by presumed corallivores is often not known (Cole et al. 2008). Our aquarium observations show that *O. longirostris* is predominantly a coral polyp feeder, selectively targeting individual polyps while avoiding the coenosarc. It is likely that this selectivity reflects the relative benefit of coral polyps as a food resource. Each coral polyp consists of a fleshy body cavity extending to the basal plate of the corallite cup, enclosed by the mouth and a ring of tentacles. In contrast, the coenosarcs is a relatively thin layer of tissue that covers the underlying skeleton between these polyps. Therefore, selectively targeting polyps should allow a greater volume of tissue to be removed per bite, offsetting any increase in search times. Other corallivores including many butterflyfishes are also assumed to preferentially consume coral polyps (Alwany et al. 2003; Cole et al. 2009). While many species, including *O. longirostris*, have jaw and mouth structures that appear adapted for removing polyps there is limited direct evidence for this, with this assumption often based on gut content analysis that may fail to distinguish between polyps and general tissue (e.g., Hiatt and Strasburg 1960; Sano et al. 1984; Harmelin-Vivien 1989). As *O. longirostris* targets polyps, variation in polyp morphology, defensive structures, or the biochemical composition of polyps that increases or decreases the amount of energy consumed could have a direct influence on prey preferences both within and between coral species. In addition, it is possible that fish target polyps that maximize the effectiveness of their specialized trophic morphology.

In the field, *O. longirostris* exhibited highly non-uniform patterns of foraging on the branching coral *A. nobilis*. Foraging theory predicts individuals should target prey that maximizes energetic return (Pyke et al. 1977). Variation in the tissue composition or surface structure within a coral colony may alter the relative prey value by increasing or reducing the efficiency with which it can be consumed or assimilated. However, no significant variation was found in the morphometric variables of the *A. nobilis* coral branches examined, suggesting that within-colony selectivity is not driven by structural differences of the corallites, at least for this coral species.

There is evidence that the biochemistry of coral tissue can vary within a colony due to metabolic processes. For instance, the concentration of lipid, which is often indicated as being particularly important for corallivorous fishes (Tricas 1989a; Rotjan and Lewis 2009), can vary within individual *Acropora* branches. Fang et al. (1989) found that polyps near the growing tip of the branching species, *Acropora formosa*, had lower lipid concentrations than polyps further down the branch, suggesting a biochemical gradient occurs as metabolites are transported up toward the growth point. While this suggests foraging near the growing tip may be less nutritionally beneficial, fish also avoided foraging near the base of branches. Foraging near the base may be less efficient due to the morphological constraints of locating suitable polyps in narrow areas where branches intersect and may require the fish to orientate itself at a suboptimal angle when searching or foraging. Midbranch, fish would have the greatest range of unrestricted motion. It is possible that predation risk may also influence feeding position; feeding near branch tips may increase potential exposure to predators, while feeding near branch bases may restrict movement and escape potential.

Behavioural experiments using simulated *A. nobilis* branches indicated that *O. longirostris* can distinguish between potential prey based on small morphological differences and, when preys are nutritionally similar, will modify their foraging patterns to preferentially select prey that are the most accessible and will presumably require the minimum effort to acquire. When simulated coral branches had identically sized artificial corallites along the branch, making food accessibility equal between segments, fish consistently fed on the central segment. This replicates the foraging patterns observed on *A. nobilis*, a species that morphometric measurements indicated has similar polyp morphology from the base to the tip of the branch. This suggests that, when there is limited structural variation, *O. longirostris* may have an innate drive to feed centrally along the branches of arborecent corals. The underlying basis for this behaviour is not known but it may relate to nutritional variation between polyps along a branch if this is consistent between branches (Fang et al. 1989) or morphological constraints that affect foraging efficiency. However, when artificial corallite extension was manipulated this central foraging pattern was overridden, with fish preferentially foraging on the segment with the shallowest artificial corallite size regardless of its location. This consistent modification of foraging selectivity implies that the shallow artificial corallites were the most attractive to fish, either due to food being closer to the surface of the corallite thereby reducing the effort needed to extract it or increasing the amount that could be removed per bite, or food being more visible and so reducing the effort needed to search between bites. This result indicates that foraging decision-making by *O. longirostris* is flexible with fish able to recognize and respond to small differences in prey characteristics, and are able to modify their foraging behaviour when presented with a novel prey to maximize foraging efficiency.

In the pairwise choice experiment using live coral fragments of two preferred *Acropora* species (*A. millepora* and *A. tenuis*), fish varied their prey preferences depending on the combination of coral species and point of origin of fragments (top or bottom sections of branches) presented. The preference patterns observed appear to reflect the morphological differences between coral fragments, specifically those that relate to polyp size and density. For instance, no significant difference was found along *A. millepora* branches with regard to any of the morphological variables recorded, and no foraging preference was exhibited by *O. longirostris*. However, fish exhibited a preference for the lower parts of *A. tenuis* branches where thecal extension was significantly less, and polyps were therefore less protected. Fish also exhibited a general preference for the bottom sections of *A. tenuis* branches over either section of *A. millepora*. While corallite density was slightly higher on *A. millepora*, *A. tenuis* was found to have larger corallites. This may increase the relative amount of tissue that can be removed per bite, increasing overall foraging efficiency (Tricas 1989a). No preference was observed between coral species when fish were provided with larger sections of coral composed of several whole branches. As *A. millepora* is known to be a preferred prey for *O. longirostris* (Chapter 2), it is therefore possible that overall both species represent equally valuable prey for these fishes. However, *A. millepora* may still be preferentially selected in the wild as fish chose the upper sections of *A. millepora* over those of *A. tenuis*, and lower sections of *A. tenuis* branches would remain difficult to access within fully intact colonies. The relationship between variation in corallite structure and prey preferences suggests that small-scale morphological differences between and within corals can affect the foraging decisions of *O. longirostris*.

Foraging selectivity is exhibited in many corallivorous species (Cole et al. 2008) with the consumption of preferred coral having beneficial effects on a variety of fitness-related parameters (Berumen et al. 2005; Berumen and Pratchett 2008; Chapter 2). It is generally assumed that these preferences relate to the nutritional content of coral tissue (Berumen et al. 2011; Pisapia et al. 2012). Despite this, attempts to relate preferences for specific corals to the relative levels of the major energetic macronutrients, such as lipids, protein, and carbohydrates, have failed to find strong correlations (Tricas 1989a; Keesing 1990). However, these studies have generally considered the biochemical profile of each sampled colony as a single replicate. When within-colony differences were assessed, namely the total reproductive effort of polyps, Rotjan and Lewis (2009) found parrotfish consumed areas of *Montastraea* colonies with high numbers of gametes, ostensibly due to their higher protein and lipid levels. If the nutritional value of coral tissue consistently varies within a colony, and corallivores only target specific parts, then relevant differences in nutritional quality between coral species may have failed to be recognized due to a sampling methodology that does not account for these within-colony foraging patterns. Future work should therefore consider the biochemical variation within corals when attempting to determine a nutritional basis for foraging preferences.

Our results provide strong support for the hypothesis that coral morphology can influence corallivore foraging preferences. Morphology has previously been indicated in the preferences of the butterflyfish, *C. multicinctus*, where fish exhibited a strong preference for the massive *Porites lobata* over the branching *Porites compressa* (Tricas 1989a), implying that the relatively flat foraging surface of *P. lobata* was the key driver of the preference. Many corallivorous fishes, including *O. longirostris*, preferentially target morphologically similar *Acropora* corals, generally digitate species with short branches and a relatively open corallite structure (Cole et al. 2008; Chapter 2). These corals may allow fish to ingest a relatively large amount of tissue per bite while requiring limited reorientation between bites. It is therefore possible that for ecologically similar corallivores, such as many butterflyfishes, coral morphology may also play a key role in determining dietary preferences. While it is likely that a variety of interacting factors influence the foraging preferences of these species, further work that determines the relative importance of nutritional quality versus accessibility may help to decipher why corallivores prefer certain corals.

In conclusion, our study shows that this corallivorous fish is a highly selective polyp feeder, with within-colony feeding selectivity probably driven by a combination of both innate preferences and responses to small-sale differences in polyp morphology that may affect foraging efficiency. *Acropora* corals appear to be highly variable in their value as prey and this can affect condition and fitness of individuals (Berumen and Pratchett 2008; Chapter 2). As obligate corallivores must achieve a nutritional balance from within a relatively narrow range of potential prey, precise behavioural mechanisms that increase foraging efficiency may help these species to maximize their performance.

Chapter 4: You are what you eat: diet-induced chemical crypsis in a coral-feeding reef fish

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4.1. Summary

The vast majority of research into the mechanisms of camouflage has focussed on forms which confound visual perception. However, many organisms primarily interact with their surroundings using chemo- sensory systems and organisms may have evolved mechanisms to 'blend in' with chemical components of their habitat. One potential mechanism is through "chemical crypsis" or the sequestering of dietary elements, causing a consumer's odour to chemically match the odour of its prey. Here I test the potential for chemical crypsis in the coral-feeding filefish, *Oxymonacanthus longirostris*, by examining olfactory discrimination in an obligate coral-dwelling crab and a predatory cod. The crabs, which inhabit the corals consumed by *O. longirostris*, were used as a bioassay to determine the effect of coral diet on fish odour. Crabs exhibited a strong preference for the odour of filefish fed their preferred coral species, suggesting coral-specific dietary elements that influence odour are sequestered. Crabs also exhibited a similar preference for the odour of filefish fed their preferred coral species relative to odour directly from that preferred coral, suggesting a close chemical match. In behavioural trials, predatory cod were less attracted to filefish odour presented alongside the coral species it had been fed on, compared with filefish odour presented alongside a coral it had not consumed, suggesting diet can reduce detectability. This first evidence of diet-induced chemical crypsis in a vertebrate suggests this mechanism could occur in many taxa.

4.2. Introduction

Many organisms have evolved a range of mechanisms to match elements of their environment to avoid detection or recognition, either by predators or prey (Stevens and Merilaita 2009). The vast majority of this research has focussed on forms of visual camouflage, such as crypsis, most likely due to our own reliance on vision (Ruxton 2009). However, organisms often rely on non-visual sensory systems to interact with, and function within, their environments (Shichida et al. 2013). There is growing empirical evidence to suggest that a wide variety of taxa have evolved mechanisms to 'blend in' with other non-visual components of their environment (reviewed in Ruxton (2009)). For instance, many species have highly developed olfactory capabilities, relying on chemical, not visual, cues to locate and identify predators or prey (Conover 2007; Ferrari et al. 2010). To counteract this, an organism could employ mechanisms that render it chemically insignificant, either by limiting the chemical cues it produces (Lambardi et al. 2007; Resetarits and Binckley 2013), reducing the ability of a receiver to exploit chemical cues (Barimo and Walsh 2006; Raffa et al. 2007), or by altering these cues to match chemical signatures present within its habitat (Piskorski et al. 2010).

One potential pathway by which an organism's chemical signature can be altered is via its diet and sequestering chemical compounds from prey species (Venzon et al. 2000; Rosell et al. 2013). If habitat-specific, diet-derived compounds are sequestered by the organism, this may infer a cryptic benefit if its chemical signature is altered such that it is either not detected, or detected but misidentified, by a potential receiver. The most compelling evidence for this mechanism has come from the herbivorous *Biston robustum* caterpillar (Akino et al. 2004). Plant-specific compounds ingested while feeding are incorporated in the caterpillar's exterior cuticle, reducing its detectability to predatory ants. This "chemical crypsis" has also been reported in other herbivorous invertebrates where dietary elements are incorporated into the exoskeleton during development (Fishlyn and Phillips 1980; Portugal and Trigo 2005). However, evidence for this mechanism in other taxa is scarce. If a similar process can occur in species without external hard structures, or non-plant based diets, this would indicate that chemical crypsis may be more widespread in the animal kingdom than is currently recognised.

In diverse coral reef ecosystems, the high number of potential interactions between predators or prey may make camouflage a particularly important process. Recent analysis has revealed that many of the apparently gaudy colour patterns seen in reef fishes have an underlying cryptic function (Marshall and Johnsen 2011) and camouflage has been implicated in the colour patterns of both of both predators (Munday et al. 2003) and prey (Marshall 2000). Reef fishes also have a high reliance on non-visual senses, such as olfaction (Ferrari et al. 2010; Dixson et al. 2012; Manassa et al. 2013), for detecting predators and prey. For many reef fishes, corals form the primary source of shelter. If a species could chemically resemble its coral habitat this may provide an advantage during predator-prey interactions.

Coral-feeding reef fishes represent a good model for testing the potential importance of chemical crypsis on coral reefs. Many fishes not only feed on corals (Cole et al. 2008), but shelter within branching corals, in a manner analogous to herbivorous insect-plant systems. One particular example, the harlequin filefish, *Oxymonacanthus longirostris* (Monacanthidae), feeds almost exclusively on corals from one genus*, Acropora,* and is also selective between species (Chapter 2). Furthermore, it associates closely with these corals, particularly during crepuscular and nocturnal periods when it shelters amongst them - visually resembling a coral branch (Brooker et al. 2011). However, whether or not it sequesters chemical compounds from its diet is unknown.

The objective of this study was to investigate if *O. longirostris* are sequestering elements from their coral diet that affect odour, and if this infers a cryptic benefit. Specifically, I (1) determined whether a filefish's odour resembled the odour of a prey coral, but differed from that of a non-prey coral, suggesting coral-specific dietary elements that affect odour are sequestered. If this was the case I (2) determined how close was the similarity between a filefish's odour and the odour of its coral prey. Finally, I (3) determined whether chemically resembling a coral can impart a cryptic benefit to the filefish by reducing its detectability to reef predators.

4.3. Methods

Study location and species

This experimental work was conducted at Lizard Island Research Station, in the northern Great Barrier Reef (GBR), Australia (14°40'S; 145°27'E), between August 2013 and February 2014. *O. longirostris* is relatively common on the reefs surrounding Lizard Island, where it feeds mostly on *Acropora* corals (RM Brooker pers. obs.). *O. longirostris* were collected from the Lizard Island lagoon using hand nets and clove oil, and maintained in aquaria.

Diet treatments

O. longirostris were subject to 2 exclusive diets, either *Acropora spathulata* or *Pocillopora damicornis*, over a four-week period. Four fish were allocated to each of four 500 L tanks, two tanks for each diet treatment, ensuring an equal size distribution of fish between treatments. As corallivorous fish tend to forage continuously during diurnal periods, each tank was supplied with sufficient coral to allow fish to feed to satiation. Diet treatments began three days prior to any experimental trials to allow accumulation of coral-specific compounds that may influence odour. As waste products released during overnight trials could affect odour cues, fish from alternate treatment tanks were used each night. Prior to use in trials, all coral was removed from the treatment tank, ensuing those fish had not fed for at least 12 hrs. The absence of faecal material in the gut after this time was confirmed from visual inspection of 5 euthanised individuals. As body condition may affect odour, differences in the length-weight relationship of fishes fed each coral was recorded. At the conclusion of experiments, each fish was starved for 12 hrs with weight and length measured. The length-to-weight ratio of fish fed each coral was used as an indication of condition and was compared using a Mann-Whitney U test. Median length/weight ratio was not significantly different between filefish fed *A. spathulata* and *P. damicornis* (U =125, z = -1.171, p = 0.252), suggesting there was no significant effect of species-specific diet on condition.

