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Competition and habitat selection in coral-dwelling fishes

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Statement on the contribution of others

This thesis includes collaborative work with my supervisors Professor Philip Munday and Professor Geoffrey Jones. During my PhD I led this collaborative project and experimental design, data collection, technical analysis, and ecological interpretations were primarily conducted by me. Both my supervisors (co-author) provided intellectual guidance, financial support, advice on experimental design and statistical analysis.

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General Abstract

Ecologists have long been interested in competition because of its potential role in population and community regulation. A large body of competition theory has accumulated, much of which remains to be empirically tested. To date, the occurrence of competition in natural communities and the mechanisms by which competing species coexist are not fully understood. The close relationship between coral-dwelling fishes and a limiting resource (coral colonies) makes them ideal models for testing hypotheses and questions about competition in natural communities. In this thesis I examine the mechanisms of competition and their influence on resource use in two ecologically similar coral-dwelling gobies (*Gobiodon histrio* and *Gobiodon erythrospilus*) that are known to compete for access to preferred coral habitat. The chapters in this thesis address four fundamental questions: 1) the mechanisms of competitive coexistence between the two species, 2) the role of resource availability in shaping the outcome of competitive interactions, 3) the fitness-associated traits of coral colonies that drive habitat preferences and competitive interactions, and 4) the influence of benthic substratum around preferred coral colonies on habitat use and competitive interactions.

Niche and lottery mechanisms of competitive coexistence have traditionally been viewed as mutually exclusive alternatives. However, recent theory suggests that a mix of these processes can facilitate coexistence between competing species. In **Chapter 2** I tested the hypothesis that the mechanism of competition between *G. histrio* and *G. erythrospilus* changes with ontogeny, from a lottery for space at settlement to niche partitioning in adults. Field observations and experiments showed that juveniles of the two species settled at the same size, had similar patterns of habitat use, and similar competitive abilities, supporting the lottery mechanism at settlement. In contrast, habitat use differed in adults suggesting that resource partitioning occurs in larger individuals. In laboratory experiments, adults of each species preferred colonies of *Acropora nasuta*, however *G. histrio* was a superior competitor and prevented *G. erythrospilus* for using *A. nasuta* in more than 70% of the trials. In a field-based transplant experiment, *G. erythrospilus* (inferior competitor) suffered less of a fitness loss when occupying the non-preferred coral (*A. spathulata*) compared with *G. histrio*, which could explain its ability to persist when displaced by the superior competitor. These results suggest that the competitive mechanism operating between the two *Gobiodon* species shifts from a lottery for space to niche-partitioning through ontogeny and that these two mechanisms of competitive coexistence are not mutually exclusive.

Competition arises from the shared use of limited resources. Consequently, spatial and temporal variation in resource availability could influence competition among coral reef fishes. In **Chapter 3** I investigated how variation in the abundance of *A. nasuta* coral colonies, the preferred habitat of *G. histrio* and *G. erythrospilus*, influences the outcome of competitive interactions between these two species. First, the relative abundance and patterns of habitat use of the two goby species was compared among sites that varied in the absolute and relative abundance of their preferred habitat. Then a recolonization experiment was used to test the prediction that the effects of competition are greatest where preferred habitat is relatively less abundant. The proportional occupancy of *A. nasuta* by the superior competitor, *G. histrio*, increased as the relative abundance of *A. nasuta* declined. In the recolonization experiment the effects of preferred coral availability differed between juveniles and adults. For juveniles, where a competitive lottery operates, the proportional use of preferred coral was the same for the two species, regardless of the relative abundance of *A. nasuta.* In contrast, for adults niche-partitioning was greater at locations that had a lower relative abundance of *A. nasuta.* These results show that changes in the relative abundance of preferred resources can influence competitive interactions between reef fishes, but the effects differ depending on the mechanism of competitive coexistence.

Competition for space affects patterns of habitat use and individual performance of coral-dwelling fishes; however, the physical attributes of corals that influence habitat preferences are uncertain. **Chapter 4** investigated the influence of coral colony size and branching structure on habitat use and growth rate of the two coral gobies, *G. histrio* and *G. erythrospilus.* The preferred coral species, *A. nasuta* had smaller interbranch width compared with an alternative coral habitat, *A. spathulata*. A binary-choice laboratory experiment demonstrated that both gobies preferred coral colonies with smaller interbranch width, except when they had the opportunity to occupy *A. nasuta* over *A. spathulata*. A field transplant experiment showed that both goby species grew faster on larger coral colonies and in colonies with smaller interbranch width. *G. erythrospilus* grew faster than *G. histrio* on *A. spathulata*, indicating that it suffers less of a fitness loss occupying this alternative habitat. The results of this chapter show that coral physical attributes are important factors driving habitat preference of coral-dwelling gobies; however, there must also be additional factors related to coral species identity that influence their habitat preferences.

The distribution and abundance of habitat specialists is often associated with the availability of preferred habitat; however, other environmental features can also influence

habitat selection. Coral-dwelling gobies depend on the availability of a few key species of coral for their survival and also possess skin toxins that reduce predation risk. In **Chapter 5** I analysed the influence of benthic substratum around preferred coral colonies on patterns of habitat use and toxicity of *G. erythrospilus* and *G. histrio*. Field surveys demonstrated that juveniles, single adults and breeding pairs of *G. erythrospilus* mostly inhabited *A. nasuta* colonies surrounded by branching corals. In contrast, *G. histrio* juveniles and single adults associated with *A. nasuta* coral colonies with adjacent epilithic algal matrix and *G. histrio* breeding pairs inhabited colonies surrounded by sand/rubble. Habitat-choice experiments showed that both gobies species prefer *A. nasuta* coral colonies with benthic substratum mainly composed by epilithic algal matrix and sand. Lastly, the substratum around preferred coral colonies also influenced the toxicity levels of the associated fishes. Gobies inhabiting *A. nasuta* coral colonies with more epilithic algal matrix and sand were more toxic than fishes collected from colonies surrounded by branching corals. Given the potential for toxicity level to reduce the risk of predation, this could explain why gobies compete for access to preferred coral species surrounded by epilithic algal matrix and sand.

This thesis empirically demonstrated that different mechanisms of competitive coexistence (such as a lotteries and niche partitioning) are not mutually exclusive and may operate at different stages in an organism's life history. Furthermore, it has shown that changes in the relative abundance of preferred resources can influence competitive interactions, but the population level effects depend on the mechanisms of competitive coexistence that operate. Additionally, this research highlights that both coral species identity and colony structural features influence the growth of coral-dwelling fishes and thus play a key role in shaping habitat preferences and competition for space in coral-dwelling fishes. Finally, the benthic composition around preferred coral species influences the toxicity of coral-dwelling gobies, and this further influences their habitat preferences and competitive interactions. This thesis answered some fundamental questions about the mechanisms of competition in animal communities with broader implications for predicting the effects of climate change and anthropogenic impacts on reef fish communities. Coral cover, benthic community composition and reef structural complexity are declining due to the combined effects of storms, crown of thorns starfish outbreaks, coral bleaching and diseases. This degradation will affect habitat use and fitness of coral associated fishes and ultimately influences the outcome of ecological process such as recruitment and competition within reef fish communities.

Table of contents

List of Tables

List of figures

Chapter 1: General Introduction

1.1. Competition and mechanisms of competitive coexistence

Competition has long been regarded as one of the most important processes structuring natural communities (Darwin 1859; Tansley 1917; Gause 1934; MacArthur and Levins 1967; Diamond 1978; Schoener 1983). It has been the cornerstone of much ecological theory and the focus of empirical research to understand its prevalence and impact in nature (Whittaker 1965; Roughgarden 1983; Connell 1983, Schoener 1983; Amarasekare 2003; Forrester 2015). Competition occurs when two or more individuals of the same or different species attempt to utilize the same resource and this resource is in limited supply, leading to a reduction in fitness of at least one of the individuals (Tilman 1982). Theory suggests that competition will influence a wide range of ecological patterns, including species richness and community structure, population size and spatio-temporal dynamics, and local to geographical scale distributions (Connell 1961; Tilman 1982; Goldberg and Barton 1992; Holt and Polis 1997; Hibbing et al. 2010; Livingston et al. 2012). While many empirical studies have demonstrated that competition within and between species can influence the distribution and abundance of species and the structure of communities (Connell 1961; Schoener 1983, Gurevitch et al. 1992, Youngentob et al. 2012; Wisz et al. 2013), many questions remain about how competing species coexist, what resources they actually compete for, and the implications of competition for individual fitness.

A key question for ecologists is what enables competing species to coexist? What prevents one species gaining an advantage that could allow it to dominate the exploitation of shared resources and ultimately prevent the persistence of other species? Resource partitioning is believed to be the most common and widespread means of competitive coexistence. Niche-based models predict that competing species are able to coexist in complex environments by partitioning essential resources, such as food and shelter (Colwell and Fuentes 1975, Ross 1986; Silvertown 2004; Gilbert et al. 2008). If a species decreases the range of resource used, thereby specializing on a narrower range of resources, this could reduce competition with other species (Armstrong and McGehee 1980). For example, MacArthur (1958) proposed that different species of wood warblers coexist by partitioning habitat space within pine trees. Each species specializes in using a particular part of the tree in order to reduce competition with other species. In many instances, such patterns of niche partitioning may represent the "ghost of competition past" (Connell 1980) as the species no longer compete due to their specialized resource requirements. Current-day competition does, however, drive niche partitioning where species have overlapping demands for shared limited resources. In this case, species may use a broader set of resources or a different set of resources when competitors are absent compared with when they are present. For example, the presence of competitors dramatically reduces the niche breadth of desert rodents (Hughes et al. 1994). A significant increase in habitat use area (i.e. new habitat types) was observed for rodents following the removal of a potential competitor. Alternatively, species may use the same range of resources but partition access to those resources in space or time. Species may use the same set resources, but differ in terms of when they exploit these resources (Armstrong and McGehee 1980; Chesson 1985; Albrecht and Gotelli 2001), or they may exploit the same resources, but in different locations (May and Hassell 1981; Chesson 2000; Lyson et al. 2011).