Experimental evaluation of the effect of coral diet on filefish odour: a bioassay

The olfactory preferences of coral-dwelling crabs were used as a biological assay to determine the effect of coral diet on filefish odour. Two specialised crab species were used; the *Pocillopora*-obligate *Trapezia cymodoce*, and the *Acropora*-obligate *Tetralia glaberimma* (Stella et al. 2011). Coral colonies containing each species were collected and held in aquaria until use. Crab olfactory responses to filefish fed on different diets, and corals themselves, were tested in a series of pairwise choice experiments (Fig. 4.1a). The effect of diet on odour was examined by first testing (i) whether coral-obligate crabs exhibited a preference for the odour of their preferred coral over that of a non-preferred coral, and if so (ii) whether crabs would exhibit a preference for the odour of a filefish fed their preferred coral over a filefish fed a non-preferred coral. The similarity between coral and filefish odour was examined by testing (iii) whether crabs would exhibit a preference for the odour of their preferred coral over the odour of a filefish fed that coral. This was examined further by testing (iv) whether crabs preferred the odour of a filefish fed their preferred coral over the odour of a non-preferred coral (Fig 4.1a).

Pairwise trials were conducted overnight in glass aquaria (L 60cm x W 25cm x H 40cm), with a deep sand bottom (10 cm) that created a flat, textured surface on which crabs could move freely. At each end, a section of perforated pipe was located, extending horizontally above the waterline, into which a coral fragment or filefish could be placed. Perforations allowed the release of olfactory cues while restricting detectable visual cues. A third non-perforated piece of pipe, located in the centre, connected to the outflow for drainage. Inflow was split so that an equal amount of water entered each perforated pipe, creating a flow gradient towards the centre as confirmed in dye tests. An air stone, added to each perforated pipe, aided mixing.

Beside all three pipes, a fragment of coral skeleton was placed as shelter. A two cm section of 15 ml pipe, placed between each end and middle fragment, allowed crabs to move between fragments while remaining covered. Prior to trials, a filefish or coral fragment was placed in each perforated tube, ensuring that the size of fish or fragments closely matched. Following sunset, an individual crab was gently removed from its coral and placed onto the sand at the centre of the aquaria, with its subsequent location recorded at first light the following morning. Its location was rechecked 10 min later to ensure it had remained in the same location. If it was located in a coral fragment, or within 2 cm of a tube, this was regarded as a choice.

The crab choice outcomes were analysed using chi-square goodness-of-fit tests (χ^2), with H_0 being that crabs would settle next to each choice (choice A, choice B, centre) in equal frequency, suggesting no preference. Where a significant χ^2 was found, standardised residuals (*sr*) were calculated to determine what choices were driving the deviation from H_0. An *sr* greater than 2.00 meant that a choice was selected significantly more often than expected under H_0, while an *sr* less than -2.00 meant that a choice was selected significantly less often (Agresti 2013).

Coral diet and ability of a predator to detect O. longirostris

A behavioural experiment using predatory cod (*Cephalopholis spp.*) examined whether a specialised coral diet can affect detectability. Each cod was run through a series of six 30 minute trials in a randomised order, with each trial consisting of combinations of two filefish odours and corals (Fig. 4.1b). Two questions were examined; (i) did treatment have an effect on how active predators were, and (ii) when presented with the odour of a filefish that matched the live coral versus the odour of a filefish that did not match the live coral, did predators spend an equal amount of time near each odour source.

Cod, collected using hand lines, were acclimated to captivity for 3 days. 24 hours prior to experimentation, individual cod were placed into large circular tanks (1.2m diameter), supplied with seawater via an inflow pipe. Each tank contained an open shelter, extending into the tank from the wall opposite the inflow pipe. For each trial, two sections of perforated tube were placed in the tank opposite each other, and at equal distance from the shelter. An air stone, placed in each tube, created an outwards flow plume, confirmed in dye tests. One filefish was placed in each tube and, when appropriate, a small coral colony was placed next to the tube. Trials were filmed using high definition video cameras (GoPro, Woodman Labs Ltd) for later analysis. Using this video, a cod's location was recorded at 30 second intervals.

Similarity between estimated and actual activity levels in a random subset of videos showed this technique provided an accurate behavioural measure.

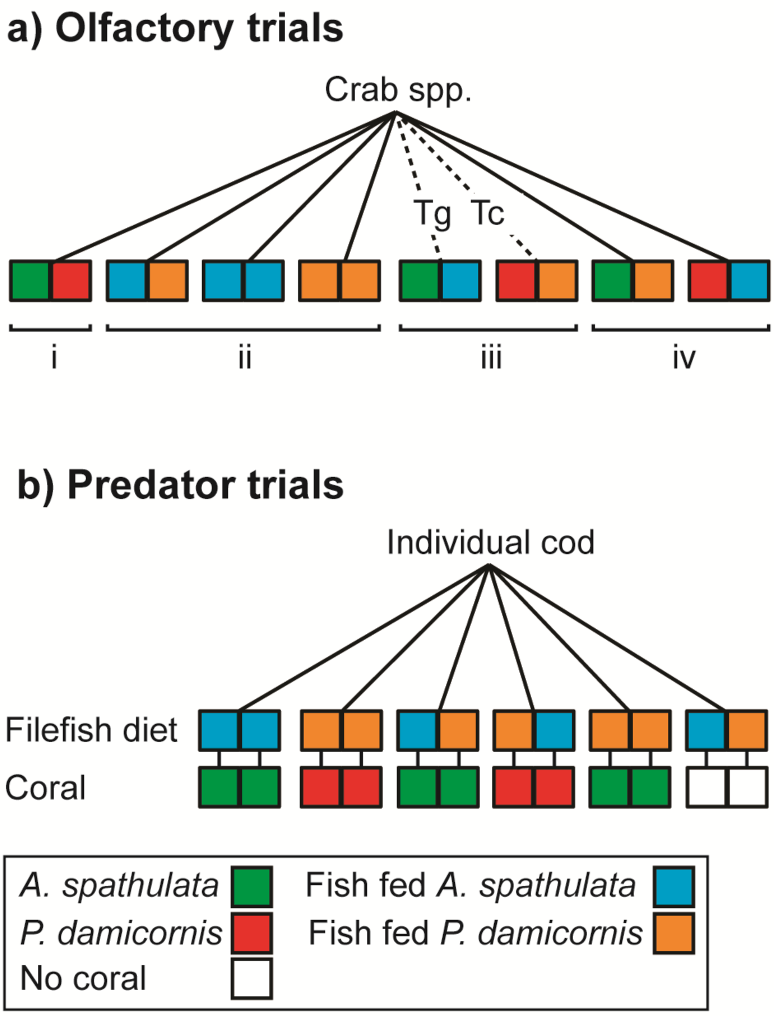

Figure 4.1. Design trees for behavioural experiments. (a) shows odour combinations used in choice trials with two species of coral-obligate crabs, as indicated in split boxes. Seven different choice trials were conducted for each crab species. Combinations conducted for both species are indicated by a solid line. Combinations indicated by a broken line were only conducted for either the *Acropora* obligate, *Tretralia glaberimma* (Tg), or the *Pocillopora* obligate, *Trapezia cymodoce* (Tc). Trial types (i, ii etc.) correspond with those in methods. (b) shows treatment combinations used in behavioural trials using predatory cod (*Cephalopholis* spp.*)*. Each treatment consisted of a choice between the odours of two filefish fed a certain coral diet, with each odour presented along with a coral colony that either matched or differed from that diet. The diet of each filefish is shown in the top row, with the

corresponding coral colony indicated directly below. Each cod was run through each of the 6 treatments in a random order.

To test the relationship between activity level and treatment, a linear mixed effects analysis was conducted using the *nlme* package in R (R Development Core Team, 2013). Treatment was included in the model as a fixed effect, with fish included as a random effect. To allow for analysis using parametric models, data was first logit-transformed following Warton and Hui (2010), using the formula *log(y+e/1-y+e)*, with *e* being the smallest non-zero proportion in the dataset. To test the relative proportion of time associated with the odour of filefish whose diet matched, or differed from, the associated coral, data from treatments 3 and 4 (Fig 5.1) were each analysed using a Kruskal-Wallis H test with post hoc comparisons performed using Dunn's test (Dunn 1964).

4.4. Results

Experimental evaluation of the effect of coral diet on filefish odour

Both crab species exhibited a strong olfactory preference for filefish that had been feeding on their preferred coral species over those fed on a non-preferred coral (Table 4.1, Fig. 4.2). As expected, both crab species preferred the odour of a preferred coral-habitat over the odour of a non-preferred coral-habitat, with *T. cymodoce* preferring the odour of *P. damicornis* and *T. glaberimma* preferring the odour of *A. spathulata* (Fig. 4.2). There was no side preference in controls.

Experimental evaluation of the similarity between filefish and coral odours

Offered a choice between the odour of their preferred coral, and that of a filefish fed that preferred coral, the majority of crabs selected coral odour. However, a number of crabs did select the filefish odour (Fig. 4.3). No significant preference between odours was identified in *T. cymodoce*, though a slightly higher proportion selected the coral odour. In *T. glaberimma*, significantly more crabs selected the coral odour than expected under H_0. However, a high percentage (37.5%) still selected the filefish odour, with the significant χ^2 driven primarily by the number that made no choice. Finally, while both species preferred the odour of their preferred coral over the odour of filefish fed a non-preferred coral, they preferred the odour of a filefish fed their preferred coral over the odour of a non-preferred coral (Fig 4.4).

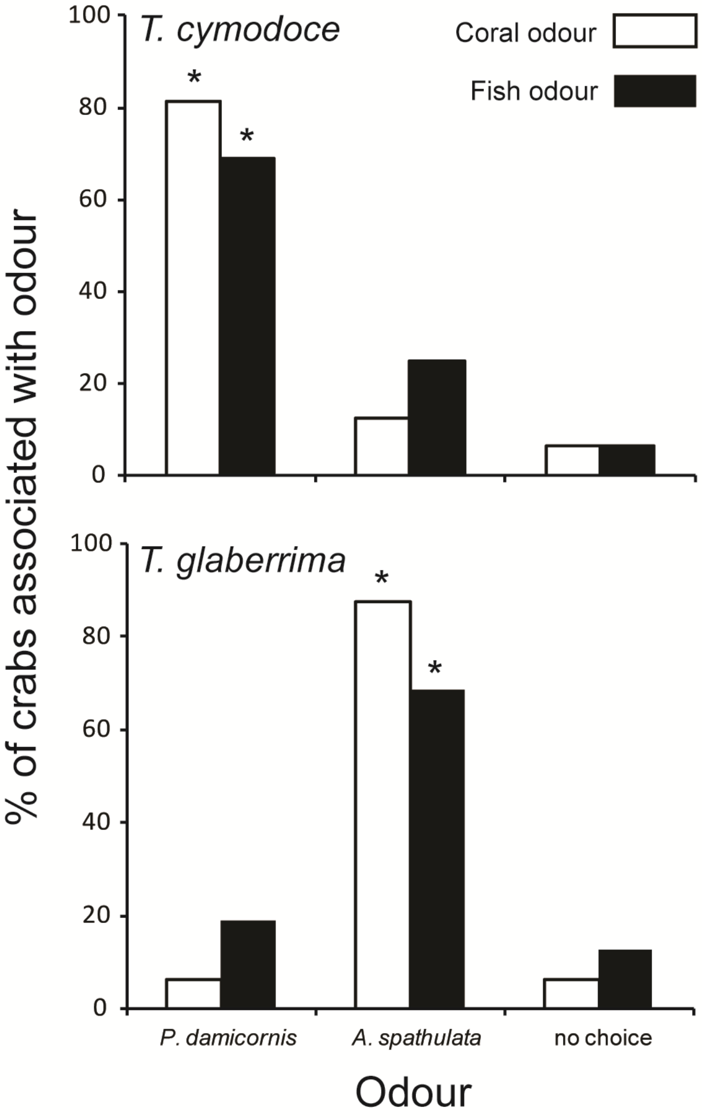

Figure 4.2. Percentage of coral-obligate crabs that associated with each odour in olfactory choice trials comparing the odours of two different corals (white), or between fish fed each different coral exclusively (black). The top graph shows results for the *Pocillopora*-obligate *Trapezia cymodoce*, while the bottom graph shows results for the *Acropora*-obligate *Tetralia glaberimma.* Coral/diet odours are *Pocillopora damicornis* and *Acropora spathulata*. An asterisk indicates a significant standardised residual was identified for that variable. Number of crabs per trial *n* = 16

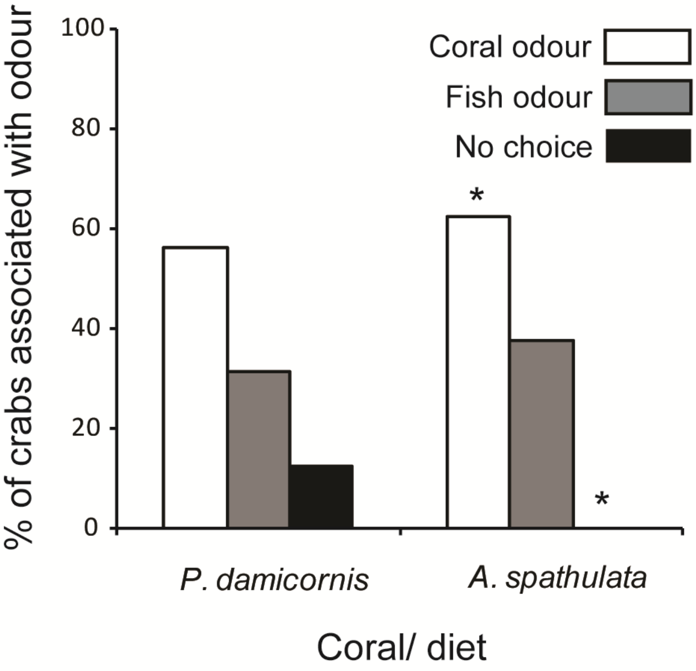

Figure 4.3. Percentage of coral-obligate crabs that associated with the odour of their preferred coral versus the odour of a filefish fed that coral exclusively. Coral versus diet trials are *Pocillopora damicornis,* using the *Pocillopora*-obligate *Trapezia cymodoce*, and *Acropora spathulata,* using the *Acropora*-obligate *Tetralia glaberimma*. An asterisk indicates a significant standardised residual was identified for that variable. Number of crabs per trial *n* = 16

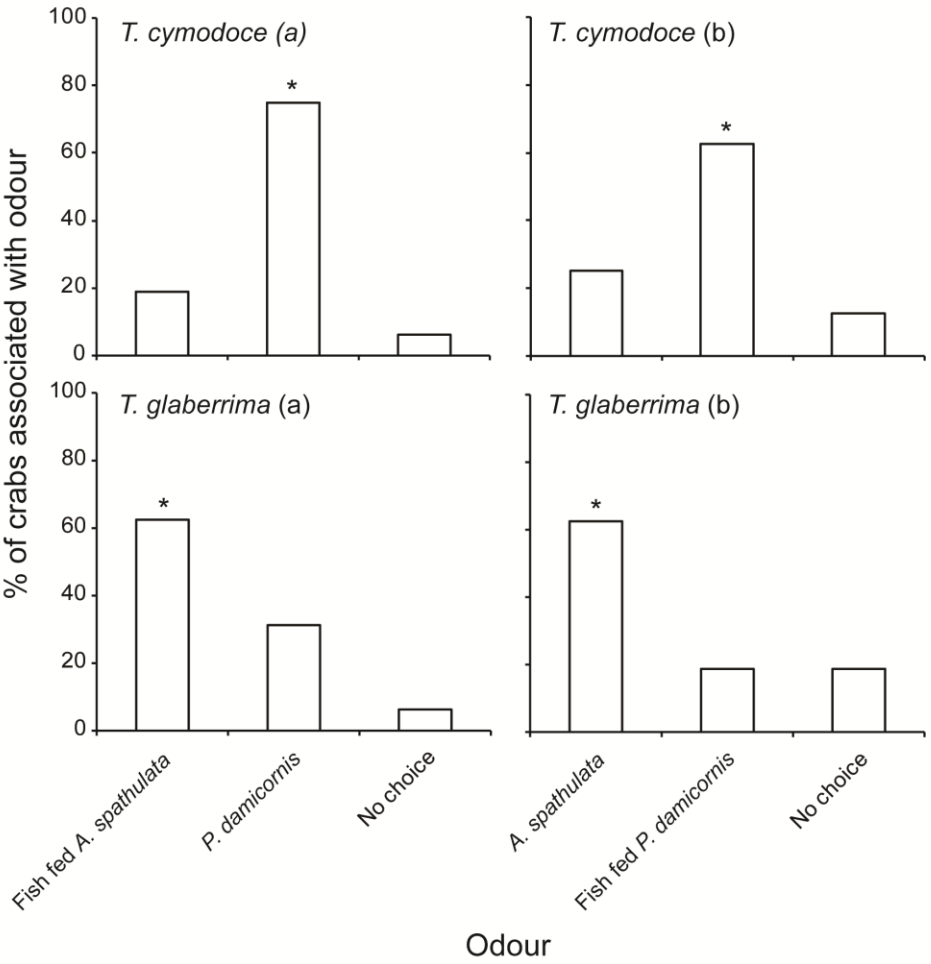

Figure 4.4. Percentage of coral-obligate crabs that associated with the odour of a non-preferred coral over the odour of a filefish fed a preferred coral, and vice versa. Coral/ diet odours are *Pocillopora damicornis,* filefish fed *P. damicornis*, *Acropora spathulata,* and filefish fed *A. spathulata*. Top row shows results of trials using the *Pocillopora*-obligate *Trapezia cymodoce*, while the bottom row shows the results of trials using the *Acropora*-obligate *Tetralia glaberimma*. An asterisk indicates a significant standardised residual was identified for that variable. Number of crabs per trial *n* = 16

Coral diet and detectability to predators

Odour treatment had a significant effect on the relative activity level of predatory cod *(F (5,130) = 15.24, p < 0.01*) (Fig 5.5). Cod were least active in treatments where all corals and filefish diets matched (*p < 0.01),* with no significant difference in activity level identified between the all *P. damicornis*, or all *A. spathulata* treatments *(p = 0.84)*. While the relative activity level of cod was significantly higher in all treatments where one or more of the fish's diets did not match the associated coral, or no coral was present, no significant difference was identified between these treatments (*p > 0.05*) (Fig 4.5). Where cod had a choice between the odour of a filefish whose diet matched, or differed from, the associated coral, cod spent more time near the filefish whose diet differed (*P. damicornis,* χ^2 (2) = 7.93, p < 0.5; *A. spathulata,* χ^2 (2) = 23.5, *p* < 0.05) (Fig 4.6). For the *P. damicornis* treatment, more time was spent near *A. spathulata*-fed filefish (Mdn = 60 %) than *P. damicornis*-fed filefish (Mdn = 10.27 %) (*p* < 0.05). For the *A. spathulata* treatment, more time was spent near *P.damicornis*-fed filefish (Mdn = 66.96 %) than *A. spathulata*-fed filefish (Mdn = 6.67 %) (*p* < 0.05), or not associated with either odour source (Mdn = 0 %) (*p* < 0.05) (Fig 4.6).

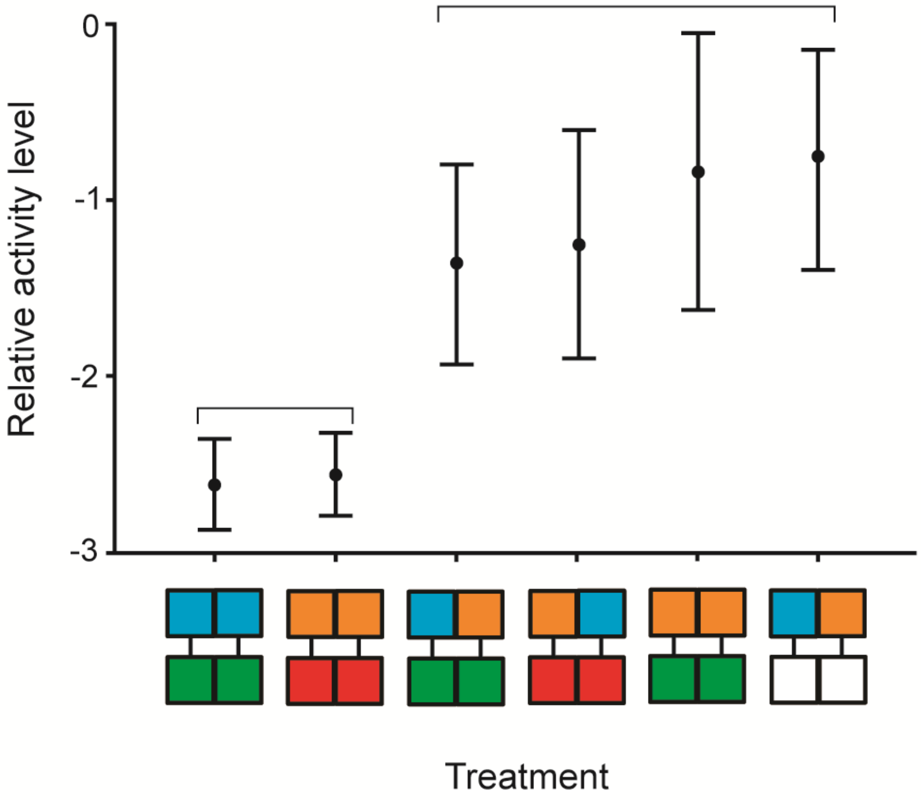

Figure 4.5. Relative activity level of predatory cod during each of the six coral/fish odour treatments. The y-axis represents logit-transformed proportional activity. Treatments are as indicated in figure 4.1 using the odours of *Pocillopora damicornis* (red), *Acropora spathulata* (green), Filefish fed *P. damicornis* (orange), and fish fed *A. spathulata* (blue). Shown are mean values with standard errors. Horizontal bars indicate treatments where relative activity level did not significantly differ in linear mixed effects analysis. Sample size per treatment *n* = 27

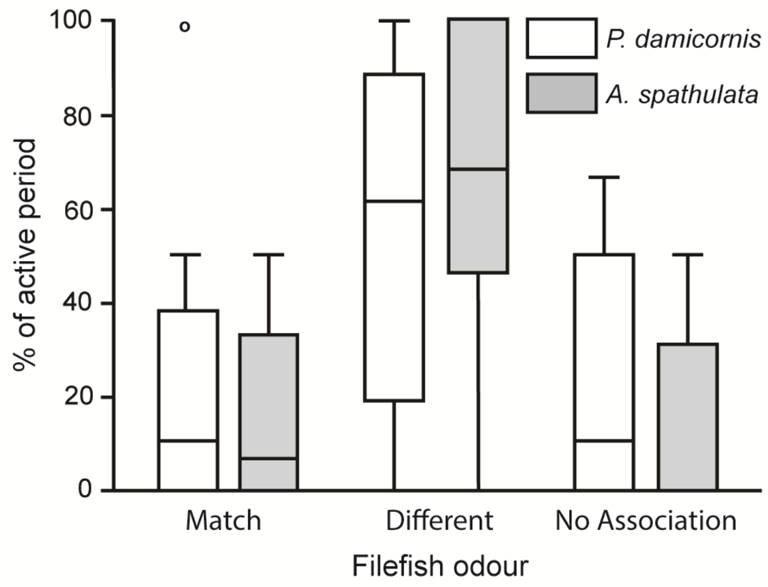

Figure 4.6. Box and whisker plot showing relative % of activity spent near the odour of a filefish whose diet matched, versus one whose diet differed from, the associated live coral during behaviour trials using predatory cod. White bars represent a treatment conducted with two live *P. damicornis*, while grey bars represent a treatment conducted with two live *A. spathulata.* Boxes represent the median and inter-quartile range, while whiskers extend out to the non-outlier upper and lower values of the data. Points indicate outliers. In each treatment, one filefish was fed *P. damicornis*, and one *A. spathulata*. NA represents the relative % of activity not associated with either odour/coral combination. Number of trials per treatment *n* = 18

Table 4.1. Summarised χ^2 goodness-of-fit test results for olfactory choice trials using two species of coral-dwelling crab; the *Pocillopora*-obligate *Trapezia cymodoce*, and the *Acropora*-obligate *Tetralia glaberimma*. Where a significant χ^2 was identified, standardised residuals (*sr*) were calculated to identify variables selected more, or less, than expected by chance. Trial codes are as indicated in figure 4.1 using the odours of *Pocillopora damicornis* (red), *Acropora spathulata* (green), Filefish fed *P. damicornis* (orange), and filefish fed *A. spathulata* (blue). Number of crabs per trial n = 16

Crab spp.	*Trial*	χ^2*(df)*	*p*	*Driven by*	*sr*
T. cymodoce	🟩🟥	16.63(2)	< 0.01	*Coral P*	3.32
	🟦🟧	9.88(2)	< 0.01	*Fish P*	2.46
	🟦🟦	1.63(2)	> 0.05	-	-
	🟧🟧	1.63(2)	> 0.05	-	-
	🟥🟧	4.63(2)	> 0.05	-	-
	🟩🟧	6.5(2)	0.04	*Fish P*	2.02
	🟥🟦	12.88	< 0.01	*Coral P*	2.89
T. glaberimma	🟩🟥	21.73(2)	< 0.01	*Coral A*	3.76
	🟦🟧	9.13(2)	0.01	*Fish A*	2.46
	🟦🟦	3.5(2)	> 0.05	-	-
	🟧🟧	0.13(2)	> 0.05	-	-
	🟩🟦	9.5 (2)	< 0.01	*Coral A*	2.02
				No choice	-2.31
	🟩🟧	6.13 (2)	0.04	*Coral A*	2.02
	🟥🟦	7.63 (2)	0.02	*Fish A*	2.02

4.5. Discussion

My results provide compelling evidence of a diet-induced chemical crypsis mechanism in *O. longirostris*. The biological assays indicate that filefish odour closely resembles that of its coral prey, suggesting coral-specific dietary elements that affect odour are sequestered. The *Acropora*-dwelling crab clearly preferred the smell of filefish feeding on *Acropora* compared to those feeding on *Pocillopora* and vice versa. The "coral" olfactory signal coming from filefish was so strong that they could barely distinguish it from the coral itself. The predator experiments clearly show that predators have difficulty using olfactory cues to distinguish filefish from the corals they eat. This is the first result of this kind, but is potentially of general significance across the range of corallivorous fishes.

The biochemical pathway from ingestion to sequestration to odour is not yet known, although fish had empty gut during trials suggesting coral-specific cues were originating from the fish itself as opposed to waste products such as faeces. In uninjured fish, odourants can originate from a number of sources, from specific chemicals released to mediate social behaviours such as pheromones, to others that are released passively as a by-product of nonrelated physiological processes (Sorensen and Stacey 2004). Small variations in the composition of these odourants could affect how distinguishable a fish is from its background (Derby and Sorensen 2008). As an example, both fish and scleractinian corals produce external mucus that is constantly being produced and sloughed off into the water column (Shephard 1994; Brown and Bythell 2005). The biochemical composition of both fish and coral mucus includes a diverse suite of amino acids (Ducklow and Mitchell 1979; Chong et al. 2005), some of which are used by fish to detect and orientate towards specific prey (Mitchel 2006). There is evidence that the amino acid composition of fish mucus can closely match that found in the diet (Saglio and Fauconneau 1985), which suggests crypsis-relevant links between diet and a fish's biochemical signature could exist. Decapod crustaceans and teleost fishes have evolved comparable chemosensory systems, using similar metabolites to gather information about their environment (Derby and Sorensen 2008). This suggests that the chemical signals used by crabs to distinguish between odours would also be those received by predatory fish.

There appears to be a clear selective advantage to sequestering coral chemical signals. In behavioural trials, predatory cod were least active when all filefish odours were presented alongside the coral they had fed on, regardless of coral species, and were more attracted to the odour of filefish that differed from the associated coral. The cognitive process underlying this behaviour was not determined, however, it is highly suggestive of crypsis as the filefish's odour was presented, as would be the case in nature, against an extensive background of coral odour rather than in isolation (Skelhorn et al. 2010). In addition, cod were more attracted to filefish odours that did not match the associated coral suggesting cod perceived a filefish's odour, when presented against a mismatched background, as potential prey. These results indicate that diet-induced chemical crypsis can have a fitness benefit by reducing detectability.

For *O. longirostris*, chemically resembling a coral would most likely be advantageous during crepuscular and nocturnal periods when individuals maintain a stationary resting position. At dusk, filefish rest amongst branching *Acropora* coral, locking themselves onto a coral branch using their dorsal spine and remaining in this position until drawn (Brooker et al. 2011). Diel patterns of predation on reefs are non uniform, with crepuscular and nocturnal periods hypothesised to be when predation risk is highest (Danilowicz and Sale 1999). Many reef piscivores are nocturnally active (i.e. the Holocentridae, Lutjanidae and Haemulidae) and these species often have adaptations to heighten sensory acuity under low light conditions, including an increased reliance on olfactory cues to locate prey (Myrberg Jr and Fuiman 2002). When stationary in amongst *Acropora*, *O. longirostris* is visually cryptic (Brooker et al. 2011), and a finely-tuned combination of visual and chemical camouflage may be an effective anti-predator strategy.

Coral reefs are home to a diverse assemblage of coral species, all of which, presumably, have unique chemical signatures. A chemical signature may also vary between coral colonies, due to condition and other factors, or even within a colony, due to biochemical differences between polyps (Fang et al. 1989). How closely the diet of *O. longirostris* needs to match the associated coral habitat to benefit the fish is not known. In this study, a mismatch between coral diet and habitat at the genus level appears to limit any benefit. However, in the wild, *O. longirostris* is known to consume a range of *Acropora* species and it is possible that simply consuming any *Acropora* corals would be sufficient to mask a fish's odour. Whether fish consciously select prey to alter their chemical signature or if this is simply a fortunate by-product of their specialised diet, is not clear. If fish do play an active role, this may explain why a large proportion of the diet is often composed of branching species of limited nutritional value (Chapter 2). Likewise, the results suggest *Pocillopora* is a nutritionally valuable prey for *O. longirostris,* but these corals are rarely consumed or used as habitat in the wild (Chapter 2; Hobbs 2013). Some nutritionally rich, non-branching species of *Acropora* appear essential for reproduction (Chapter 2). Adult *O. longirostris* are presumably less vulnerable to predation than juveniles, and may need to trade-off maximising any diet-induced anti-predator defence with the high energetic requirements of reproduction.

My results suggest that similar mechanisms of sequestration could have evolved wherever there is a close coupling between an organism's food and habitat. On coral reefs, a diverse range of fishes feed on scleractinian corals (Cole et al. 2008). While many species are highly mobile as adults, they are often very site-attached as juveniles. For example, following settlement to the reef corallivorous butterflyfish juveniles (Chaetodontidae) often use a single coral colony exclusively for shelter and food (Pratchett et al. 2008b). Scleractinian corals are also home to a diverse assemblage of small corallivorous invertebrates (Stella et al. 2011), which may incorporate cnidarian-specific elements into their tissue via digestion (Burghardt et al. 2005; Greenwood 2009). There is, therefore, potential for a wide variety of corallivorous organisms to be, either actively or passively, incorporating this mechanism into their anti-predator defences. In addition, these findings show diet-induced crypsis can occur in vertebrates, without the need for the signal-receiver to come into direct contact with the cryptic individual for a benefit to occur, increasing the likelihood of similar mechanisms occurring in a range of aquatic, and potentially terrestrial, systems.