Competitive hierarchies are common in niche-based competition and directly influence which species have access to which resources (Connell 1983; Bonin et al. 2015). Dominant competitors are expected to have preferential access for preferred resources; whereas subordinate competitors will be forced to use inferior resources. Previous studies have shown that inferior competitors either shift to resources that are normally not used by the dominant species (e.g. niche displacement) (Brown 1988; Svanbäck and Bolnick 2007), or there may be a competition-performance trade-off, such that subordinate competitors outperform dominants when using alternative resources (Biging and Dobbertin 1995; Caley and Munday 2003). Reduced access to preferred resources for subordinate competitors could reduce their performance and ultimately fitness (Tanner 1997; Cusumano et al. 2015). Despite considerable research, it is uncertain how subordinate competitors persist in instances where they do not attain better fitness on alternative habitats and additional stabilizing mechanisms (e.g. neutral model assumptions) could be the explanation.

In 1978, Peter Sale presented an alternative to the niche-partitioning paradigm of competitive coexistence, called the lottery hypothesis. The *lottery hypothesis* argues that competing species with identical resource requirements can coexist through chance colonization of vacant space. This theory assumes that space is a limiting resource, that vacant space is recolonised by the first-available recruit (analogous to a winning lottery ticket) and that species have similar competitive abilities. In a competitive lottery, recruitment to vacant habitat operates on a first-come-first-served basis and there is no subsequent displacement. The lottery hypothesis was further developed to the *lottery model* by showing that spatial or temporal variation in the relative abundance of recruits is necessary to prevent one species gaining a numerical advantage that could lead to competitive exclusion of other species through time (Chesson and Warner 1981). A lottery for space is potentially ineffective at producing long-term coexistence between species without additional stabilizing mechanisms, such as spatiotemporal environmental variation that alternatively favours recruitment rates for the different species (Chesson and Warner 1981).

The lottery hypothesis was first developed using reef fishes as a model, however experimental test of the hypothesis have found little evidence for competitive lotteries in reef fish communities (Robertson 1995). Nevertheless, competitive lotteries do appear to operate in some plant (Henri et al. 1997), parasite (Janovy et al. 1992) and marine benthic invertebrate communities (Shinen and Navarrete 2014), and at least one study has recently found support for lottery-based competition in reef fishes (Munday 2004). Although there is ample empirical evidence for competitive coexistence by niche partitioning in plant and animal communities, the conditions that favour competitive coexistence by the lottery mechanism remain unresolved (Amarasekare 2003).

Subsequent extensions and derivations of the lottery model, such as competition-colonization trade-offs (Levins and Culver 1971; Horn and MacArthur 1972) and spatial patch dynamic models (Wu and Levin 1994) offer additional mechanisms that promote coexistence of competing species. For example, the competition-colonization trade-off model proposes that species that are better competitors are inferior colonizers and vice versa (Levins and Culver 1971; Horn and MacArthur 1972). Inferior competitors are better at colonizing vacant space, but superior competitor can generally displace the subordinates in time (Amarasekare et al. 2004). Competition–colonization trade-off models have been used to explain species coexistence of virus (Ojosnegros et al. 2012), parasites (Nowak and May 1994) and plants (Calcagno et al. 2006). However, the importance of competition-colonization trade-offs explaining species coexistence has also been questioned (Yu and Wilson 2001; Amarasekare et al. 2004). Yu and Wilson (2001) applied at the individual patch level, the classic competition-colonization models of species coexistence assuming that propagules of superior competitors can displace adults of inferior competitors (displacement competition). However, they found that trade-offs between different stages of colonization could be far more common in nature than a trade-off between competitive ability and colonization ability.

The development of the unified neutral theory of biodiversity and biogeography ("Unified Theory" or "UNTB") has intensified the interest and debate about the mechanisms of competition in natural communities. Neutral models (Hubbell 2001) suggest that ecological differences between species are irrelevant to the maintenance of biodiversity. Instead, chance variations in demographic (births, deaths and immigration) and evolutionary rates (speciation and extinction) are responsible for the generation and maintenance of biological diversity (Bell 2000; Hubbell 2001). Recruitment into the population in the neutral model is governed by a simple lottery for space, species have equal competitive ability, and any differences in resource use are unrelated to competitive effects. In other words, there is no niche partitioning due to competition and no competitive hierarchies. Despite controversy over the neutral model (Whitfield 2002; Mikkelson 2005) and some studies refuting its assumptions (Adler 2004; Dornelas et al. 2006; Ricklefs and Renner 2012), a lively debate about niche versus neutral models still persists in ecology (Gravel et al. 2011; Connolly et al. 2014).

1.2. Competition and resource availability

Competitive interactions arise from the shared use of limited resources and resource availability is one of the main factors determining the dynamics of populations (Wilson and Tilman 1993; Dyer and Rice 1999; Schoolmaster Jr et al. 2014). Consequently, fluctuations in resource availability can influence the intensity of competition (Wilson and Tilman 1993; Briones et al. 1998; Delong and Vasseur 2013). When resources are abundant, individuals have greater access to preferred resources and thus competitive effects may be negligible. Conversely, when resources become scarce, competition for these resources may be intense, affecting fundamental demographic traits, such as growth, survival and reproduction (Robertson 1996; Dyer and Rice 1999; Pollitt et al. 2011). For example, Robertson et al. (2015) demonstrated that a reduction in the availability of feeding habitats proportionally increased competition for food in European badger, a mustelid mammal that lives in territorial social groups, but forages alone. Additionally, in environments where resource fluctuations are frequent and severe, a high responsiveness for suddenly released resources is expected and species coexistence can be favoured by repeated fluctuation in resources availability (Wright 2002; Pekkonen et al. 2013). Therefore, spatiotemporal fluctuations in resource availability can influence the intensity of competition as well as species coexistence.

How resource availability influences the outcome of competitive interactions should also depend on the mechanisms of competition in action. In a competitive hierarchy (*niche partitioning*), changes in resource availability could affect patterns of resource use and relative fitness among species because superior competitors should gain greater access to preferred resources when they are scarce, whereas subordinate competitors are forced to use inferior resources. However, in lottery competition, changes in resource availability should not actually alter patterns of resource use. Change in resource availability may affect absolute abundance, but not the relative performance of different species, because each species will still have an equivalent chance to use remaining resources. Hence, the mechanisms of competitive coexistence are critical to understand the consequences of interactions between the intensity of competition and resource availability. Surprisingly, no study to date has explored the relationship between mechanisms of competitive coexistence and how species will respond to fluctuations in resource availability.

Cryptic density-dependence (Shima and Osenberg 2003) is another important concept that deals with the correlation of resource availability/quality, species abundance and competitive outcomes. This hypothesis argues that if sites differ spatially and temporally in quality (*e.g.* supply of a limited resource) then species abundance will become positively correlated with resource availability. The cryptic density-dependence phenomenon has been described in site-attached reef fishes (Overholtzer-McLeod 2004; Schmitt and Holbrook 2007), crabs (Donahue 2006) and aphids (Helms and Hunter 2005). Heterogeneity in site quality can affect species recruitment, causing species abundance to become positively correlated with resource availability. The connection between the strength of density dependence and resources availability can then give the false idea that all sites have the same capability of support similar populations. Because survival is density dependent, habitat quality can mask the effects of competition, making it more difficult to detect (Shima and Osenberg 2003).

1.3. Competition in reef fish communities

Coral reefs are one of the most important and ecologically diverse ecosystems on Earth and are home of astonishing and almost unmatched diversity of species (Reaka-Kudla 1997). The occurrence of competition and its role in structuring communities has been a particularly controversial topic in reef fish ecology (Jones 1991; Forrester 2015; Bonin et al. 2015). Early researchers assumed that competition for space was ubiquitous in reef fish communities, but differed in their opinion over whether competitive hierarchies led to changes in resource use by niche-partitioning (Smith and Tyler 1972, 1975; Robertson and Lassig 1980) or whether reef fish were competitive equivalents, successfully exploiting the same limited resources by the lottery mechanism (Sale 1977, 1978). By the 1980's competition had lost favour as an ecological process explaining the diversity and dynamics of reef fish communities. Space and food were no longer considered to be limiting factors in the recruitment limitation hypothesis (Doherty 1983) and predation (Talbot et al. 1978) hypothesis. The recruitment limitation hypothesis (Doherty 1983) stated that larval mortality of reef fishes is so high, and subsequently settlement so low, that local populations of juveniles and adults never reach abundances where they compete for space or other resources. Alternatively, the predation hypothesis asserts that predation on new recruits, juveniles, and adults results in such low population sizes that resource limitation and competition are essentially precluded. However, more recent laboratory and field experiments have since demonstrated that space is a limiting factor for at least some reef fishes (Clarke 1992; Munday et al. 2001; Holbrook and Schmitt 2002; Munday 2004; Forrester et al. 2006; Bonin 2009) and that competition for space can affect demographic traits such as growth and survival (Shulman 1984; Robertson 1996; Munday 2001). While the majority of studies suggest the presence of competitive hierarchies and niche partitioning among competing species (Robertson and Gaines 1986; Clarke 1989; Munday et al. 2001; Geange et al. 2013), there is also evidence for competitive lotteries in some reef fish taxa (Munday 2004; Pereira et al. 2015).