In conclusion, this study adds a new component to the already complex array of predator avoidance mechanisms observed on coral reefs. Given that visual camouflage is often a central component of predator-prey interactions, it seems logical that organisms existing in multi-sensory environments would also employ non-visual mechanisms to conceal themselves. This study showed that, via digestion, a corallivorous fish was able to chemically resemble its coral habitat, which reduced its detectability to predators. This is the first evidence that diet-induced chemical crypsis as a mechanism can meaningfully be applied to vertebrates, and provides further evidence that non-visual camouflage plays an important role in predator-prey interactions in a variety of ecosystems.

Chapter 5: Habitat preferences of a corallivorous reef fish: predation risk versus food quality

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5.1. Summary

Many animals preferentially select a habitat from a range of those potentially available. However, the consequences of these preferences for distribution and abundance, and the underlying basis of habitat preferences are often unknown. The present study, conducted at Great Keppel Island, Australia, examined how distribution and abundance of an obligate corallivorous filefish, *Oxymonacanthus longirostris*, relates to coral architecture and diversity. The main drivers of the distribution and abundance of *O. longirostris* among reefs were coral species richness and availability of branching coral. Feeding territories had a higher percentage of *Acropora* coral than surrounding habitat. In addition, feeding territories had a higher percentage of the structurally important branching coral, *Acropora nobilis*, and a primary prey species, *Acropora millepora*. A series of pairwise choice experiments in which both structural complexity and coral tissue quality were independently manipulated showed that habitat choice was primarily based on structural complexity and shelter characteristics. In addition, the choice for the preferred coral (*A. nobilis*) was stronger in the presence of a piscivorous fish. These results indicate that species-diverse coral habitats, which provide sufficient structural complexity along with nutritionally important prey, are essential for population persistence of this small corallivorous reef fish.

5.2. Introduction

Habitat selection is a significant behavioural decision that has many ecological implications, from an individual’s fitness (Huey 1991; Franklin et al. 2000) to a species distribution and abundance (Crowe and Underwood 1998). The increasing human footprint on habitat quality has underscored how little we know of the underlying basis of habitat choices (Sala et al. 2000; Creel et al. 2005; Hoekstra et al. 2005). Habitats vary in numerous characteristics and it can be a challenge to identify the critical factors involved in habitat preferences and establish why they are important. Individuals are expected to exercise habitat preferences that maximise potential fitness by either (a) increasing foraging efficiency through prey quality or abundance (Mittelbach 1981) or (b) reducing mortality risk or threat of predation (Gilliam and Fraser 1987). All animals have specific feeding requirements and habitat selection may simply reflect the presence of preferred food resources (Werner et al. 1983). However, if the risk of predation varies among habitat types, habitat choice may have more to do with minimising the risk of being eaten (e.g. Cowlishaw 1997; Downes and Shine 1998; Heithaus and Dill 2002). The inherent riskiness of a habitat is dependent on various factors including predator density and the quality of shelter. Many species exhibit preferences for structurally complex habitats (Bell and Westoby 1986; Martin and Salvador 1995; McNett and Rypstra 2000), which can reduce mortality risk by restricting movement or visual acuity of predators by providing shelter or refuge (Anderson 1984; Nemeth 1998; Elkin and Baker 2000). Given that the optimal habitat for minimising predation risk may or may not differ from that for maximizing nutritional benefits, controlled experiments are necessary to determine which factors are important.

Many coral reef fishes are closely associated with their underlying coral reef habitat, and the distribution and abundance of species has been related to coral cover (Bell and Galzin 1984; Jones et al. 2004), coral diversity (Hughes et al. 2002; Bellwood and Meyer 2009; Messmer et al. 2011), and the structural complexity of the habitats (Friedlander and Parish 1998; Wilson et al. 2007; Graham and Nash 2013). The relative importance of biotic and physical factors in habitat choice has not been resolved. Many species exhibit a high degree of apparent habitat specialisation on a small number of coral species (Elliott et al. 1995; Munday et al. 1997; Gardiner and Jones 2005; Bonin 2012; Coker et al. 2012) from which they can derive multiple resources, including food and shelter (Jones et al. 2004; Munday 2004; Cole et al. 2008). However, the specific features of the coral that are important are difficult to separate; whether it is the coral tissue quality, the structural characteristics, or both. Complex branching corals can clearly represent an important refuge from predators, with increased survivorship associated with higher complexity (Beukers and Jones 1997; Almany 2004; Noonan et al. 2012). For other species, choice of coral refuge may reflect greater access to food resources, such as the supply of plankton or benthic invertebrates (Brooker et al. 2010; Stella et al. 2011). Understanding the relative importance of food and shelter in habitat choice can provide critical insight into the processes that limit a species distribution and abundance.

The potential trade-off in habitat selection between the quality of the coral habitat for food and shelter may be most extreme in corallivorous reef fishes. The vast majority of studies (~75 %) on the ecology of coral-feeding fishes have primarily focused on the butterflyfishes (Chaetodontidae) (Cole et al. 2008), a conspicuous and diverse family of perciform fishes noted for this feeding mode. Various studies have suggested that the spatial distribution, abundance, and condition of coral-feeding butterflyfishes may relate to the availability of preferred prey resources (i.e. Bouchon-Navaro and Bouchon 1989; Tricas 1989b; Berumen et al. 2005; Pratchett et al. 2008). However, corallivory has also been reported in at least 11 other reef fish families (Cole et al. 2008), and many of these species are relatively small and trophically unlike butterflyfishes. The importance of other habitat variables to corallivores, such as habitat complexity, has seldom been considered. During vulnerable juvenile stages, many butterflyfishes are highly dependent upon the shelter provided by structurally complex corals (Pratchett et al. 2008b). The question as to which is the most important in habitat selection—food acquisition or predator avoidance—has yet to be addressed.

The objective of this study was to investigate the critical factors involved in habitat selection of the corallivorous filefish, *Oxymonacanthus longirostris*, and examine the consequences for patterns of distribution and abundance. While the close association between this filefish and coral cover, and its susceptibility to coral loss, is well known (Kokita and Nakazono 2001), the relative importance of coral structural complexity and preferred coral prey has not been investigated. To understand the relationship between habitat use and intrinsic habitat preferences it is important not only to describe natural habitat associations in the field, but also experimentally test for preferences under conditions of equal habitat availability (Singer 2000; Underwood et al. 2004). To separate the effects of coral physical structure from nutritional factors, controlled experiments are necessary. In this study the specific tasks were to: (1) examine the distribution and abundance of *O. longirostris* in the field to identify specific habitat characteristics likely to be important to the distribution and abundance of *O. longirostris* among reefs, (2) determine whether territories of *O. longirostris* are associated with areas of high structural complexity or high nutritional value, (3) experimentally test if *O. longirostris* distinguishes between coral habitats based on structural complexity, and (4) experimentally test if preferences between coral habitats are primarily dependent on prey quality or structural complexity, and if the presence of predators influences these choices.

5.3. Methods

Study species and sites

The harlequin filefish, *O. longirostris* (Monacanthidae), is distributed on shallow coral reefs throughout the Indo-Pacific. It is an obligate corallivore that feeds almost exclusively on corals from the genus *Acropora*, and is known to be severely impacted by processes that damage coral habitat (Kokita and Nakazono 2001). Adults are generally monogamous, with heterosexual pairs sharing a feeding territory (Kokita and Nakazono 1999). Recent work has shown that individuals exhibit strong dietary preferences for certain *Acropora* species, particularly *Acropora millepora* (Chapter 2).

The field components of this study were conducted at Great Keppel Island (GKI) on the southern Great Barrier Reef (GBR), Australia, during September 2009 and October 2010. GKI (23° 10.7'; 150° 57.6'E) is a large continental island located approximately 18 km from the mainland. Two aquarium choice experiments were conducted: the 1st at Reef HQ Aquarium, Townsville, Australia (19° 15.3'S; 146° 49.3'E), in May 2010, and the 2nd at Lizard Island, northern GBR, Australia (14° 40'S; 145° 27'E), in May 2012. Where applicable, data analysis was performed with SPSS v. 21 using a significance value of $p \leq 0.05$.

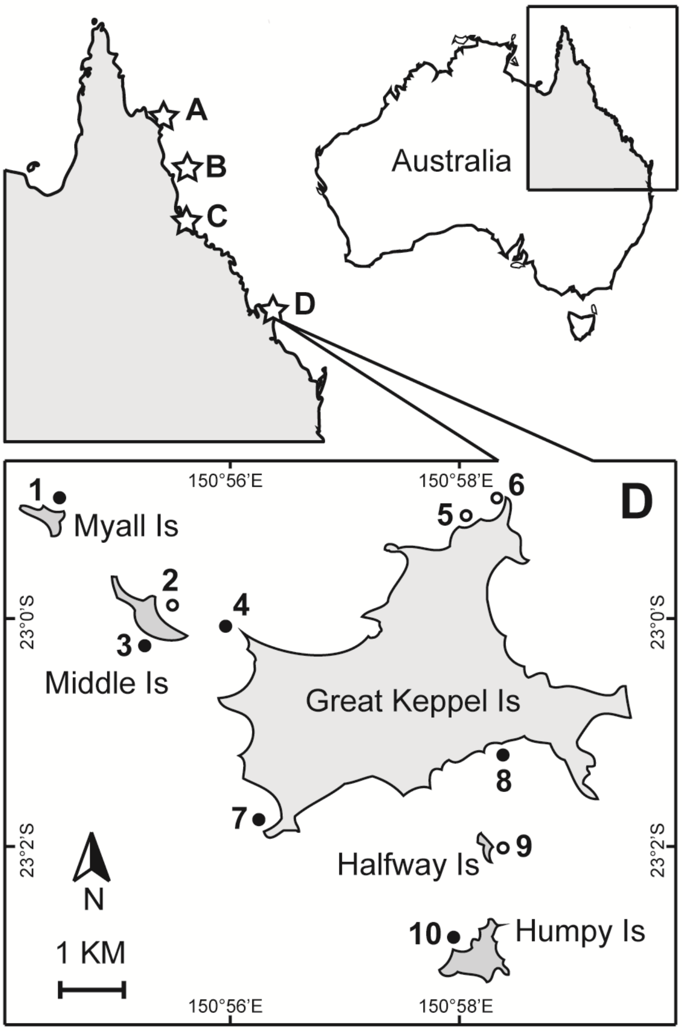

Figure 5.1 Map of study locations. Top section shows location of Lizard Island (A), Cairns mid-shelf reefs (B), Reef HQ, Townsville (C), and Great Keppel Island (D) within Australia. Bottom section shows location of the 10 surveyed reefs surrounding Great Keppel and associated islands. Reefs were east Myall Island (1), east Middle Island (2), west Middle Island (3), Passage Rocks (4), Butterfish Bay (5), Big Peninsula (6), Monkey Point (7), Clam Bay (8), east Halfway Island (9), and north Humpy Island (10). Reefs where *O. longirostris* were observed are marked with open circles

Relationship between distribution, abundance and habitat variables

A field study examined patterns of distribution and abundance of *O. longirostris* and the relationship to substrate composition. Fish abundance at 10 fringing reef locations surrounding GKI was surveyed (Fig. 5.1). To estimate the relative abundance of *O. longirostris* between each reef location, five replicate 50 m belt transects were conducted at each reef recording all *O. longirostris* observed 1 m either side of each transect. To determine coral cover and benthic community structure, the relative abundance of habitat types was measured at the same locations that the fish were surveyed. Ten replicate 10 m line intercept transects were deployed at each site, and the substrate directly under the transect recorded every 10 cm. Habitats were divided into live scleractinian coral, live soft coral, macroalgae, dead coral, hard reef substrate, and sand. Scleractinian corals were categorised into coral genera with those in the genus *Acropora* further recorded to species. For each site, additional environmental variables were recorded. These were current direction, wave exposure, and marine protected area (MPA) status. Significant differences in the benthic composition between sites were determined using ANOVA and MANOVA (SPSS v. 21). The environmental factors that best explained the distribution and abundance of *O. longirostris* were identified, using regression tree analysis (De'ath and Fabricius 2000). Density of *O. longirostris* was used as the dependent variable, with current direction, exposure, management status (marine protected area or not), macroalgal cover, branching *Acropora* cover, and *Acropora* species richness used as explanatory variables. Branching *Acropora* cover was chosen as opposed to total *Acropora* cover due to proportional dominance at all sites. Due to limited sample size, the number of leaves in the analysis was restricted to two (Brieman et al. 1984).

Habitat selectivity

To determine whether *O. longirostris* associates with areas of reef with particular habitat characteristics, the habitat composition within the feeding territories of 20 *O. longirostris* breeding pairs was compared with the overall habitat composition at Big Peninsula Reef, GKI. To calculate the area within a feeding territory, each pair of *O. longirostris* was followed on SCUBA for a period of 20 min from when it was first encountered. Pairs were followed from a distance of 2 m and showed no signs of disturbance, taken as a sign of acclimation to the diver's presence. Every time the pair moved across the substrate, their original position was marked along with the bearing and distance swum. The feeding territory was defined as the minimum convex polygon created by the marked positions. The habitat composition within each feeding territory was measured using 10 replicate 1 x 1 m quadrates placed haphazardly within the marked area. The substrate under 10 randomly determined points within each quadrat was recorded. Habitat categories were the same as those used in the field distribution and abundance study, discussed above. MANOVA and post hoc t tests were used to compare the mean proportional cover of habitat components within feeding territories with the overall habitat composition quantified during the abundance study.

Experimental evaluation of habitat preferences

Two choice experiments were conducted to determine whether *O. longirostris* has a preference for a specific coral morphology, and to evaluate the relative importance of habitat structure versus prey quality in driving habitat preferences.

Experiment 1

This ‘‘cafeteria-style’’ experiment was conducted to test the hypothesis that fish could exhibit a preference based on coral morphology, independent of coral tissue quality. Adult fish were collected from mid-shelf reefs off Cairns, Australia and held at Reef HQ aquarium, Townsville, Australia. Collection was conducted on SCUBA using clove oil and hand nets (Munday and Wilson 1997). Fish were maintained in flow through tanks during transport to shore and bagged with 100 % O2 during transport to Reef HQ. Fish ranged in size from 50 to 80 mm total length. Prior to the commencement of experiments, fish were fed ad libitum with pieces of *Acropora* species of differing morphologies supplied in equal abundance, supplemented with a standard conditioning diet consisting of prawn meal. Following experimentation fish were maintained at the Reef HQ aquarium facility. Experiments were conducted in a flow through tank (1.2 m x 1.2 m x 0.5 m) lined with coral sand. Replicate individuals were presented with four pieces of dead coral skeleton of different morphologies. This included three *Acropora* species with analogous colony morphologies to those that *O. longirostris* associates with in the field: the branching *Acropora formosa* (analogous to *Acropora nobilis*), the digitate *Acropora spathulata* (analogous to *A. millepora*), and table forming *Acropora cytherea* (analogous to *Acropora hyacinthus*), and one nonacroporid, a *Porites* (submassive with low complexity). Dead coral skeleton of analogous species was used to isolate the morphology of each coral and remove any innate preference due to feeding selectivity. Coral skeletons were clean of any algae or other organisms, which may have affected preferences. Each piece of coral was approximately equal in size, covering a 20 x 20 cm area of the tank base. However, vertical extension varied between morphologies. To account for intraspecific structural variation within each morphological type, three pieces of coral of each morphology were used in the overall experiment with one piece per morphology randomly selected for each trial. For each trial, the four coral pieces were arranged in the tank in a random order with one piece per corner. Each piece was 20 cm from each side of the tank. In this arrangement, each piece was approximately 40 cm from the neighbouring pieces. Each fish was released into a 20 cm diameter mesh cylinder with a 15 x 15 mm mesh size at the centre of the experimental enclosure and left to acclimate for a 10 min period. The cylinder’s large mesh construction allowed the fish to observe each coral fragment during the acclimation period. The cylinder was then removed, and the location of the fish was recorded every 15 s for a 10 min period. A fish was considered to associate with a particular coral if it was within 15 cm of it and in either a stationary or slow swimming position. A fish was considered to be not associated with any coral if it was beyond 15 cm of any coral skeleton. During trials, fish were not able to see the observer. A total of 21 fish were used in this experiment. Due to non-independence of corals, this cafeteria experiment was analysed using a nonparametric Kruskal–Wallis test (SPSS v. 21), with post hoc comparisons performed using Dunn's test (Dunn 1964).

Experiment 2

To investigate the relative importance of structure versus prey quality, and if predation risk influences this choice, a series of 6 pairwise trials were conducted in which choices among live and dead colonies of two coral species were compared (Fig. 5.2). Pairwise trials were repeated comparing the strength of choice in the presence and absence of a small predatory fish, giving a total of 12 experimental combinations (Fig. 5.2). The two coral species were the branching *A. nobilis* and the digitate *A. millepora*. These species were chosen because although *O. longirostris* often associates with structurally complex *A. nobilis* colonies, under controlled conditions it exhibits a strong feeding preference for *A. millepora* (Chapter 2). Both live and dead coral skeleton treatments for each coral species were included to isolate the role of morphology from feeding responses. This experiment tested the hypothesis that *O. longirostris* selects habitats primarily due to structural characteristics, and that the presence of predation risk would increase its association with structurally complex corals.

Adult fish were collected from the Lizard Island lagoon using hand nets and clove oil. Fish were ranged in size from 50 to 70 mm total length. For the duration of the experiment, each fish was housed in a 50 L tank constantly supplied with fresh sea water and aeration to maintain water quality. Experimental trials were conducted within a circular tank (1.5 m diameter) lined with coral sand. At one end, a 6 L glass predator-holding aquarium was placed on top of a concrete block so that the water level matched that of the main tank. For each trial, a fish was presented with two *Acropora* pieces and its association with each recorded. Coral pieces were approximately 40 cm diameter. To account for intraspecific structural or biochemical variability, three live pieces of each species were used with one randomly chosen for each trial. Post-experiment, all live corals were returned to reef of origin. For each trial, a fish was first placed within a 20 cm diameter mesh cylinder with a 15 x 15 mm mesh diameter at the centre of the 50 L experimental tank and left to acclimate for 30 min. The large mesh size allowed the fish to observe both coral habitats and allowed water from the tank to enter the cylinder. In this way, it did not block visual or olfactory cues. This cylinder was then removed allowing access to both coral habitats with the location of the fish recorded every 15 s for a period of 10 min. At this point, for risk trials, three *Cheilodipterus artus* were added to the internal predator-holding aquarium, and fish location was recorded every 15 s for an additional 10 min. For control trials, no predators were added. Each fish was run through all combinations of species, condition, and predation risk (i.e. 12 trials per individual) in a randomised order, with one trial conducted per day. Preferences for food were determined using the Wilcoxon signed-rank test (SPSS v. 21). A preference for branching coral independent of prey quality and the effect of predator risk were analysed using logistic regression (SPSS v. 21) with presence of preferred prey, *A. millepora* (y/n) and predator (y/n) as fixed factors.

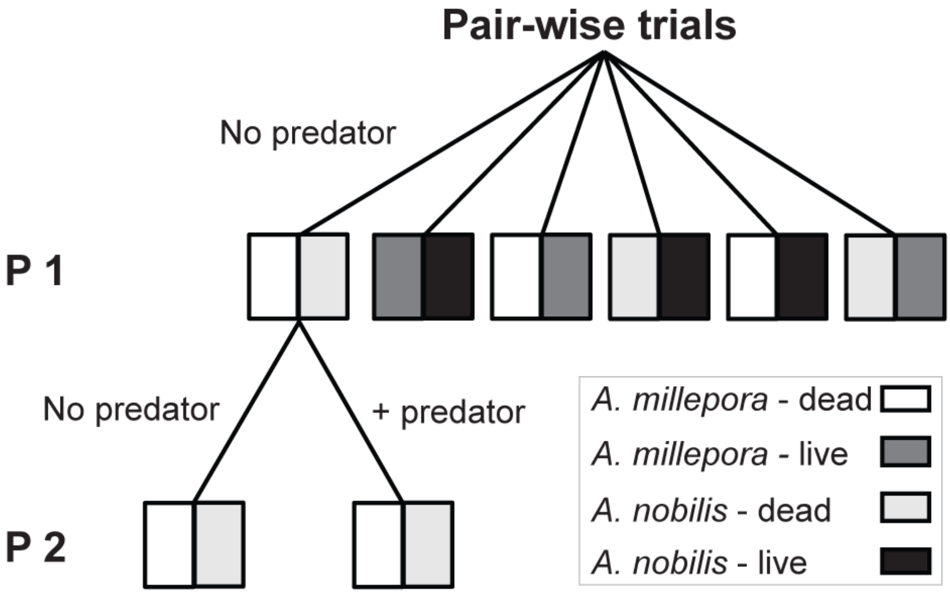

Figure 5.2. Design tree for experiment 2 with coral combinations used in pairwise trials shown in split boxes. Each trial consisted of two periods; period 1 (P1) did not include any predator, while period 2 (P2) was either consistent with P1 or introduced a predator. Following this design, a total of 12 pairwise trials were conducted for each replicate individual

5.4. Results

Relationship between distribution and abundance, and habitat variables

Abundance and composition of live coral varied among reef sites (MANOVA, Pillai's trace = 1.39, *df* = 36, 36, $p < 0.01$). *Acropora* corals were the most dominant coral genus observed. However, *Acropora* cover varied significantly among sites (ANOVA, F = 18.8, *df* = 1, 9, $p < 0.01$). *O. longirostris* was observed at four of the 10 reefs sampled; Big Peninsula, Butterfish Bay, Halfway Island, and Middle Island (Fig. 5.1). Regression tree analysis revealed that *Acropora* species richness and branching morphology accounted for the majority of variation in *O. longirostris* density among reefs (Fig. 5.3). Sites were first split by *Acropora* species richness, with no *O. longirostris* observed at sites with limited *Acropora* diversity (< 7.5 spp.). Sites where fish were observed were split by proportional abundance of branching *Acropora*, with the highest abundances recorded at sites where branching coral accounted for over 51 % of the benthos.

Habitat selectivity

The habitat inside *O. longirostris* feeding territories was significantly different from the overall habitat of Big Peninsula Reef with regard to coral cover and composition (MANOVA, Pillai's trace = 0.67, *df* = 4, 25, $p < 0.01$) (Fig. 5.4). Feeding territories had a significantly higher percentage of total *Acropora* coral cover (87.4 ± 2.34 %), *t* (28) = 5.66, $p < 0.05$, and significantly less dead coral (9.4 ± 1.98 %), *t* (-4.77) = 16.38, $p < 0.05$, than found on the reef overall (69.6 ± 2.28 % and 25.7 ± 2.83 %, respectively). The area inside of feeding territories also had higher percentage cover of two *Acropora* species. The percentage of branching *A. nobilis* was significantly higher inside feeding territories (76.2 ± 4.03 %), *t* (28) = 2.41, $p < 0.05$, than the reef overall (63 ± 3.3 %). The percentage of digitate *A. millepora* was also higher inside feeding territories (6.6 ± 1.76 %), *t* (3.13) = 10.46, $p < 0.05$, than the overall habitat (1.6 ± 0.37 %). The percentage cover of all other *Acropora* species, as well as other coral genera, recorded inside of the feeding territories did not differ significantly from the overall habitat composition. There were no differences in the percentage cover of other non-coral substrates.

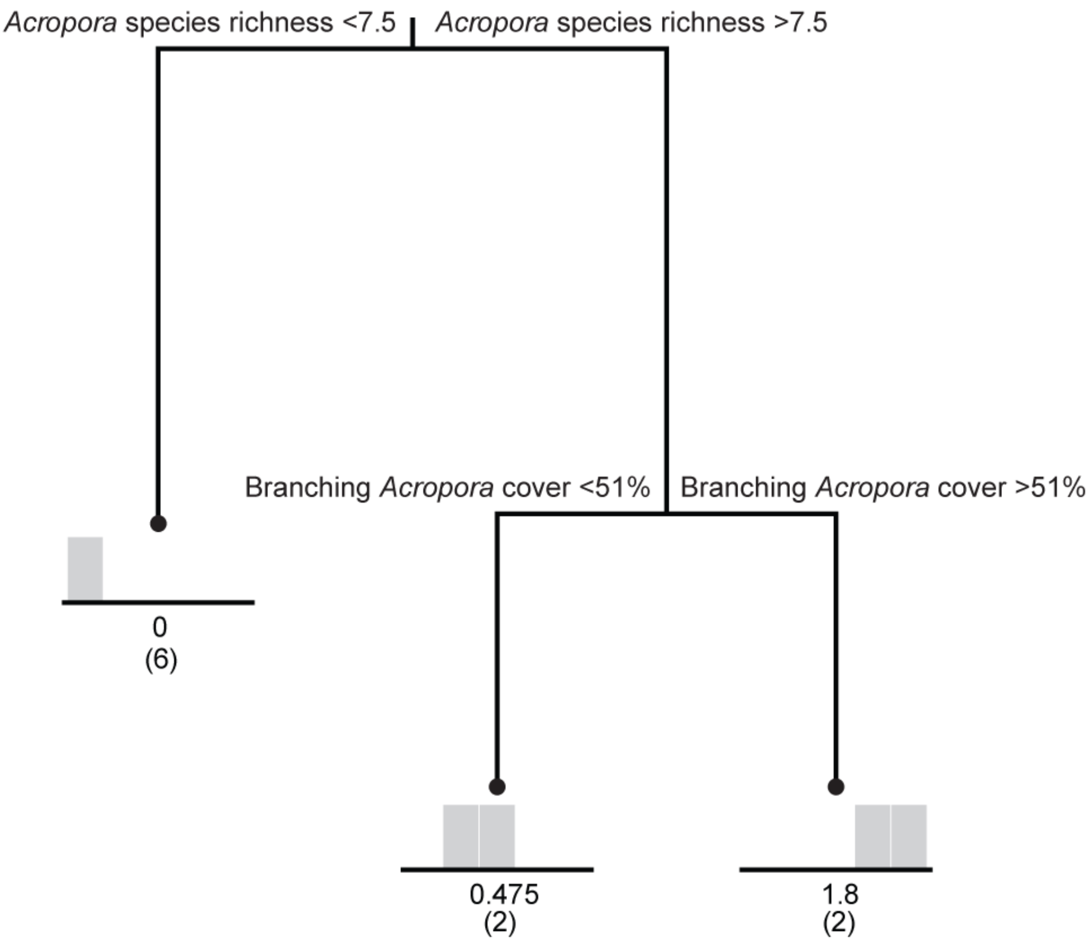

Figure 5.3. Univariate regression tree output explaining the spatial distribution and abundance of *O. longirostris* at Great Keppel Island, Australia. The length of the line from each split indicates the relative proportion of the sum of squares explained by that split. Values beneath nodes represent mean total abundance, and value in brackets is the number of replicate sites

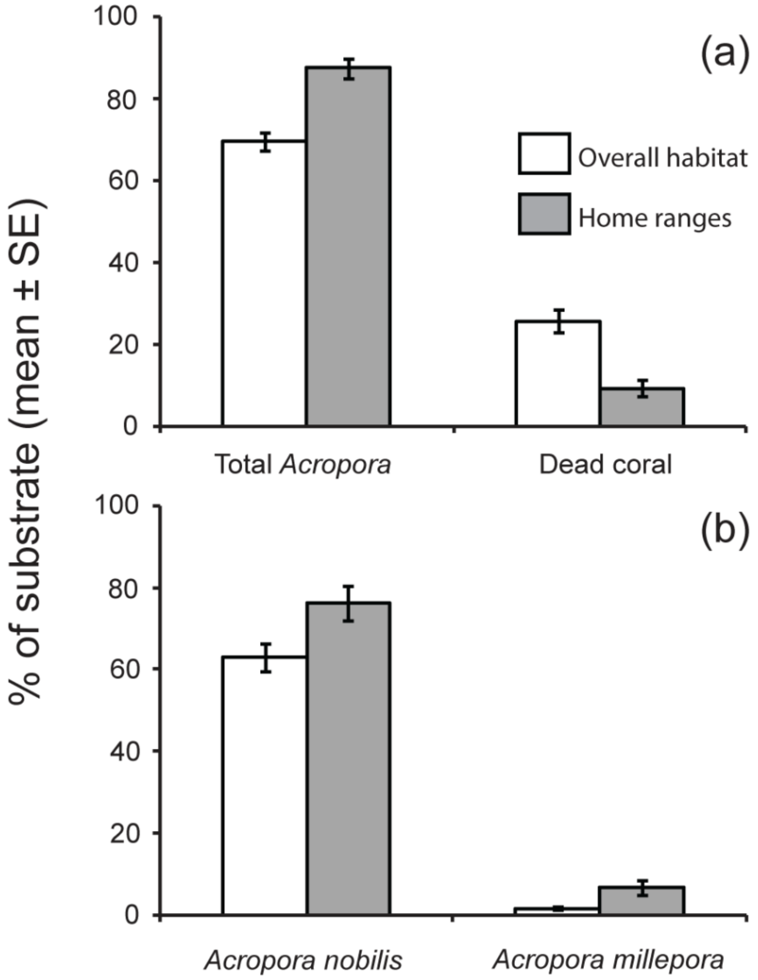

Figure 5.4. Relative per cent cover (mean ± SE) of major habitat categories within *O. longirostris* feeding territories compared with overall habitat composition at Big Peninsula Reef, Great Keppel Island, Australia. Only habitat categories found to differ significantly between feeding territories and overall reef habitat are shown. (a) Major habitat categories. (b) Specific *Acropora* species. Number of feeding territories = 20

Experimental evaluation of habitat preferences

Experiment 1

In the cafeteria experiment, fish were highly selective between morphologies (Kruskal–Wallis *H* test: χ^2 (3) = 59.46, $p < 0.01$). Post hoc comparisons indicated that fish were significantly more associated with the skeleton of the branching coral than all other morphological types presented (Fig. 5.5). The association with branching coral was much stronger than any other coral presented (mean % of time = 48 ± 6.6 % SE), with the next highest being the table morphology (mean % of time = 15.4 ± 3.8 % SE). The amount of time spent not associated with any coral was significantly higher than digitate and submassive morphologies (mean % of time = 27.8 ± 4 % SE).