Competition appears to be especially prevalent in small coral-dwelling fishes (Robertson 1996; Munday et al. 2001; Almany 2004; Coker et al. 2009; Forrester 2015), presumably because shelter space in coral colonies is a vital, but limited, resource. Some highly diverse fish families, such as Pomacentridae, Gobiidae and Apogonidae rely extensively on live coral habitat during most of their life (Jones and Syms 1998; Pratchett et al. 2008; Coker et al. 2014). The complex architecture of coral colonies created by their branching structure constitutes the living space for these species (Coker et al. 2014). For instance, *Acropora* coral colonies provide refuge from predators, nesting sites and also food resources for many fishes. The complex branching structure of these corals can influence survival rates and fitness-associated traits such as growth and reproductive success (Thompson et al. 2007, Schiemer et al. 2009; Noonan et al. 2012). Therefore, coral-dwelling fishes are expected to select coral types that benefit individual fitness and may compete for access to these habitats (Munday et al. 2001; Holbrook and Schmitt 2002).

However, competitive hierarchies are also evident on coral-dwelling fishes, such that superior competitors gain greater access to preferred habitats and inferior competitors are forced to use suboptimal habitat, regardless of their natural preference. For example, following the removal of the superior competitor (*Stegastes planifrons*) in a damselfish assemblage, adult *S. partitus*, which are less aggressive and half the size of *S. planifrons*, doubled in number and expanded their range into a microhabitat previously used almost exclusively by *S. planifrons* (Robertson 1996). A third species, *S. variabilis*, which is less aggressive and 20% smaller than *S. planifrons*, also increased in abundance following the removal of *S. planifrons*. By contrast, removal of *S. planifrons* had no effect on the abundances and patterns of resource use of *S. diencaeus* and *S. leucostictus* because these two species use different microhabitats to *S. planifrons* and thus do not compete directly (Robertson 1996). Additionally, Geange et al. (2013) recently demonstrated competitive networks among three closely related species of wrasse. Resource monopolization and patterns of distribution and abundance among species in competitive networks (at least 1 species of lower rank out-competes ≥1 species of higher rank) differed from those in competitive hierarchies (all species of higher rank out-compete all species of lower rank) during a field-based experiment (Geange et al. 2013).

Competitive hierarchies and competitive displacement also have consequence for fitness-associated traits in reef fishes (*e.g.* growth and reproduction). For example, Clarke (1992) demonstrated that competition between the spinyhead blenny, *Acanthemblemaria spinosa*, and the roughhead blenny, *Acanthemblemaria aspera*, influenced both growth and fecundity. The dominant spinyhead blenny tend to exclude the inferior competitor, roughhead blenny, for superior habitats and a manipulative experiment conducted showed a significant reduction in spawning frequency for the inferior competitor as a result of inhabiting lower quality microhabitats (Clarke 1992). In addition, Forrester et al. (2006) manipulated the densities of two sand gobies and suggested competitive effects on growth due to increased metabolic costs during foraging at sites with high density.

There has been a surge of interest in competition in reef fish communities in recent years and two new reviews on competition among coral reef fishes have recently been published (Bonin et at. 2015; Forrester 2015). Bonin et at. (2015) demonstrated the prevalence and importance of competition among coral reef fishes compiling and synthesizing the results of 173 experimental tests of competition from 72 publications. The authors argue that evidences for competition are pervasive both within and between species, with 72% of intraspecific tests and 56% of interspecific tests demonstrating a demographically significant consequence of competition (e.g. a decrease in recruitment, survival, growth or fecundity). An important conclusion from Bonin et at. (2015) is that it is time to move beyond the debates of the past about *whether* competition occurs and embrace the pluralistic notion that competition is one of the many factors that shape reef fish communities. Forrester (2015) also highlights the relevance of competition and discuss how the effects of competition are influenced by body size, priority effects, predator and prey behaviour, reef shape and quality, as well as spatiotemporal resource availability. An important new dimension outlined by Forrester (2015) is how reef fish competitive interactions will be affected by the ongoing degradation of the coral reefs, which is altering resource availability. Forrester (2015) argues that as a result of competition for gradually diminishing supply of resources, it is likely that some reef fish species experience rising levels of density-dependent mortality.

To date, most studies on habitat use of coral-dwelling fishes has been focused on habitat features such as coral colony size, coral health and physical structure (Friedlander and Parrish 1998; Feary et al., 2007; Noonan et al. 2012; Holbrook et al. 2015). However, other resources (i.e. surrounding habitat) around coral colonies could also influence fish preference, performance and competition. For example, Wen et al. (2013) observed that the recruits of three predator reef fishes (*Plectropomus maculatus, Lutjanus carponotatus* and *Epinephelus quoyanus*) were found mostly associated with *Acropora* coral colonies located over sand substratum. Similarly, the abundance of the coral-dwelling damselfish, *Dascyllus aruanus* was directly correlated with the presence of the preferred habitat *Pocillopora damicornis* located on a sandy substratum (Chase et al. 2014). Consequently, there is some evidence to suggest that the benthic composition around preferred coral colonies could directly influence the habitat preference of coral-dwelling fishes, and this may influence competitive interactions; however, this has never been tested.

1.4. Coral gobies as models for ecological investigations

Gobies in the genus *Gobiodon* are obligate coral-dwelling fishes that live among the branches of *Acropora* coral colonies using them for shelter, breeding sites and food (Munday et al. 1999; 2004; Brooker et al. 2010). Some goby species are highly specialized, inhabiting just one or two species of *Acropora*, whereas other species are more generalist and use a variety of *Acropora* species (Munday et al. 1997, Dirnwoeber and Herler 2007). The close relationship of *Gobiodon* with their *Acropora* coral hosts makes them excellent models to investigate ecological and evolutionary patterns within reef fish communities. In addition, coral-dwelling gobies are some of the best reef fish models for ecological field experiments, due to their short pelagic larvae duration, restricted movement and easiness of collection and tagging.

Coral-dwelling gobies compete for habitat space and some species have similar preferences and therefore compete for access to preferred coral colonies. Munday et al. (2001) found that the presence of a superior competitor influenced habitat use of subordinate species of coral-dwelling gobies. Following the removal of a superior competitor, *G histrio*, the subordinate competitor, *G. brochus*, increased its use of the preferred coral *A. nasuta*, where it has faster growth, increased survival, and reaches a larger maximum size and thus has higher fecundity (Munday 2001; Herler et al. 2011). Competition also controls spatial distribution and social organisation of *Gobiodon histrio*, an obligate coral-dwelling goby that inhabits the branching coral *Acropora nasuta*. Hobbs and Munday (2004) demonstrated a positive relationship between fish size and coral size, with small, single *G. histrio* mostly occupying small corals and larger paired fish inhabiting large corals. A manipulative experiment involving small and large corals demonstrated that this positive relationship between fish size and habitat size was due to size-based competition for large coral colonies (Hobbs and Munday 2004).

Previous studies also indicate that gobies coexist by a variety of mechanisms. For instance, some coral-dwelling gobies appear to coexist by niche partitioning either among coral species or among reef zones (Munday et al. 2001). Species also differ in their competitive ability, resulting in a competitive hierarchy that influences patterns of habitat use and access to preferred coral habitat (Munday et al. 2001). In contrast, other coral-dwelling gobies appear to coexist though a lottery for space. Munday (2004) suggested that two ecological similar species (*G. histrio* and *G. erythorspilus*) have similar patterns of habitat use and identical ability to compete for vacant corals, and thus may coexist by a lottery for space at settlement. However, not all assumptions of lottery competition have been confirmed and it is not known if patterns of habitat use established at settlement persist into adulthood or if there are any ontogenetic changes in the relative competitive strength of the two species.

Another unique characteristic of coral-dwelling gobies is that they possess toxic skin secretions that can act as a chemical defense from predators (Schubert et al. 2003; Gratzer et al. 2013). However, the origin of these toxins is not clear as well as the extent of variation among different goby species and habitat types. A recent study by Dixson and Hay (2012) suggests that the gobies may sequester these toxins from algae that grow nearby their host coral colony. If skin toxins reduce the risk of predation, then gobies may also select coral colonies in locations that are likely to offer the best opportunities to feed outside of the coral colony and graze on benthic substratum that enhance their chemical defense. Yet, no studies to date have tested if the benthic composition around preferred coral colonies could influence the habitat use and also toxicity of these gobies.

1.5. Aims and thesis outline

The overall aim of this study is to investigate the mechanisms of competition, habitat selection and resource use in two ecological similar coral-dwelling gobies (*Gobiodon histrio* and *Gobiodon erythrospilus*). Although *G. histrio* and *G. erythrospilus* have previously been considered the same species (Munday et al. 1999) they can be distinguished by differences in color pattern and the presence or absence of minute cycloid scales on the side of the body (Suzuki et al. 1995). Molecular analysis has confirmed that they are two different species (Munday et al. 2004; Duchene et al. 2013). *G. histrio* and *G. erythrospilus* can be found in neighbouring coral colonies, but rarely occupy the same coral colony, and have not been observed to form a breeding pair (*personal observation*). The thesis focuses on the two species because they provide a unique opportunity to investigate competition on coral reef fishes. These two species are ecologically similar sister species (Duchene et al. 2013) that overlap broadly in their geographical distribution. At Lizard Island on the GBR they occur in similar abundances and have broadly similar patterns of habitat use; both species are known to inhabit the same species of coral (*A. nasuta*) and occupy the same reef habitats (Munday et al. 1997; 2001). Therefore, *G. histrio* and *G. erythrospilus* compete for preferred coral habitat, *A. nasuta*.

The chapters in this thesis address four fundamental questions: 1) the mechanisms of competitive coexistence between the two species, 2) the role of resource availability in shaping the outcome of competitive interactions, 3) the fitness-associated traits of coral colonies that drive habitat preferences and competitive interactions, and 4) the influence of benthic substratum around preferred coral colonies on gobies' patterns of habitat use and toxicity. Each chapter is written as a stand-alone publication.

Chapter 2 tested the hypothesis that the mechanism of competition on ecologically similar goby species changes with ontogeny, with a lottery for space operating at settlement and niche partitioning occurring in adults. Recent theory suggests that a mix of lottery and niche processes can facilitate coexistence between competing species, but this has not been empirically tested. Field and laboratory experiments with two ecologically similar fish species, *G. histrio* and *G. erythrospilus* on different life phases, were used to test this hypothesis.

Resource limitation underpins competition theory; consequently, changes to resource availability are predicted to influence the outcome of competitive interactions in natural communities. In **Chapter 3**, I explore how variation in the relative abundance of *A. nasuta* coral colonies influences the outcome of competitive interactions between *G. histrio* and *G. erythrospilus* in a system where the mechanisms of competitive coexistence changes through ontogeny. *G. histrio* and *G. erythrospilus* provided a unique opportunity to test how resource availability influences the outcome of competition for habitat space under different mechanisms of competitive coexistence.

G. histrio and *G. erythrospilus* prefer *A. nasuta* coral colonies during laboratory experiments and it has also been shown that both goby species compete for *A. nasuta* coral colonies; whereas *A. spathulata* is used as an alternative habitat. However, it is not yet understood which coral attributes drive this specific preference for *A. nasuta,* and coral complexity and size could be determinant factors. **Chapter 4** examine how coral identity, coral colonies size and branching structure influence habitat use and fitness of coral reef fishes.

The distribution and abundance of habitat specialists is often associated with the availability of preferred habitat; however, additional environmental features can also influence their spatial distribution. Coral-dwelling fishes depend on the availability of a few species of coral for their survival, but whether the location of preferred coral habitats influences habitat selection is unknown. In **Chapter 5** I investigate the influence of benthic substratum around preferred coral habitat on patterns of habitat use and toxicity levels of *Gobiodon erythrospilus* and *Gobiodon histrio*.

Chapter 2: Competitive mechanisms change with ontogeny in coral-dwelling gobies

This chapter was published in Ecology. Authors: PHC Pereira, PL Munday and GF Jones.

2.1 Summary

Recent theory suggests that a mix of lottery and niche processes can facilitate coexistence between competing species, but this has not been empirically tested. Previous research indicates that a competitive lottery for space promotes coexistence between two ecologically similar fish species, *Gobiodon histrio* and *Gobiodon erythrospilus*. However, not all the assumptions of lottery competition have been tested and patterns of habitat use by adults suggest niche partitioning. Here, we investigated the hypothesis that the mechanism of competition changes with ontogeny, with a lottery for space operating at settlement and niche partitioning occurring in adults. Patterns of resource use in the field were compared for juveniles and adults of the two species. Pelagic larval duration (PLD) and size-at-settlement was also estimated to determine if size differences at settlement could affect the outcome of competitive interactions among juveniles. Habitat preference and size-based competitive ability were then tested for juveniles and adults in laboratory experiments. Finally, a transplant experiment was performed to test the fitness-associated consequences of niche partitioning among adults and its implications for coexistence of the two species. *G. histrio* had a similar PLD (20.7 ± 2.0 days) to *G. erythrospilus* (18.5 ± 1.9 days), and there was no difference in size-at-settlement between the species. Juveniles of the two species had similar patterns of habitat use and similar competitive abilities, supporting the lottery mechanism at settlement. However, adults differ in their habitat use, supporting the prediction that resource partitioning increases with ontogeny. In laboratory experiments, adults of each species preferred colonies of *Acropora nasuta*, however *G. histrio* was a superior competitor and prevented *G. erythrospilus* for using *A. nasuta* in more than 70% of the trials. In the field transplant experiment, *G. erythrospilus* (inferior competitor) suffered less of a fitness loss when occupying the non-preferred coral (*A. spathulata*) compared with *G. histrio*, which could explain its ability to persist when displaced by the superior competitor. These results suggest that the competitive mechanism operating between the two *Gobiodon* species shifts

from a lottery for space to niche-partitioning through ontogeny and that these two mechanisms of competitive coexistence are not mutually exclusive.

2.2 Introduction

Competition is a fundamental ecological process, influencing population size, biomass, species richness and community structure (Elton 1946; Dayton 1971; Levin 1974; Connell 1983; Tilman 1994). The traditional view of interspecific competition was that one species would dominate, leading either to resource partitioning between the species, or the elimination of the weaker competitor from the habitat (Colwell and Fuentes 1975). While a number of theoretical studies have advanced alternative ideas to account for the coexistence of ecologically similar species in animal communities (Sale 1977; Abrams 1984; Warner and Chesson 1985; Chesson 2000; Hubbell 2001), these hypotheses have not always been adequately tested (Yu and Wilson 2001; Salomon et al. 2010). In fact, a limitation to understanding the role of competition in structuring ecological communities is that theoretical explanations for competitive coexistence have generally advanced more rapidly than empirical investigations and more field observations and experiments are necessary to test predictions of existing hypotheses (Amarasekare 2003; Siepielski and McPeek 2010; Hixon 2011; Shinen and Navarrete 2010).

Traditional niche-based models of competition propose that competing species coexist through resource partitioning (Colwell and Fuentes 1975; Diamond 1978). These models predict that species are able to coexist in complex environments by partitioning resources, such as food (Hyndes et al. 1997; Pimentel and Joyeux 2010; Pereira et al. 2015) and shelter (Ross 1986; Schmitt and Holbrook 1999). If a species decreases the range of resource used, thereby specializing on a narrower range of resources, this could result in reduced levels of competition with other species (Armstrong and McGehee 1980). Consequently, coexistence in a spatially heterogeneous environment is possible by species specialization on different resources (Colwell and Fuentes 1975; Amarasekare 2003). However, competitive abilities may also differ among species, with superior competitors gaining access to preferred resources, whereas inferior competitors are forced to use less favorable resources (Hardin 1960; Violle et al. 2011). As a result, there can be fitness-associated consequences of resource partitioning that favour selection over evolutionary timescales for the ability of inferior competitors to maintain their performance across a range of resources (Lynch and Gabriel 1987; Futuyma and Moreno 1988).

Sale (1977, 1978) proposed an alternative idea, the *lottery hypothesis*, which argues that competing species with identical resource requirements can coexist through chance colonization of vacant space. The lottery hypothesis assumes that space is a limiting resource, that vacant space is recolonised by the first-available recruit (analogous to a winning lottery ticket) and that species have similar competitive abilities. The lottery hypothesis was further developed to the *lottery model* by showing that spatial or temporal variation in the relative abundance of recruits is necessary to prevent one species gaining a numerical advantage that could lead to competitive exclusion of other species through time (Chesson and Warner 1981). A lottery for space is potentially ineffective at producing long-term coexistence between species without additional stabilizing mechanisms, such as environmental variation that alternatively favours recruitment rates in the different species (Chesson and Warner 1981). Although there is ample empirical evidence for competitive coexistence by niche partitioning in plant and animal communities, there is much less evidence for competitive coexistence by the lottery mechanism (Robertson 1995; Amarasekare 2003). Therefore, the conditions under which these two competitive mechanisms are likely to be favoured have not been resolved for either aquatic (Munday 2004; Salomon et al. 2010; Shinen and Navarrete 2014) or terrestrial systems (Hubbell 2001; Lin et al. 2009; Kalyuzhny et al. 2014).

Interest and debate about lottery models intensified with the development of the neutral model (Hubbell 2001), which proposed that differences between species in ecological communities are irrelevant to the maintenance of biodiversity. The core assumption of the neutral model is that chance variations in demographic (births, deaths and immigration) and evolutionary rates (speciation and extinction) are responsible for the generation and maintenance of biological diversity (Bell 2000; Hubbell 2001). Recruitment into the population in the neutral model is governed by a simple lottery for space. Competition models have subsequently been classified into those based on: (1) *stabilizing mechanisms* (known as *niche theory*), such as competitive hierarchies and resource partitioning, which are the most widely accepted mechanisms of species coexistence, and (2) *fitness equivalence* (known as *neutral theory*), where stabilizing mechanisms are absent, species have equivalent fitness, and coexist through demographic stochasticity (Adler et al. 2007; Bode et al. 2012). Neutral models challenge the niche paradigm by proposing that similarities, not differences, explain the high diversity of natural communities. Despite controversy over the neutral model (Whitfield 2002; Mikkelson 2005) and some studies refuting its assumptions (Adler 2004; Dornelas et al. 2006; Ricklefs and Renner 2012), a lively debate about niche versus neutral models persists in ecology (Gravel et al. 2011; Connolly et al. 2014).

Theory and experimental tests of competition typically assume that just one competitive mechanism operates between species (Colwell and Fuentes 1975; Amarasekare 2003). However, niche and neutral theory are not mutually exclusive, and both niche and neutral processes could potentially influence the coexistence of competing species (Gravel et al. 2006; Silvertown et al., 2006; Adler et al., 2007). Chesson (2000) proposed that the magnitude of niche-based differences required to stabilize long-term coexistence depends on how similar species are in average fitness. If species have similar average fitness they require only small niche differences to coexist. Neutral mechanisms are the special case where species have equivalent fitness and there are no stabilizing, niche-based processes. Recent theory suggests that niche and neutral theories are the extremes of a continuum and that aspects of both could operate in many communities (Gravel et al. 2006). In this context, niche and lottery processes could operate simultaneously to promote coexistence, or their relative importance could change through time, with similar fitness and a lottery operating in one life stage and differential fitness and niche-partitioning operating in another life stage. Ecological and life history changes through ontogeny could affect both fitness consequences of resource use patterns and the potential competitive mechanisms involved. Ontogenetic shifts in habitat (Dahlgren and Eggleston 2000) and food preference (Schmitt and Holbrook 1984; Pereira and Ferreira 2013) could potentially alter the degree of resource overlap between species and their competitive abilities. It is well known that the strength of competitive effects can be stage-dependent (Werner 1994; Callaway and Walker 1997; Connolly and Muko 2003). However, to our knowledge, no study has empirically demonstrated ontogenetic changes in the competitive mechanisms operating in animal communities.