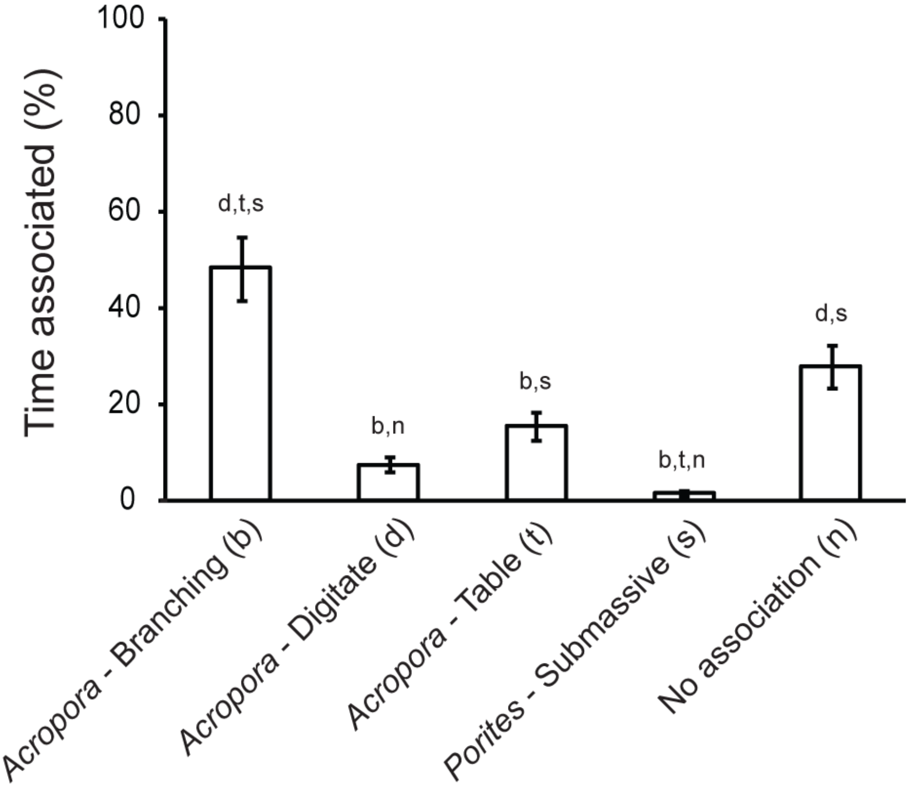

Figure 5.5. Percentage of time (mean ± SE) *O. longirostris* spent in association with each coral morphology during cafeteria-style experiment. No association represents the mean percentage of time fish were not associated with any of the coral morphologies present. Above each bar are the representative letters of alternatives which were found to differ significantly from the given morphology in pairwise comparisons. Sample size = 21

Experiment 2

During pairwise trials, fish exhibited a significant preference for live coral over skeleton of the same species (Wilcoxon signed-rank test, $Z = 4.3$, $p < 0.01$) (Fig. 5.6). However, when coral species were mixed, fish preferably associated with the branching *A. nobilis* irrespective of whether the preferred prey, *A. millepora*, was available (Wald statistic = 0.35, $p = 0.55$). While fish preferably associated with *A. nobilis* in the presence or absence of a predator (Wilcoxon signed-rank test, $Z = 7.5$, $p < 0.01$), the proportional association with *A. nobilis* was slightly higher when a predator was present (Wald statistic = 4.74, $p = 0.03$). In addition, between periods one and two, fish increased their proportional association with *A. nobilis* more frequently when a predator was introduced (Wald statistic = 7.86, $p < 0.01$).

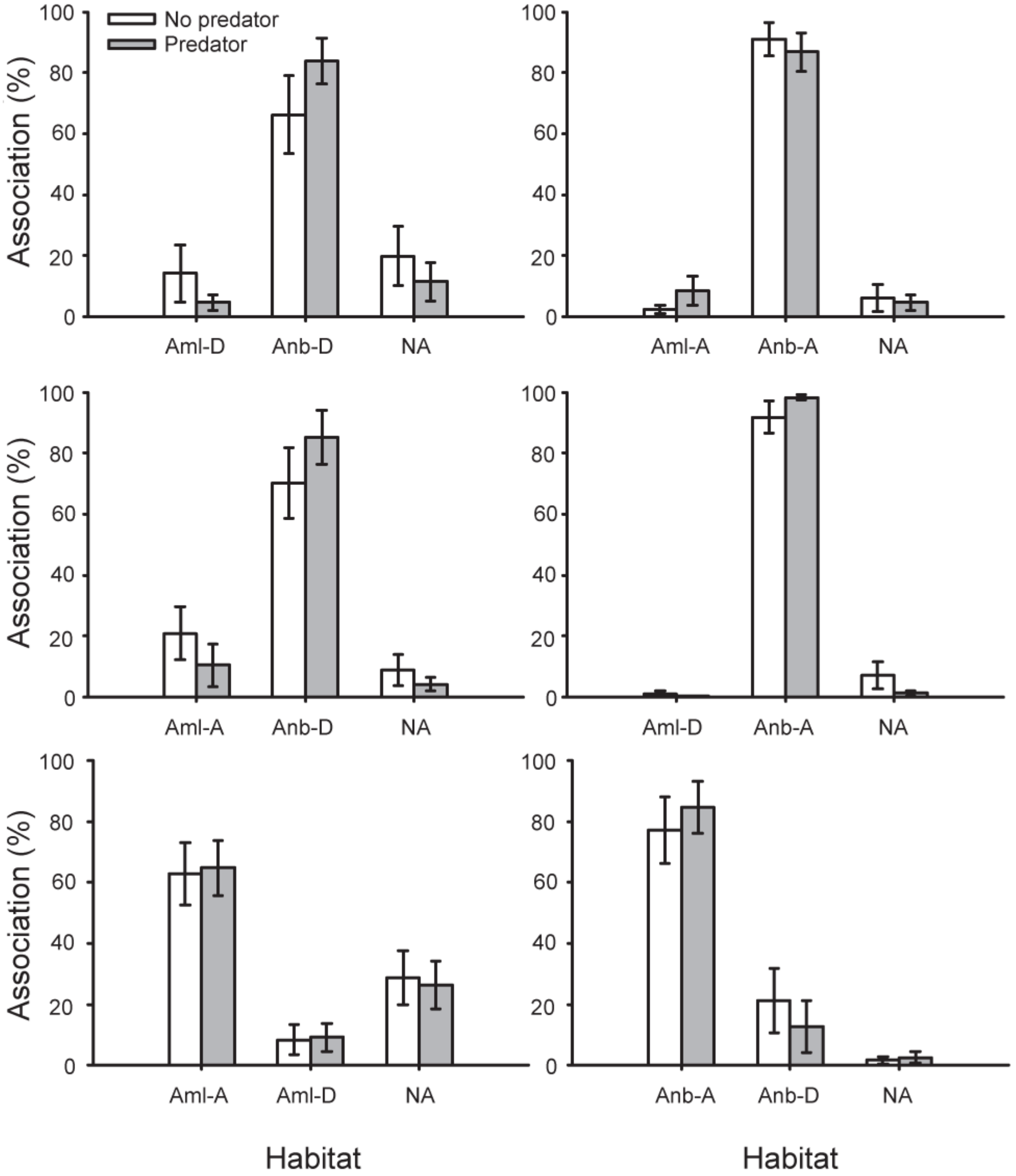

Figure 5.6. Percentage of time (mean ± SE) spent in association with each coral during the second 10 min period for each pairwise trial combination when a predator was present (grey) or absent (white). Coral types are *A. millepora* alive (Aml-A), *A. millepora* dead (Aml-D), *A. nobilis* alive (Anb-A), *A. nobilis* dead (Anb-D). NA represents the mean percentage of time fish were not associated with any of the coral morphologies present. Sample size per trial = 12

5.5. Discussion

This study indicates that *O. longirostris* exhibits a strong association with a few branching *Acropora* species, and this association appears to be a key driver of their distribution and abundance. While distribution appeared to relate to *Acropora* diversity, abundance was determined primarily by branching coral cover. At the reef scale, the presence of *O. longirostris* was associated with *Acropora* rich sites, and abundance was greatest on reefs with a high proportion of the branching *A. nobilis* and a key prey species *A. millepora*. Results of preference experiments showed that *O. longirostris* can distinguish between corals due to morphological characteristics, exhibiting a preference for branching coral skeletons over other forms. When live and dead coral were mixed, fish continued to exhibit a preference for branching coral independent of whether this coral was alive or if a preferred food resource, *A. millepora*, was available. The introduction of a predator increased the association with branching coral. Together, these results suggest that structural characteristics of the corals are a primary factor in habitat selection.

The distribution and abundance of *O. longirostris* among reefs was associated with *Acropora* species richness and branching coral cover. Obligate corallivores must often allocate a considerable proportion of their energy budget to foraging (Gregson et al. 2008); therefore, habitats where potential prey is close and abundant should maintain foraging efficiency. It is also possible that, as its dietary range is restricted (Chapter 2), access to a more nutritionally heterogeneous environment on species-rich reefs could allow *O. longirostris* to better maintain its nutrient balance, thereby promoting persistence. Reef habitats surrounding GKI are frequently dominated by branching *Acropora* corals such as *A. nobilis* that likely provide shelter from predators. Abundant shelter may allow a higher proportion of recruits to avoid predation during highly vulnerable juvenile stages, resulting in a higher abundance of resident adults. In addition, *O. longirostris* is often territorial and actively defends a feeding territory from conspecifics (Kokita and Nakazono 1999). Providing prey resources are sufficient, the increased structural complexity these corals provide may also promote abundance by reducing intraspecific competition for territory, as well as providing protection from predators (Bell et al. 1991; Almany 2004).

Feeding territories of *O. longirostris* were in areas with abundant live *Acropora* and with a higher percentage of *A. nobilis*. However, *A. nobilis* appears to be of limited nutritional value to *O. longirostris*. Chapter 2 showed that *O. longirostris* could persist on *A. nobilis*, but there was a marked reduction in condition and reproductive output over a period of 4 weeks. The presence of territories in areas with a high cover of *A. nobilis*, despite its limited nutritional value, supports the hypothesis that corals with a complex branching structure are important for shelter. Other branching *Acropora* species may also provide shelter for *O. longirostris*. Importantly, feeding territories also had a higher abundance of the preferred prey species *A. millepora*. These results suggest fish are associating with areas of reef with high structural complexity along with key prey species.

From both experiments it is clear that *O. longirostris* distinguishes between corals based on structural characteristics, and exhibits a preference for branching coral as habitat primarily due to its morphology. In experiment 1, fish selected the branching habitat independent of food availability suggesting a preference for its structural complexity. In experiment 2, where fish were offered a choice between superior branching habitat (*A. nobilis*) and superior food quality (*A. millepora*), fish continued to preferentially associate with *A. nobilis* independent of whether it was alive or dead. This also suggests that, for *O. longirostris*, structural complexity is the primary driver of habitat selection, not prey quality. The introduction of a predator only slightly increased the proportion of time spent associated with branching coral. This suggests that while *O. longirostris* does recognise predatory fishes as a threat, its association with branching coral is not an immediate response to a predator's direct presence.

As fish are particularly vulnerable to predation when feeding, the complex architecture of branching *Acropora* may provide more refuge than less complex morphologies (Beukers and Jones 1997; Almany 2004), increasing fitness potential by reducing mortality risk (Lima and Dill 1990). *O. longirostris* has the ability to manoeuvre within the architecture of branching corals, but this is not possible within denser morphologies with tightly packed branches such as *A. millepora*. In addition to the superior shelter provided by branching coral, camouflage may also influence habitat preferences. Evidence suggests *O. longirostris*' colouration and body form allow individuals to optically resemble branching coral as a predator avoidance strategy (Brooker et al. 2011). As crypsis is generally context dependent (Skelhorn and Ruxton 2010), individuals will benefit from active association with their model background. Associating in pairs may reduce the risk of attack from predators, allowing paired individuals to associate more closely with preferred prey such as *A. millepora*. Both experiments were conducted outside of the summer breeding season of *O. longirostris*. It is possible that greater energetic requirements during gonad development may increase individuals association with preferred prey species, such as *A. millepora*, during certain periods.

Unlike *O. longirostris*, the distribution and abundance of many larger coral-feeding fishes appears to correspond primarily to the availability of preferred prey corals and not the morphological complexity of the habitat. For instance, the specialist butterflyfish, *Chaetodon trifacialis*, generally inhabits highly exposed outer reef crests where its preferred coral, *A. hyacinthus*, is common (Reese 1981). In addition, Lawton and Pratchett (2012) found that abundances of both dietary generalist and specialist butterflyfishes were best predicted by dietary resource availability over large spatial scales. Differences in habitat requirements may directly relate to relative predation risk. Juveniles of both *O. longirostris* and many chaetodontids maintain close associations with live coral (Pratchett et al. 2008; RM Brooker pers. obs.), which provide food and shelter during this vulnerable life phase (Cole and Pratchett 2011). However, as butterflyfish reach adult size, mortality due to predation appears to decline, due in part to their comparatively large, high-bodied morphology and sharp dorsal and anal fins which deter piscivorous predators (Hourigan 1989), and a body-caudal fin gait which permits rapid acceleration (Fulton 2007). Reduced predation pressure may therefore allow mature butterflyfish to maximise feeding opportunity by selecting prey rich habitats, and closely associating with preferred prey species, independent of diurnal shelter availability. In comparison, the risk of mortality for *O. longirostris* likely remains high in adults due to their small size and an inflexible body morphology that likely limits startle-response speeds (Korsmeyer et al. 2002), thereby leaving fish vulnerable to lethal attack by opportunistic predators such as serranids (RM Brooker pers. obs.). Predation risk may therefore restrict the movement of *O. longirostris*, and other small dietary specialists, to within habitats that not only provide required prey but also adequate shelter to reduce mortality risk.

Specialised resource requirements may restrict *O. longirostris* to habitats which have a necessary combination of essential characteristics. Many obligate corallivores are selective between *Acropora* species, and access to preferred species has been shown to positively affect growth, condition, and reproduction (Berumen et al. 2005; Berumen and Pratchett 2008; Chapter 2). Preferred prey species of tissue feeding corallivores such as butterflyfishes and *O. longirostris* tend to be of digitate or plate forming morphologies consisting of tightly packed, upright branches that provide limited shelter opportunities leaving individuals exposed while feeding, but which may be more efficient to consume as fish require limited reorientation between bites. Where *O. longirostris* was observed in this study, the benthos was dominated by monospecific stands of branching coral interspersed with a variety of plate and digitate species. This suggests that sites which provide branching corals for shelter interspersed with nutritionally rich prey species may provide optimal conditions for these fish, allowing them to access valuable prey corals while maintaining adequate contact with shelter.

In conclusion, the combination of field observations and laboratory choice experiments indicates that habitat choice is primarily determined by the structural characteristics of corals. We hypothesise that this will be important to a range of fishes that live in or recruit into branching corals. We suggest sufficient branching *Acropora* along with key prey species will be required for persistence of *O. longirostris* populations. If so, they are the species particularly at risk from small changes in the structure and diversity of coral reef habitats.

Chapter 6: Local extinction of a coral reef fish explained by inflexible prey choice

This paper is in review with the journal Coral Reefs. Authors: RM Brooker, PL Munday and GP Jones.

6.1. Summary

While extinctions of marine species are infrequent, local extinctions are becoming common. However, the role of habitat degradation and resource specialisation in explaining local extinction is unknown. On coral reefs, coral bleaching is an increasingly frequent cause of coral mortality that can result in dramatic changes to coral community composition. Coral-associated fishes are often specialised on a limited suite of coral species and are therefore sensitive to these changes. This study documents the local extinction of a corallivorous reef fish, *Oxymonacanthus longirostris,* following a mass bleaching event. Local extinction only occurred on reefs that also completely lost a key prey species, *Acropora millepora,* even though coral cover remained high. In an experimental test, fish continued to select bleached *A. millepora* over the healthy, but less preferred prey species that resisted bleaching. These results suggest that behavioural inflexibility may limit the ability of specialists to cope with even subtle changes to resource availability.