The coral-associated gobies from the genus *Gobiodon* are some of the most specialized fishes on coral reefs. These fishes associate almost exclusively with corals from the genus *Acropora*, from which they derive multiple resources including shelter, food and breeding sites (Munday et al. 1997; Hobbs and Munday 2004; Brooker et al. 2010). The close relationship of the gobies with *Acropora* coral hosts makes them an excellent model group to analyze competitive interactions within reef fish communities. Munday et al. (2001)

demonstrated that some coral-dwelling gobies compete for space (*Acropora* coral colonies) and that species coexist by a variety of mechanisms. Most species coexist by niche partitioning, at one or more spatial scales, and interspecific differences in competitive ability result in a competitive hierarchy among species. However, it appears that some coral-dwelling gobies may coexist by the lottery mechanism. Munday (2004) found that two ecologically similar species (*G. histrio* and *G. erythrospilus*) have similar patterns of habitat use and that juveniles have similar size-based ability to compete for vacant corals. Removal of one species from coral colonies, resulting in vacant space, caused enhanced recruitment of the other species, demonstrating that habitat space is limited. However, not all the assumptions of the lottery hypotheses were tested. For example, it is not known if the two species recruit to coral habitat at the same size, which could influence their competitive ability. Similarly, it is not known if habitat preferences and competitive abilities remain the same or change through ontogeny. Coexistence of these goby species could involve a mix of both lottery and niche processes if competitive abilities change with ontogeny.

In this study we tested, for the first time, the hypothesis that the competitive process changes from a lottery for space at settlement to niche partitioning in adults. There were four components to evaluating this hypothesis. Firstly, newly settled juveniles were collected to estimate the pelagic larval duration (PLD) and size-at-settlement for each species from otoliths (ear bones). This was to determine if differences in size at settlement could affect the outcome of competitive interactions among juveniles. Secondly, we compared patterns of resource use by the two species to examine potential resource partitioning by either juveniles or adults. To do this we compared the primary biotic and abiotic factors, such as coral species inhabited, size of the coral colonies inhabited, and reef location, that have been found to be important to resource partitioning of gobies in previous studies (Munday 2000; Munday et al. 2001; Hobbs and Munday 2004). Thirdly, habitat preference and size-based competitive abilities were tested for juveniles and adults of both species in laboratory experiments to determine if there was competitive equivalence or a competitive hierarchy. Finally, a transplant experiment tested if individual performance in preferred and non-preferred habitat differed between the two species, which could provide an explanation for the coexistence of the two species if a competitive hierarchy developed with ontogeny. We hypothesized that coexistence could be achieved if the relative fitness (i.e. growth rate) of the inferior competitor in the non-preferred habitat is greater than that of the superior competitor in that habitat.

2.3 Methods

Study location and species

Field surveys and laboratory experiments were conducted in May and September 2012 at Lizard Island in the northern section of the Great Barrier Reef (GBR), Australia (14° 38'S - 145° 26'E). *Gobiodon histrio* and *Gobiodon erythrospilus* are ecologically similar sister species (Duchene et al. 2013) that overlap broadly in their geographical distribution. At Lizard Island on the GBR they occur in similar abundances and have broadly similar patterns of habitat use (Munday 2004). *G. histrio* and *G. erythrospilus* can be found in neighbouring coral colonies, but rarely occupy the same coral colony.

Pelagic larval duration and size at settlement

Munday (2004) showed that juvenile *G. histrio* and *G. erythrospilus* have similar competitive strength when size matched. However, it is unknown if these species actually settle at the same size. Differences in PLD could enable one species to grow larger than the other, leading to a competitive hierarchy at settlement despite similar size-based competitive ability. To estimate size at settlement, sagittal otoliths were removed from 25 juveniles of each species collected from the most commonly inhabited corals, *Acropora nasuta* and *Acropora spathulata* at Lizard Island. Otoliths were processed using standard methods as described by Epperly et al. (1991) and Secor (1992).

PLD was determined by counting daily growth increments of processed otoliths from the first fine-lined, dark increment to the settlement check mark. The settlement mark was identified by the increment transitions, represented by a zone where the increments are indistinct from one another (Victor 1986; Wilson and McCormick 1999). Otolith radius was measured from the nucleus to the settlement mark and from the nucleus to the otolith edge, along a consistent axis.

Individual fish sizes (standard length – SL) at settlement were then back-calculated using the biological intercept procedure (Campana & Jones 1992), given by $L_a = L_c + (O_a - O_c)\ (L_c - L_0)\ (O_c - O_0)^{-1}$, where L_a is the estimated fish length at age a, L_c is fish length (standard length) at capture, O_c is otoliths radius at capture, L_0 and O_0 are the fish length at hatching and otolith size at hatching, respectively. The biological intercepts of L_0 and O_0 were fixed at

3.0 mm fish length and 0.20 mm otolith radius (author's pers. obs.). R script was used to perform back calculation. A t-test was used to compare mean PLD and size at settlement between the two species.

Habitat use and partitioning

Coral-dwelling gobies can partition habitat either among the coral species they inhabit, or among reefs with different exposure to prevailing wind (Munday 2000; Munday et al. 2001). Therefore, different species may inhabit different coral species on the same reef, or they may inhabit the same coral species, but on different reef types (*i.e.* exposed versus sheltered locations). Pattern of habitat use of juveniles and adults was examined in three reef zones, based on their exposure to the prevailing south easterly trade winds; (1) sheltered lagoon, (2) leeward side of island, and (3) windward side of island. Three replicate sites were selected within each zone (Figure 2.1). At each site we recorded habitat use of 50 randomly selected individuals of *G. histrio* and 50 individuals of *G. erythrospilus*. To do this, a diver conducted a haphazard swim in the depth range where suitable *Acropora* corals are most abundant (0-10m). All sighted *Acropora* coral colonies were inspected and the coral species identity and coral colony size was recorded for each coral colony containing one or more individual of *G. histrio* or *G. erythrospilus*. Gobies were recorded by life phase (juveniles and adults) using criteria stipulated by Munday et al. (1997). *Acropora* coral colonies were identified to species level according to Wallace (1999) and Veron (2000). Any colonies with doubtful identification were photographed for further identification. Colony size was recorded as the distance across its widest axis, using a tape measure. Coral colonies were subsequently categorized as small (0 - 20 cm), medium (20 - 40 cm) or large (40 - 60 cm).

A chi-square test of independence was used to compare the frequency with which *G. histrio* and *G. erythrospilus* used different coral species. Juveniles and adult were analysed separately. Univariate regression trees (URT) using Tree Plus were then used to explore potential resource partitioning among the habitat variables measured for the two *Gobiodon* species. *Acropora* species inhabited, colony size, prevailing wind exposure and location were the explanatory variables. URT is well suited for describing patterns in complex ecological datasets because they separate the variables in a series of binary splits and continuous and categorical variables can be compared in the same analyses (Death and Fabricius 2000).

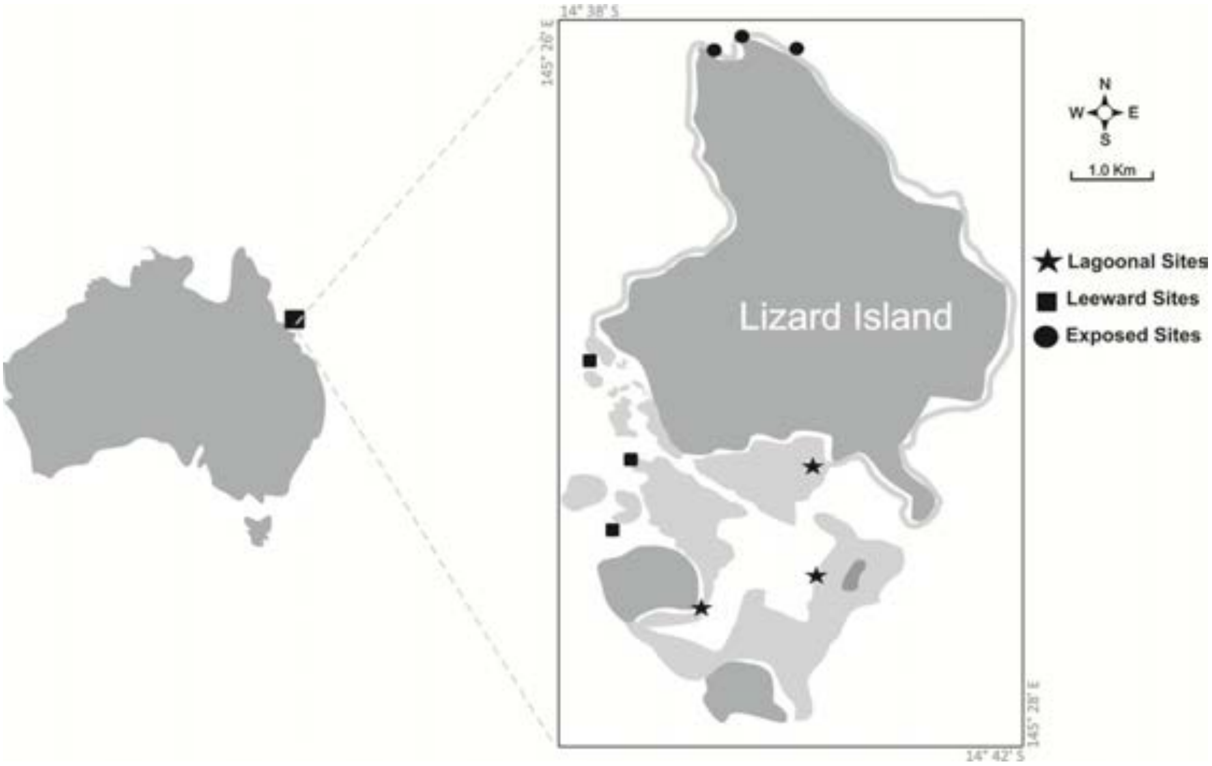

Figure 2.1 - Map of study area (Lizard Island - Northeast Australia) showing the sites surveyed for gobies

Habitat preference (laboratory experiments)

Preliminary observations confirmed that *Acropora nasuta* and *A. spathulata* were the two most commonly used coral species by *G. histrio* and *G. erythrospilus* in the field (see also Munday 2004). To determine the preference for these two coral species in the absence of competition, juveniles and adults of each species of *Gobiodon* were given the choice between two coral colonies, one *A. nasuta* and one *A. spathulata*. The protocol used was identical to that used by Munday (2004) for juveniles. Small colonies (15–20 cm diameter) of these two coral species were carefully removed from the reef, transported alive to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). One colony of each coral species (approximately equal size) was placed at opposite ends of a glass aquarium (50 x 30 x 30 cm). The position of each coral species on either the left or right side of each aquarium was changed regularly during the experiment and coral colonies were replaced if their condition visibly deteriorated. Gobies were collected from the field by lightly anesthetizing them with clove oil (Munday and Wilson 1997). A single individual of *G. histrio* or *G. erythrospilus* (ranging from 1.5 to 3.8 cm) was released between 1800 and 1900 in the middle of glass aquarium and their choice of coral recorded between 0600 and 0700 the following morning. Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 h. Habitat preference was tested for 24 individuals of each species. A chi-square test of independence was used to compare the habitat preference of *G. histrio* and *G. erythrospilus*.

Competition experiment

A laboratory experiment was used to test the relative competitive abilities of *G. histrio* and *G. erythrospilus* for preferred habitat. This was performed for both juveniles and adults to determine if there was a shift in competitive ability between life stages. While Munday (2004) has previously reported similar competitive abilities in juveniles, it was important that we repeated this experiment with juveniles at the same time that we tested adult competitive ability. One similar-sized individual of each species was simultaneously placed into a glass aquarium with a colony of *Acropora nasuta* in the middle. The species occupying the coral was recorded after 12 hours. The individual occupying the test coral was considered the superior competitor. *Acropora nasuta* was the coral species used in this experiment because it is the preferred species of coral for both *G. histrio* and *G. erythrospilus* at Lizard Island (Munday et al. 1997, 2001). Coral colonies used in the experiment were carefully removed from the reef, transported to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). To provide shelter for evicted fish, a similar-sized piece of coral that had been bleached to remove all living tissue was placed at one end of each aquarium.

In order to test whether the origin of individuals (e.g. *Acropora* species they were collected from) affected the competition ability of adults, *G. histrio* and *G. erythrospilus* were collected from *A. nasuta* and *A. spathulata* and held in separate aquaria. Two different combinations were established: (1) Both individuals from *A. nasuta* or (2) *G. histrio* individuals from *A. nasuta* and *G. erythrospilus* from *A. spathulata.* This second combination was chosen because adult *G. erythrospilus* commonly inhabited *A. spathulata* in the field, and this might affect its competitive ability against *G. histrio*, whereas *G. histrio* less frequently inhabited *A. spathulata*. Individuals in each trial were matched for size. Fish were released onto the corals between 1800 and 1900 hours and the outcome recorded at 0700 hours the following morning. A total of 24 trials were performed for juveniles and a total of 24 trials of each combination were performed for adults. A chi-square test of independence was used to compare the frequency of wins in the competition experiment for juveniles and for adults.

Growth experiment

A transplant experiment was performed to test if patterns of habitat use differentially affect individual performance of *G. erythrospilus* and *G. histrio*. Specifically, we predicted that the inferior competitor, *G. erythrospilus*, should experience a relative fitness advantage compared with the superior competitor, *G. histrio,* when occupying a non-preferred habitat, *A. spathulata*. Consequently, *G. erythrospilus* may persist because it suffers less of a decline in fitness-associated traits compared with *G. histrio* when forced to use non-preferred habitat.

We compared the growth rates of *G. erythrospilus* and *G. histrio* on preferred (*A. nasuta*) and non-preferred coral species (*A. spathulata*) over a three-month period between January and April 2014. A total of 50 individuals of both goby species were collected from *A. nasuta* by lightly anesthetizing them with clove oil. Collected fishes were transported to the laboratory, measured (SL to 0.1 mm) and individually marked with a small fluorescent-elastomer tag injected into the dorsal musculature (Munday 2001). Tagged fishes were held for 24 hours in aquaria to ensure recovery. Fishes were then transported to the reef and released on approximately equal sized coral colonies of either *A. nasuta* or *A. spathulata*. A total of 25 individuals of each goby species were transplanted to each of the two coral species. Coral colonies were tagged for subsequent identification and any resident fishes present were removed before a goby was released onto a coral colony. After three months, all the remaining fishes were collected from the marked coral colonies and SL of each tagged fish was measure in the laboratory to determine the increase in size.

A t-test was used to compare the size of the transplanted gobies at the beginning of the experiment between the two species. Analysis of variance (ANOVA) was then used to compare growth of the two goby species in the two coral species. We predicted that there would be significant interaction between the main factors (goby species and coral species) if the inferior competitor was better able to maintain performance (i.e. growth) in the non-preferred habitat compared with the dominant competitor.

2.4 Results

Pelagic larval duration and size at settlement analyses

G. erythrospilus had a mean PLD of 18.5 ± 1.9 days, and *G. histrio* had a mean PLD of 20.7 ± 2.0 day, which was not significantly different (t = 10.76, df = 1, *P* = 0.1). Similarly, there was no significant difference in size at settlement estimated for the two species (t = 6.19, df = 1, *P* = 0.7). *G. erythrospilus* was estimated to settle at 6.66 ± 0.44 mm and *G. histrio* at 6.98 ± 0.49 mm.

Habitat use

Gobiodon histrio and *G. erythrospilus* inhabited a total of 11 *Acropora* species (Figure 2.2). Despite this diversity, 62.9% of juveniles and 86.1% of adults occurred in just two main coral species; *Acropora nasuta* and *A. spathulata*. Juveniles of the two species exhibited nearly identical patterns of habitat use (chi-square = 3.68, df = 10, *P* = 0.97), especially for the two primary coral species (Figure 2A). However, adults of the two species exhibited significant differences in habitat use (chi-square = 89.21, df = 10, *P* = 0.002) (Figure 2.2A). For adults, *G. erythrospilus* was most frequently observed in association with *A. spathulata* (44.1% of observations) whereas *G. histrio* was mostly associated with *A. nasuta* (71.3% of observations) (Figure 2.2B).

Univariate regression tree analysis for adults resulted in a 7-leaf tree explaining 35.5% of the total variation (Figure 2.3A). Coral species inhabited was the most important variable, explaining more than 80% of the explained variation in habitat use between *G. histrio* and *G. erythrospilus* (Figure 2.3B). In the first split, *G. erythrospilus* was grouped with *Acropora spathulata*, *A. gemmifera* and *A. humilis*; whereas *Gobiodon histrio* was associated with *A. nasuta*, *A. cerealis, A. digitifera* and *A. millepora*. The next split in order of importance was colony size with *G. erythrospilus* more frequent on large and medium colonies and *G. histrio* more frequent on small colonies (22.5% of the variation). Exposure explained just 6.06% of the variance, indicating that patterns of habitat use by the two species differed little among reefs from different exposure regimes. *G. erythrospilus* tended to be more associated with exposed sites and *G. histrio* exhibited a slight preference for sheltered areas (Figure 2.3A-B).