6.2. Introduction

The global decline in terrestrial biodiversity has primarily resulted from extinctions of highly specialised species as a direct consequence of habitat loss (Clavel et al. 2010). While an evolutionary trend toward specialisation can be expected in a stable world, it can rapidly become the Achilles heel when conditions change rapidly. In the marine realm, recent global extinctions have been infrequent events (Dulvy et al. 2003). However local extinctions are becoming increasingly common (Estes et al. 1989; Monte-Luna et al. 2007; Harnik et al. 2012), and, in face of increasing environmental change, may represent the early stages of extinction. The role of habitat degradation and specialisation in explaining the local extinction of marine organisms is poorly understood. This is mainly because there is little information on what resources species are specialised on and how they respond to specific changes in resource availability.

On coral reefs, exposure to extreme environmental conditions can cause corals to bleach - expelling their symbiotic zooxanthellae and turning white. An increasing occurrence of mass bleaching has been linked to climate change and is a major cause of mortality in reef building scleractinian corals (Hoegh-Guldberg 1999). As corals vary in their susceptibility to bleaching (Marshall and Baird 2000), these events have the potential to not only reduce overall coral cover, but also alter the composition of coral communities. Many coral reef associated organisms depend on live corals to some degree (Jones et al. 2004; Stella et al. 2011) making them particularly vulnerable to changes to the underlying habitat (Munday et al. 2008). Declines in coral cover have led to dramatic declines in the abundance of some species and evidence of local extinctions (Munday 2004), whereas others appear to be far more tolerant to coral loss. The mechanisms that lead to extinctions in some species and persistence in others are poorly understood (Purvis et al. 2000; Graham et al. 2011).

Coral feeding fishes are often highly specialised, showing strong preferences for particular coral genera or species (Pratchett 2007; Cole et al. 2010) which appears to reflect prey quality (Berumen and Pratchett 2008; Chapter 2). Dramatic declines in the abundance of some corallivorous fishes have been observed following catastrophic reductions in coral abundance (Kokita and Nakazono 2001), while others appear to be resilient to these changes (Pratchett et al. 2004). The magnitude of the responses to coral loss may reflect specific changes in the composition of coral communities, and the degree of flexibility fish have in terms of prey selectivity. However, the ability of apparently specialised species to shift to less preferred corals is unknown. Following disturbance, fitness and population persistence may be negatively affected if fishes continue to target preferred corals in declining condition, or if key coral species are lost altogether. In addition, prey selectivity has the potential to influence coral community composition following disturbance. If fishes continue to target preferred corals in poor condition, necessary reallocation of energetic resources towards repair (Henry and Hart 2005) may further reduce recovery potential (Meesters and Bak 1993). Alternatively, if feeding pressure shifts to remaining healthy corals, resulting declines in condition may increase these corals susceptibility to subsequent disturbances.

The harlequin filefish, *Oxymonacanthus longirostris* (Monacanthidae) is an obligate corallivore that occurs on coral rich Indo-Pacific reefs. On the Great Barrier Reef (GBR) it feeds almost exclusively on *Acropora* corals, exhibiting strong prey preferences for specific species such as

Acropora millepora (Brooker et al. 2013a). While we know this species can be highly sensitive to disturbance that removes the majority of live coral (Kokita and Nakazono 2001), and there is some evidence that its dietary range can vary between geographic locations (Hobbs 2013), empirical evidence of its ability to change diet in response to the loss of its preferred species is missing. In 2011, following extensive flooding, a large freshwater plume caused extensive and almost immediate coral bleaching and loss of *A. millepora* (Tan et al. 2012; Jones and Berkelmans 2014) on the southern GBR. Here, we investigated how this disturbance affected *O. longirostris* and whether it exhibited a flexible feeding response. Field surveys were undertaken pre- and post-bleaching to determine if changes in fish abundance reflected changes to the composition of associated coral communities. We then carried out a controlled feeding experiment to test whether bleaching altered prey selection.

6.3. Methods

Fish abundance and habitat structure before and after coral bleaching

Surveys were conducted to examine if changes to *O. longirostris* abundance post- bleaching reflected changes to coral composition. In October 2010, prior to the bleaching event, *O. longirostris* was observed on four reefs surrounding Great Keppel Island (GKI) (23^{o}10.7’S; 150^{o}57.6’E), a site < 50 km from the major source of freshwater input. To estimate initial abundance at these reefs, five replicate 50 m belt transects were conducted, recording all *O. longirostris* within 1 m of each side. To determine benthic community structure at each reef, ten replicate 10 m line-intercept transects were deployed in the same area with the substrate beneath recorded every 10 cm (see Berumen et al. 2005; Chapter 5). Scleractinian corals were categorised to genera, with *Acropora* further recorded to species level. In December 2011, surveys of fish abundance and benthic community composition were repeated at each of the four reefs. At each reef, each survey was conducted in the same general area used in the pre-bleaching survey using an identical methodology. Variation in the abundance of *O. longirostris* between sites pre- and post-bleaching were analysed using a generalised linear model in R (R Development Core Team 2013), with a Poisson error distribution and the variables site and bleaching status treated as fixed effects. To allow for analysis of habitat variables using parametric models, proportion data was first logit-transformed following Warton and Hui (2011), using the formula log(y+e/1-y+e), with e being the smallest non-zero proportion in the dataset, and then tested using two-way ANOVA. Where transformed data violated the assumption of normality (Shapiro-Wilks test, $p < 0.05$) or homogeneity (Levene’s test, $p <$

0.05), a Friedman test was conducted. Unless stated, analysis was performed using SPSS v.21 using a significance value of $p \leq 0.05$.

Coral bleaching and prey preferences

To determine how bleaching affects feeding behaviour, an experiment was conducted at Reef HQ Aquarium, Townsville, Australia. Individual fish were offered a choice between healthy or experimentally bleached fragments from two *Acropora* species. The species, *A. millepora* and *Acropora nobilis*, were both relatively abundant at GKI, although *O. longirostris* preferentially feeds on *A. millepora* (Chapter 2). 16 fish were run through six randomly ordered pair-wise trials representing all combinations of species and condition, with one trial conducted per day. During experimentation, fish were not fed outside of trials and were housed individually to ensure they were subject to all trials. Coral fragments consisted of 3 cm lengths of individual branches and were removed from colonies collected from Pioneer Bay, Orpheus Island, Australia (18^{o}36'S; 146^{o}29'E). To account for genotypic and phenotypic variation between colonies, three colonies of each species (20 cm diameter) were haphazardly collected from varying locations along the reef. To account for within-colony variation that may affect preferences (Chapter 3), fragments used in the experiment were randomly selected from within these colonies. A random subset of coral fragments were experimentally bleached using a hyposaline treatment based on Cole et al. (2009) resulting in disassociation between zooxanthellae and the coral host. Fragments were placed in aerated, 10 ppt salinity water for 40 min then returned to fresh seawater. After 24 hours, fragments exhibited a uniform pale-white coloration indicating expulsion of zooxanthellae. Fragments where tissue necrosis occurred were not used. Following removal, untreated fragments were also left in fresh seawater for 24 hours prior to trials.

For each trial, two coral fragments were placed upright within a circular, 80 cm diameter tank at two haphazardly selected, opposite points. Twenty minutes later, fish were introduced via a 20 cm diameter, mesh cylinder placed in the centre. Following a 10 minute acclimation period, during which fish could observe each fragment, this cylinder was removed and bites on coral were recorded for 10 minutes following the first bite. Selectivity was determined using the Wilcoxon signed-rank test.

6.4. Results

Changes in fish abundance associated with habitat degradation

Prior to the bleaching event, *O. longirostris* abundance did not differ significantly between the four reefs ($p > 0.05$), although the mean abundance was slightly higher at two sites (Fig. 6.1a). A decline in abundance following bleaching was identified by the generalised linear model, which determined significantly higher abundance pre-bleaching ($p < 0.01$). While fish were still observed following bleaching at Butterfish Bay and Big Peninsula, fish densities were reduced to zero at Halfway and Midway with extensive searching indicating that they had disappeared from these sites.

Acropora composition was dominated by the branching *A. nobilis* at all sites (mean 84% ± 2.5 SE). While the proportion of benthos occupied by *Acropora* corals was significantly higher at Butterfish and Big Peninsula compared with Halfway and Midway sites, both pre- [$F_{(3, 72)} = 31.92$, $p < 0.01$], and post-bleaching [$F_{(3, 72)} = 9.9$, $p < 0.01$] (Fig. 6.1b), substantial *Acropora* cover did remain at all sites post-bleaching (Fig. 6.1b). However, while the proportion of benthos occupied by a preferred coral species for the filefish, *A. millepora,* did not vary significantly among sites pre-bleaching [$X^2_{(3)} = 3.1$, $p > 0.05$], it did post-bleaching [$X^2_{(3)} = 8.6$, $p < 0.05$]. It was still present at Butterfish and Big Peninsula, but had completely disappeared from the Halfway or Midway sites (Fig. 6.1c), confirmed through extensive searching.

Coral bleaching and prey preferences

Prey choice varied depending on *Acropora* species and tissue condition (Fig. 6.2). When offered a choice between healthy or bleached fragments of the same species, fish preferred healthy fragments of both *A. millepora* ($z = -2.85$, $p < 0.01$) and *A. nobilis* ($z = -3.54$, $p < 0.01$) (Fig. 6.2a). Between *A. millepora* and *A. nobilis* in the same condition, fish preferred *A. millepora* regardless of whether fragments were healthy ($z = 3.62$, $p < 0.01$) or bleached ($z = 3.55$, $p < 0.01$) (Fig. 6.2b). Fish also preferred healthy *A. millepora* over bleached *A. nobilis* ($z = 3.52$, $p < 0.01$) (Fig. 6.2c), consistent with the results of previously discussed trials. However, when the condition was reversed, fish continued to prefer bleached *A. millepora* and did not switch to healthy *A. nobilis* ($z = 3.42$, $p < 0.01$) (Fig. 6.2c).

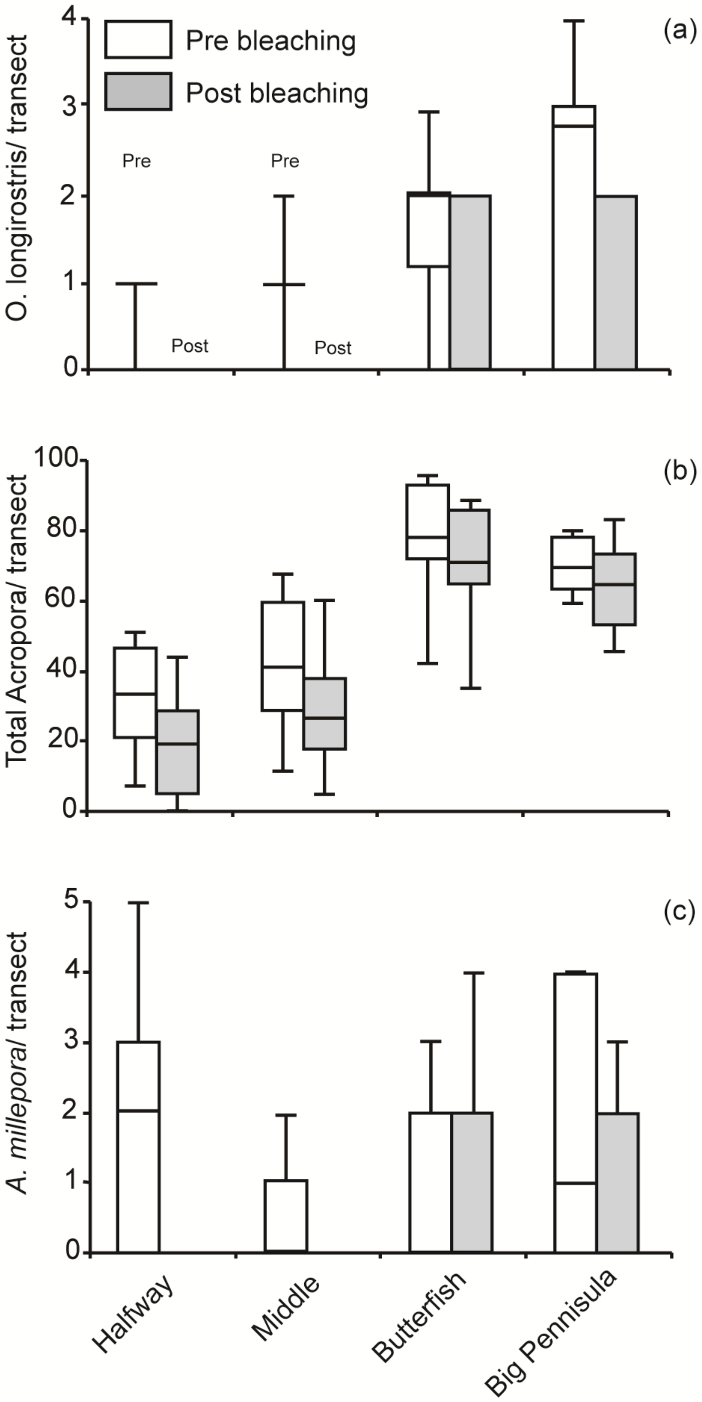

Figure 6.1. Box-and-whisker plots showing abundance of *Oxymonacanthus longirostris* and key habitat variables between Boxes represent the median and inter-quartile range, while whiskers extend out to the upper and lower values of the data. GKI sites, pre- and post- 2010-11 bleaching event. (a), number of *O. longirostris* observed per transect, (b) is the proportion of transects occupied by *Acropora* coral and (c) is the proportion of transects occupied by a key prey species, *A. millepora* (±SE).