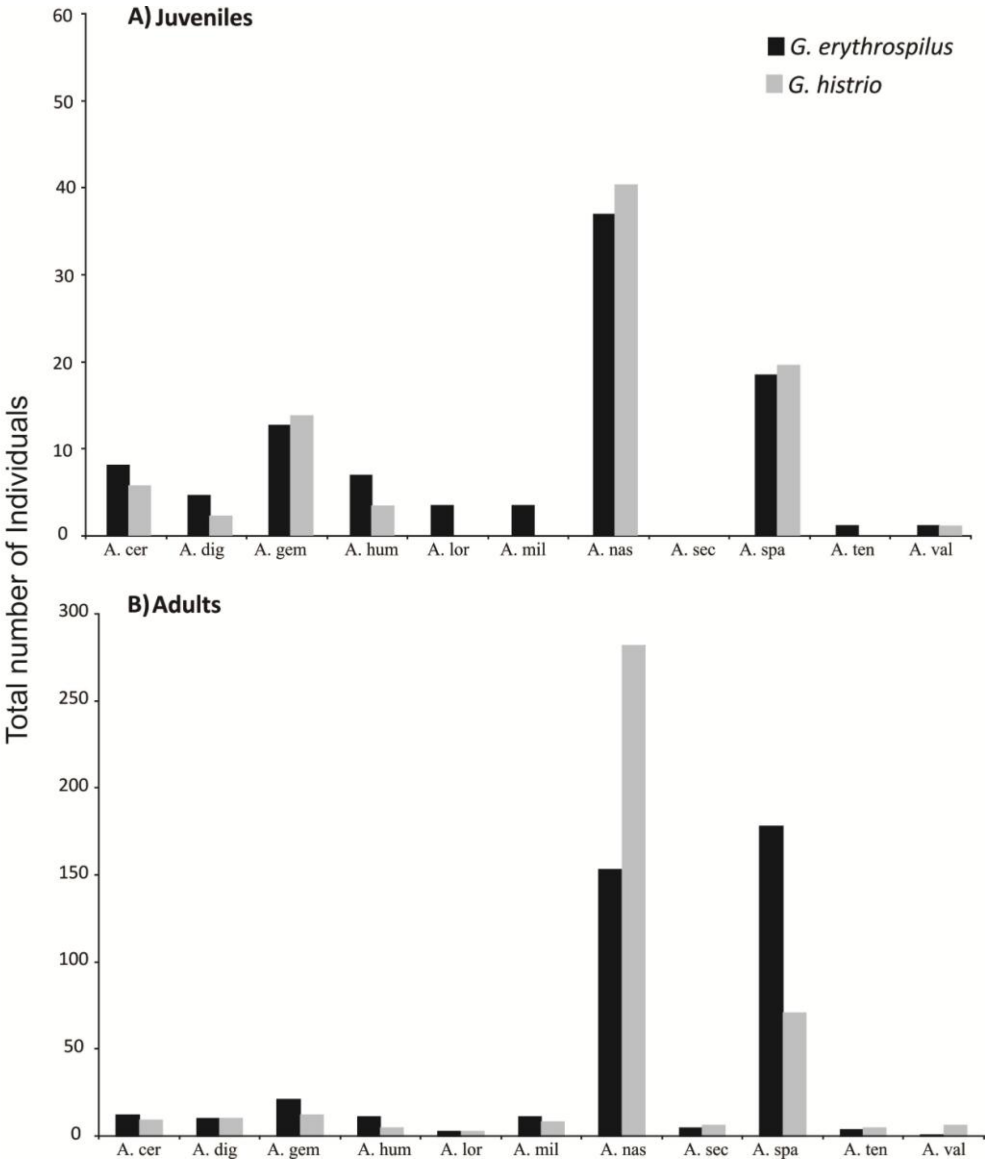

Figure 2.2 – Habitat use of juveniles (A) and adults (B) of *Gobiodon histrio* and *Gobiodon erythrospilus*. Coral abbreviation: **A. cer** = *Acropora cerealis*; **A. dig =** *Acropora digitifera*; **A. gem** = *Acropora gemmifera*; **A. hum** = *Acropora humilis*; **A. lor** = *Acropora loripes*; **A. mil** = *A. millepora*; **A. sec** = *Acropora* secali**; A. nas** = *A. nasuta*; **A. Spa** = *Acropora spathulata*; **A. ten** = *Acropora tenuis***; A. val** = *Acropora valida.*

Habitat preference

Despite the difference in *Acropora* use in the field, both *G. histrio* and *G. erythrospilus* exhibited a strong preference for *A. nasuta* in laboratory trials, with no significant difference in habitat preference between the species (chi-square = 0.76, df = 1, P = 0.66). *G. histrio* preferred *A. nasuta* in 22 of 24 (91.6%) trials and *G. erythrospilus* in 20 of 24 (83.3%) trials.

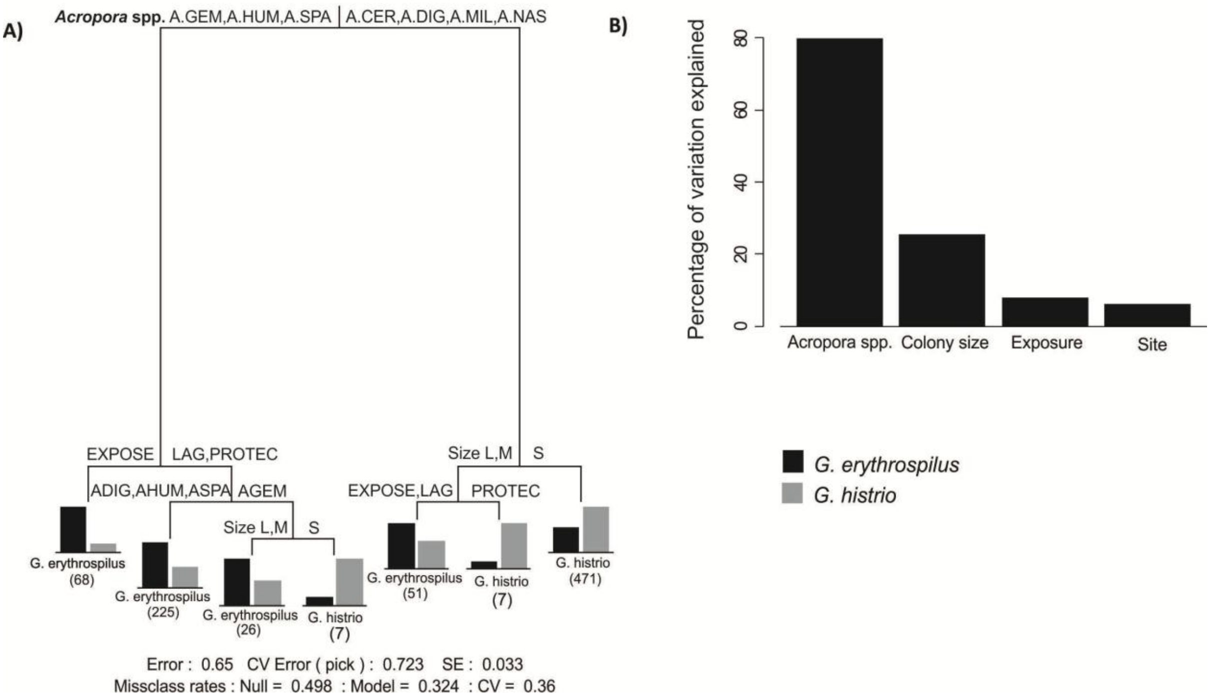

Figure 2.3 - Univariate Regression Trees of habitat use by *Gobiodon histrio* and *Gobiodon erythrospilus.* (A) Seven leaf regression tree showing distribution of *Gobiodon histrio* and *Gobiodon erythrospilus* among the coral species, colony sizes, wind exposure and locations samples. Each split in the tree indicates the number of recorded gobies in each situation (parenthesis), length of vertical lines proportionally indicate the percentage of variation explained. B) Bar graph showing proportion of variation explained by *Acropora* species inhabited, colony size, prevailing wind exposure and location.

Competition experiments

Juvenile *G. erythrospilus* and *G. histrio* exhibited similar ability to compete for preferred coral habitat (*A. nasuta*). In 24 trials, where similar-sized fishes were released simultaneously onto a coral colony, *G. histrio* won 13 and *G. erythrospilus* won 11 trials (chi-square = 1.35, df = 1, P = 0.45) (Figure 2.4A). In contrast, for adults, *G. histrio* proved to be the superior competitor compared to *G. erythrospilus*, winning the majority of the trials regardless of the coral of origin (chi-square = 6.03, df = 2, *P* = 0.001) (Figure 2.4B). When both individuals were from *A. nasuta, G. histrio* won 16 of 24 trials (chi-square = 5.63, df = 2, *P* = 0.002) with 3 draws. Moreover, when *G. histrio* individuals were from *A. nasuta* and *G. erythrospilus* from *A. spathulata*, *G. histrio* won 19 of 24 trials (chi-square = 10.35, df = 2, *P* = 0.005) with 3 draws. A draw occurred when both gobies occupied the *A. nasuta* coral colony in the experimental arena.

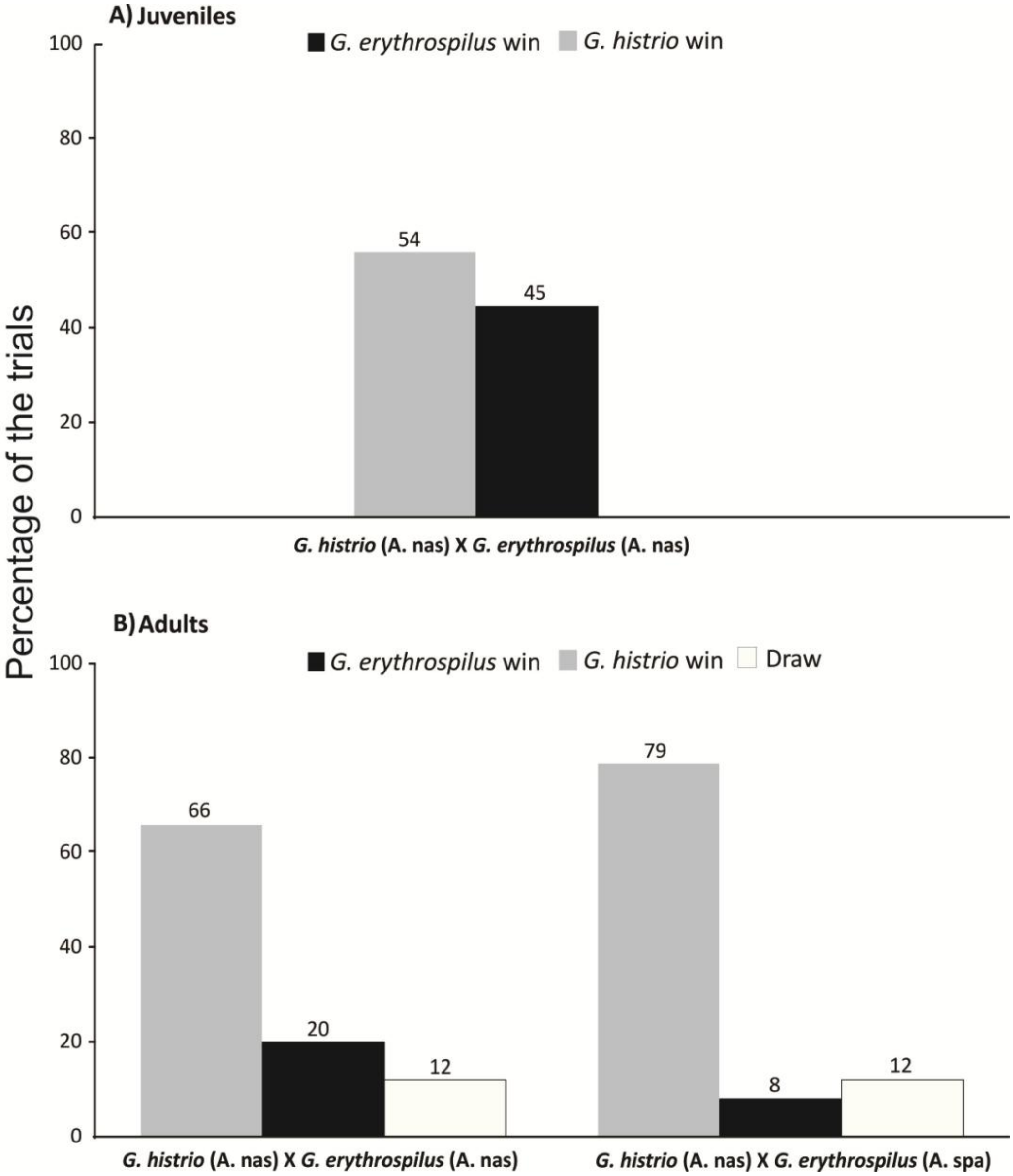

Figure 2.4 – Outcome of competition experiments for juveniles (A) and adults (B) of *Gobiodon histrio* and *Gobiodon erythrospilus*. For adults (B) *G. histrio* was collected from *A. nasuta* and *G. erythrospilus* was collected from either *A. nasuta* (left-hand side) or *A.*

spathulata (right-hand side). N= 24 trials for each combination. **A.nas** = *Acropora nasuta*; **A.spa** = *Acropora spathulata*.