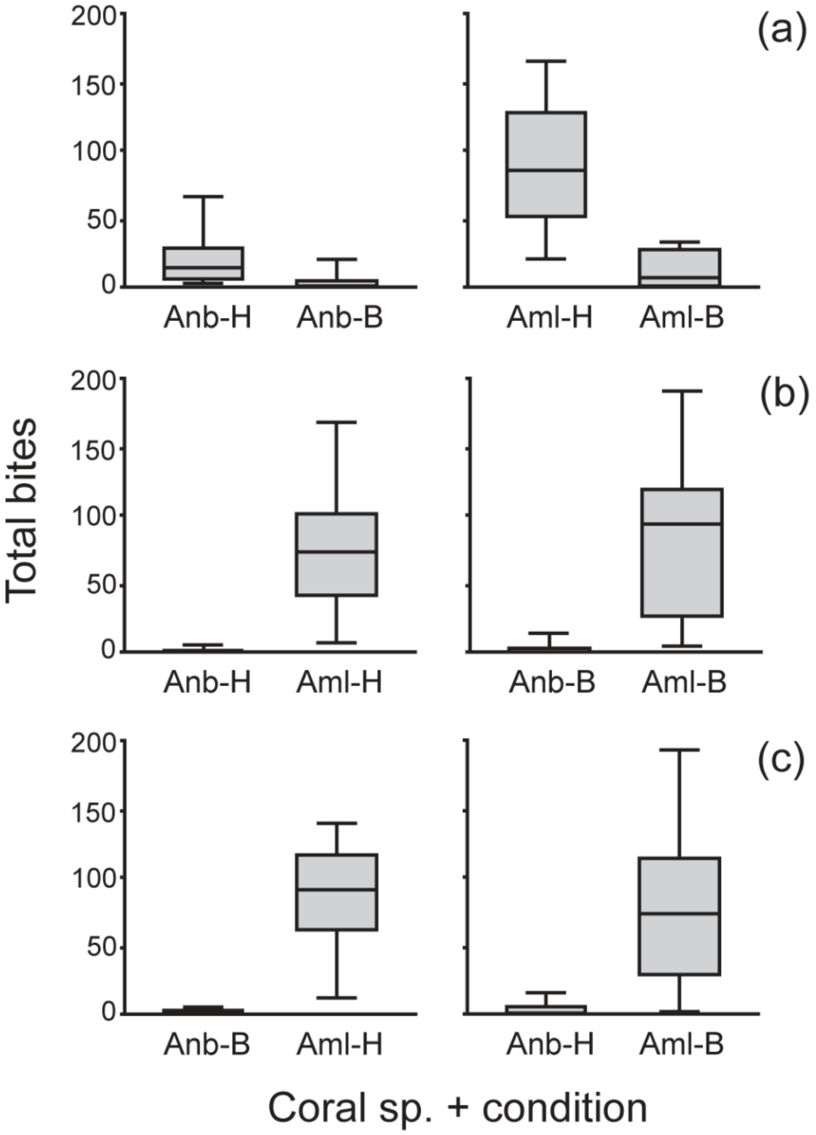

Figure 6.2. Box-and-whisker plots showing the number of bites taken by *Oxymonacanthus longirostris* on coral fragments during pair-wise trials. Boxes represent the median and inter-quartile range, while whiskers extend out to the upper and lower values of the data. Row (a) = same coral species but different condition (healthy or bleached), row (b) = different species but same condition, and row (c) = different species and different condition. Coral fragments were *Acropora millepora* – healthy (Aml-H), *A. millepora* – bleached (Aml-B), *Acropora nobilis*- healthy (Anb-H), and *A. nobilis* – bleached (Anb-B). Number of observations = 16 per combination of prey types.

6.5. Discussion

The local extinction of *O. longirostris* from reefs that also lost the preferred coral species, *A. millepora*, suggests that this coral may be an essential resource for this species in limited-diversity systems such as GKI. Although the filefish can consume other coral species, there is something about *A. millepora* that appears necessary for survival. The fate of the filefish may be linked to this single coral, or species with similar traits, and the vulnerability of these corals to increasing threats impacting on reef ecosystems.

Our data show that the bleaching event had a particularly negative impact on *A. millepora* (see also Tan et al. 2012). Mass coral bleaching has occurred with some frequency at GKI, most notably in 2006 where high sea surface temperatures resulted in up to 89% of corals bleaching on some reefs (Diaz-Pulido et al. 2009). While *Acropora* cover did quickly return to pre-bleaching levels, communities were dominated by fast growing, branching forms (Diaz-Pulido et al. 2009). While *O. longirostris* can feed on these species, they appear to be of limited nutritive value (Chapter 2). If key prey species are removed by bleaching and their return impeded, the resulting reduction in habitat quality may reduce the potential for *O. longirostris* to successfully repopulate former habitats.

Low rates of feeding on bleached corals may reflect the altered biochemical composition, visual appearance, or polyp behaviour of bleaching corals (Cole et al. 2009). Following bleaching, reduced photosynthetic activity increases corals reliance on heterotrophy and energetic reserves (Grottoli et al. 2006), and as these reserves become depleted, bleached corals may become less valuable prey. Continued selection of bleached *A. millepora* suggests that either a) this coral represents a superior resource even when bleached, or b) inherent preferences remain consistent irrespective of prey condition. Some characteristics that could affect foraging efficiency, i.e. skeletal morphology (Gochfeld 2004; Chapter 3), would remain consistent following bleaching which may explain continued selection of bleaching tissue. However, if the nutritive value of preferred coral declines to the point that fish cannot derive sufficient energy to survive, and cannot make this up feeding on other species, this will have serious consequences for their continued persistence.

This study suggests that even moderate disturbances may have lethal consequences if they remove key resources or alter habitat composition beyond thresholds required to support specialists. The fate of this filefish may be determined by the fate of a single coral species.

Chapter 7: General discussion

Determining the factors that drive specialisation for specific resources, as well as the effects of resource specialisation on key ecological processes, is essential for understanding how specialised organisms interact with their habitat. Establishing these relationships can, in turn, identify what specific resources are required for persistence, and how vulnerable these organisms may be to changes in resource availability. By exploring the determinants of resource specialisation in the corallivorous filefish, *Oxymonacanthus longirostris*, the present study showed how behavioural and physical adaptations can maximise the efficiency with which a specialised organism can use the resources available to it. These findings suggest that habitats which provide a specific mix of corals are critical for *O. longirostris*, and this will have important implications for the persistence of the species given predicted global declines in coral abundance and diversity (Pandolfi et al. 2003).

7.1. Resource specialisation: causes and consequences

The findings of this study suggest that *O. longirostris* is even more specialised than previous research has indicated (i.e. Barlow 1987; Kokita and Nakazono 2001). It has evolved finely tuned behavioural mechanisms that allow it to maximise how efficiently it can exploit the scleractinian corals that it associates with. It is able to distinguish between coral prey, preferring those with characteristics that maximise nutritional intake (Chapter 2). This is important as only certain corals appear capable of providing the nutritional return necessary for critical processes such as reproduction. In this regard, *O. longirostris* appears more specialised than many other corallivores (Pratchett 2007). However, studies on corallivore prey selectivity have often grouped prey by genus, or by colony morphology, rather than to species (see Cole et al. 2008). Therefore, various other corallivores may exhibit similar levels of specialisation once resource use is re-evaluated in greater detail. Preferred corals appear to have morphological characteristics that increase the volume of tissue that can be removed relative to effort (Chapter 3). The importance of morphology as a driver of prey selection in corallivorous fishes has seldom been considered, and the results presented here may explain why correlations between the biochemical composition of coral tissue and selectivity patterns have failed to produce conclusive results (Cole et al. 2008). The underlying drivers of prey preference most likely incorporate elements of both biochemical value and foraging efficiency, and so studies that incorporate both may find a clearer connection between prey biochemistry and preference. The intriguing findings of the chemical crypsis experiments (Chapter 4) highlight that an organisms diet may also have important implications beyond meeting energetic requirements. As the prey consumed could influence the effectiveness of this mechanism, chemical crypsis could play an important role in prey selection.

This study also highlights that the preferred resource for one requirement, such as food, may not be the preferred resource for another, such as shelter, and that habitats that contain a range of different, but equally essential, resources may be needed for persistence (Chapter 5). Understanding that organisms can be specialised for different resources along different axes is important for determining how they interact with their habitat, and this factor should be incorporated into studies that attempt to link resource specialisation to essential processes, or establish potential vulnerability. The results of this study also emphasise the importance of conducting controlled behavioural experiments alongside field observations when determining the basis of resource specialisation in species such as *O. longirostris*.

7.2. Vulnerability to anthropogenic disturbance

The ability of a specialised organism to persist through changes to its environment and the loss of preferred resources relies on its ability to successfully exploit alternatives. With this in mind, the results of this study suggest that *O. longirostris* will be extremely vulnerable to the predicted declines in coral abundance and diversity caused by anthropogenic disturbance and climate change. While coral abundance has often been used as a measure of reef health, this study highlights just how variable scleractinian corals can be in terms of their quality as both prey and habitat. Substantial differences in growth and reproduction were observed when *O. longirostris* were fed preferred or non-preferred corals from within the same genera (Chapter 2). However, these highly nutritious corals do not also necessarily represent the preferred habitat for this species (Chapter 5). Differing resource requirements may therefore restrict this species to habitats that provide a specific range of essential resources for both shelter and food.

While this study emphasised the importance of *Acropora millepora* for *O. longirostris* at Great Keppel Island (Chapter 6), it is likely that a range of corals with similar morphological or biochemical characteristics could support *O. longirostris* across its range. For instance, within the *Acropora* genus, there are a variety of species with large fleshy polyps of a comparable or greater size to those of *A. millepora* (Wallace 1999). However, within coral communities characterised by comparatively low *Acropora* diversity, such as those surrounding Great

Keppel Island, the range of potential prey species that could meet the nutritional requirements of *O. longirostris* may be limited. The *O. longirostris* populations in these areas may, therefore, have an increased reliance on the presence of individual coral species for persistence, putting them at particular risk if these corals are also especially vulnerable to predicted disturbances. Similarly, high coral species richness may reduce vulnerability to changes in resource availability by increasing the range of potential resources available, and providing a form of buffer should a specific coral species, such as *A. millepora*, be lost.

However, while associating with habitats with a greater diversity of corals may reduce the potential for the decline of an individual prey species to have catastrophic effects, the *O. longirostris* populations in these areas still remain highly vulnerable. If coral species richness declines globally as is predicted (Pandolfi et al. 2003), those *O. longirostris* populations currently in areas of high coral diversity will also become reliant on an increasingly narrow range of resources. In addition, *Acropora,* along with *Pocillopora* on which *O. longirostris* will occasionally feed (Hobbs 2013; RM Brooker pers. obs.), are amongst the most sensitive to anthropogenic impacts (Marshall and Baird 2000), and a shift towards reefs dominated by less sensitive coral genera, such as massive *Porites*, is expected (Pratchett et al. 2011). Apart from one report of *O. longirostris* feeding on *Montipora* (Barlow 1987) there is little evidence that these fish are able to extend their dietary scope beyond *Acropora* and *Pocillopora* corals. If the predicted mass decline of these corals from the Indo-Pacific does occur, it is likely that *O. longirostris* will become increasingly scarce and may eventually disappear from much of its original range.

7.3. Future research questions

As mentioned above, scleractinian corals appear highly variable in terms of their quality as prey. Given that *O. longirostris* modifies it’s foraging to maximise its energy intake, dietary selectivity could vary as energetic requirements change ontogenetically. For instance, reproductive individuals that have higher relative energetic requirements may be more reliant on nutritionally rich species such as *A. millepora.* This may, in turn, directly influence patterns or resource use, as well as the underlying preferences that drive them. However, if feeding on relatively exposed digitate species such as *A. millepora* increases direct predation risk, reduces the effectiveness of chemical crypsis, or requires defending these corals from conspecifics and other potential competitors, these nutrient rich corals may be avoided in favour of structurally complex corals, such as *Acropora nobilis*, by juveniles or sub-adults for which avoiding predation is the key driver of resource preference.

Corallivorous fishes often display variable patterns of prey selectivity between different geographic locations, most likely due to differences in prey availability (Lawton et al. 2012). While the *O. longirostris* population from Great Keppel Island exhibited a particular pattern of selectivity in the field, the extent to which prey selectivity varies across its geographic range is not known. If the foraging patterns seen at Great Keppel Island are representative of the species as a whole, with *O. longirostris* targeting the same narrow range of coral species throughout the Indo-Pacific, this will have direct consequences for its distribution, as well as its vulnerability if those corals are lost. As the morphological characteristics of corals influence prey value, it is possible that prey selection may vary depending on coral availability although corals with similar characteristics will be consistently targeted. Habitats with a specific range of essential characteristics appear to be crucial for supporting *O. longirostris* populations. Determining how consistent or variable patterns of resource selection are over larger spatial scales will help to build a more complete picture of this species global vulnerability.

The initial evidence of diet-induced crypsis in *O. longirostris* raises many additional questions with regards to the nature of this mechanism. For example, the biochemical pathway from prey ingestion to a fish's odour was not established, and determining exactly what dietary compounds are sequestered is a logical next step. There are a number of potential candidate compounds. For instance, various classes of amino acids, such as free amino acids (FAAs) and myco-sporine like amino acids (MAAs), are found within both coral tissue and fish mucus and are known to be used by predators for locating and orientating towards prey. Alternatively, the microbial communities associated within the gut or exterior mucus of fish may play a role if the biochemical signatures they produce change depending on diet. Whether there is an active behavioural role in this mechanism, or if it is simply a by-product of a specialised diet, remains to be tested. If fish actively select prey corals that maximise the effectiveness of this crypsis rather than to maximise energetic intake, this could have important implications with regards to resource use by this species. Also unknown is how generalised this mechanism is, i.e. how closely a fish's diet needs to match its habitat for a cryptic benefit to occur. In a broader sense, these results suggest that similar mechanisms could occur in a disparate range of taxa, wherever there is a close coupling between diet and habitat. Future investigations into this mechanism's occurrence throughout the animal kingdom will likely yield fascinating results.

7.4. Concluding remarks

Stable environmental conditions can allow organisms to evolve specialised morphological and behavioural adaptations to exploit specific resources within their habitat. For instance, *O. longirostris* has evolved precise behavioural mechanisms to select coral prey that will maximise its nutritional intake. Prey selection can occur on fine scales, to within a single coral branch, and appears to largely reflect foraging efficiency. *O. longirostris* has also evolved the ability to use its diet as an anti-predator defence, by sequestering coral-specific compounds to chemically resemble its coral prey. The ability to exploit a resource more effectively than generalist species occupying the same habitat can provide specialists with a competitive advantage when access to these resources is not limited. However, if environmental conditions change and preferred resources become scarce, specialist species become increasingly vulnerable if they cannot exploit alternatives. This study highlights how variable corals can be with regards to their quality as both habitat and food, and that *O. longirostris* appears to require diverse coral communities to provide the resources it needs for persistence. This leaves it vulnerable to even subtle changes in the composition of coral communities, as well as the loss of key coral species. Given the projected declines in the abundance and diversity of corals on reefs, due to direct anthropogenic disturbance and the effects of climate change, this species is at particular risk. The results of this study suggest that predicting the vulnerability of coral-specialists based on traditional measures such as total coral abundance may be of limited value. To truly understand how at risk these species are, the entire ecology on the organism needs to be considered.

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Appendix 1: Publication list

A1.1. Publications derived from the thesis

Brooker RM, Jones GP, Munday PL (2013). Prey selectivity affects reproductive success of a corallivorous reef fish. *Oecologia* **172**, 409-416

Brooker RM, Jones GP, Munday PL (2013) Within-colony feeding selectivity by a corallivorous reef fish: foraging to maximise reward? *Ecology and Evolution* **3**, 4109-4118

Brooker RM, Munday PL, Chivers DP, Jones GP (In Review) You are what you eat: diet-induced chemical crypsis in a coral feeding reef fish. *Proceedings of the Royal Society B: Biological Sciences*

Brooker RM, Munday PL, McLeod IM, Jones, GP. (2013) Habitat preferences of a corallivorous reef fish: predation risk versus food quality. *Coral Reefs* **32,** 613-622

Brooker RM, Munday PL, Jones GP (In Press) Local extinction of a coral reef fish explained by inflexible prey choice. *Coral Reefs*

A1.2. Additional publications during PhD candidature

Brooker, R. M., Munday, P. L. & Jones, G. P. (2011). Coral obligate filefish masquerades as branching coral. *Coral Reefs* **30,** 803-803

Brooker, R. M., Munday, P. L. & Ainsworth, T. D. (2010). Diets of coral-dwelling fishes of the genus *Gobiodon* with evidence of corallivory. *Journal of Fish Biology* **76**, 2578-2583

McLeod IM, McCormick MI, Munday PL, Clark TD, Takahashi M, **Brooker RM**, Wenger AS, Jones GP (In Review). Latitudinal variation in larval development of coral reef fishes: implications for a warming ocean. *Marine Ecology Progress Series*