Growth experiment

The average size of transplanted fishes at the beginning of the experiment was 27.4 mm SL for *G. histrio* and 27.7 mm for *G. erythrospilus,* and there was no difference in the size of the transplanted gobies between the two species (t = 0.28, df = 38, $P = 0.77$).

There was a significant effect of goby species ($F_1 = 7.25$; $P = 0.01$), coral species ($F_1 = 10.77$; $P = 0.002$) and their interaction ($F_1 = 4.19$; $P = 0.047$), on growth rate of fish transplanted to colonies of *A. nasuta* and *A. spathulata*. Importantly, there was a significant interaction, with the change in growth between the two coral species higher in *G. histrio* compared with *G. erythrospilus* (Figure 2.5). *G. histrio* suffered a 37% decline in growth on *A. spathulata* compared with *A. nasuta*, whereas *G. erythrospilus* suffered only a 21% decline in growth on the non-preferred coral.

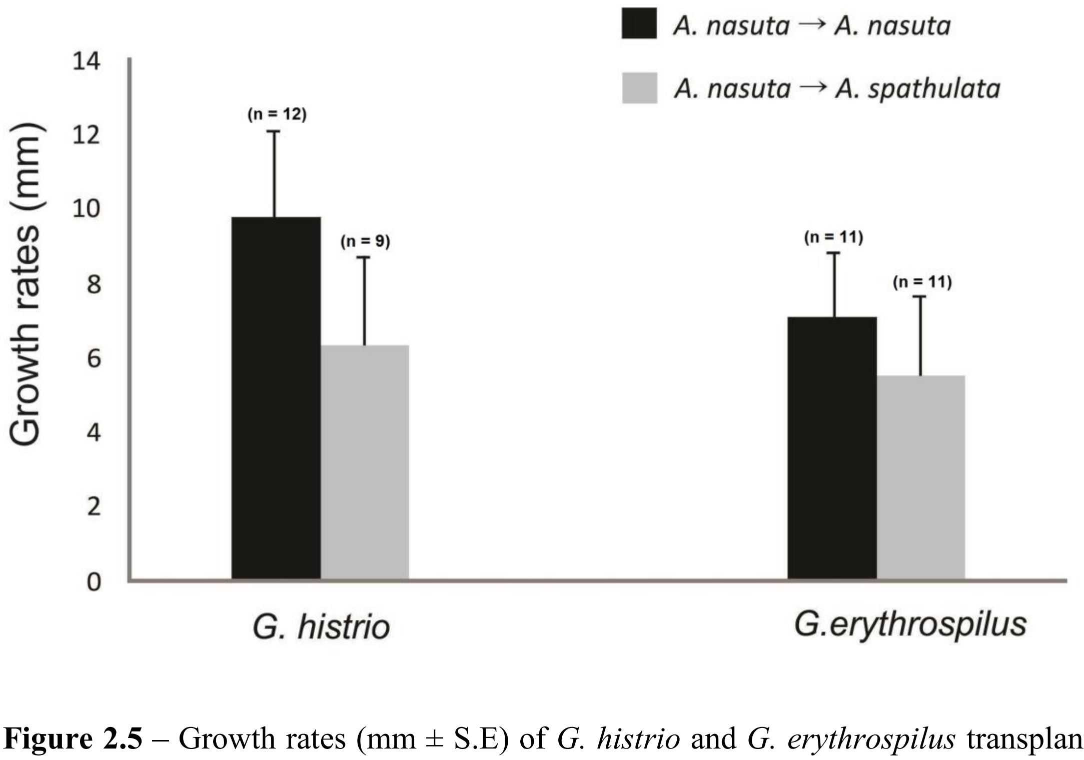

Figure 2.5 – Growth rates (mm ± S.E) of *G. histrio* and *G. erythrospilus* transplanted for *A. nasuta* and *A. spathulata* after a three months transplants experiment on Lizard Island. Numbers above error bars represent the total number of recollected fishes.

2.5 Discussion

Our results support the conclusion that a competitive lottery between *Gobiodon histrio* and *G. erythrospilus* occurs at settlement. We show that both species settle at the same size and that juveniles have identical patterns of habitat use. Moreover, a laboratory competition experiment found similar competitive ability between juveniles of the two fish species, as previously suggested by Munday (2004). Consequently, recruitment to preferred corals is likely to operate on a first come, first served, basis. However, we show that this situation changes later in life. By the adult stage, differences in habitat use have arisen, with *G. histrio* tending to dominate the preferred coral species *A. nasuta*. Competition experiments clearly show that *G. histrio* is the dominant species at this life stage, indicating that differences in habitat use among adults is likely due to competitive displacement. Our results uniquely demonstrate that both niche-partitioning and lottery mechanisms of competitive coexistence could operate between ecologically similar species and that the relative importance of these processes may change with ontogeny.

Stabilizing and neutral mechanisms of competition are typically viewed as diametrically opposed alternatives. However, recent theory suggests that they are extremes on a continuum that can simultaneously influence species coexistence in natural communities (Chesson 2000; Gravel et al. 2006; Adler et al 2007). Using site attached reef fishes we show, for the first time, that a lottery for living space occurs at settlement and niche partitioning take places in the adult stage. In the past, these two alternative mechanisms were considered mutually exclusive, and the ensuing debate has been one of the most enduring in the literature on reef fishes through the last few decades (Smith and Tyler 1972; Sale 1977, 1978; Robertson 1995; Forrester 2015). While theoretical and empirical studies have often assumed that the coexistence of two competing species is explained by just one mechanism, there is no *a priori* reason why this should be true. Attributes that might influence fitness differences between species and their competitive ability, such as growth rates, aggressiveness and specialization levels can change with ontogeny, as observed for a range of different taxa (De Roos et al. 2003, Huston and Smith 1987, Wilson et al. 2010, Gagliano et al. 2007; Pereira and Ferreira 2012). Therefore, it is not surprising that the mechanisms of coexistence may change with development in these reef fishes.

The lottery hypothesis still remains controversial and there are few studies that fully tested all of its assumptions. Results presented here using site attached reef fishes support an earlier study showing a competitive lottery for space at settlement for two coral-dwelling gobies. Similar to Munday (2004) we found that juveniles of both species exhibited nearly identical size-based ability to compete for preferred habitat. The present study tested and confirmed additional facets of the lottery hypothesis (sensu Sale 1977, 1998); (1) *G. histrio* and *G. erythrospilus* settle at the same size, so there is no potential for a size-based outcome of competitive ability, and (2) there is no niche partitioning between juveniles of the two species. Juvenile of the two species have nearly identical patterns of resource use and inhabit *Acropora* coral species in the same proportion. This combination of results suggests that chance alone determines which of the two species occupies a vacant space at settlement. The lottery hypothesis assumes that once space is colonized there is no displacement through a competitive hierarchy (i.e., there is a strong priority effect). Priority effects are important during settlement in reef fish assemblages (Shulman et al. 1983; Geange and Stier 2009) and Munday (2004) showed a priority effect for juveniles of *G. histrio* and *G. erythrospilus* where the first species to occupy a vacant coral excluded an interspecific intruder of similar body size; further supporting a competitive lottery during early life stages. Differences in colonization ability and dispersal can also influence coexistence among species with similar competitive abilities (Salomon et al. 2010). For example, if the subordinate competitor (*G. erythrospilus*) spawns earlier and consequently colonizes vacant habitats before the superior competitor (*G. histrio*) a priority effect could be established that favours the persistence of *G. erythrospilus*. However, there is no evidence, either from the present study or from other surveys and experiments over the last 10-20 years at Lizard Island that there are any differences in the timing of spawning or settlement of these two species of goby (Hobbs and Munday 2004; Munday 2004; Pereira, P.H.C. unpublished data). Furthermore, the two goby species have similar pelagic larval durations, which suggest that differences in dispersal abilities are unlikely to be involved in competitive coexistence.

Although the laboratory experiments demonstrated that adults of *G. histrio* and *G. erythrospilus* preferred the same species of coral (*A. nasuta*) they exhibited a different pattern of resource use in the field. *G. histrio* used *A. nasuta* more often than *A. spathulata*. In contrast, *G. erythrospilus* used the less preferred *Acropora spathulata* more often than *A. nasuta*. In adults, *G. histrio* appears to become the superior competitor, occupying *A. nasuta* at the expense of *G. erythrospilus,* which is displaced onto less preferred coral habitats. The use of alternative coral species due to limited habitat availability is common for *Gobiodon* spp. (Munday et al. 1997; Dirnwöber and Herler 2007). Habitat partitioning among the two goby species could be explained either by eviction of *G. erythrospilus* from *A. nasuta* colonies by *G. histrio* once competitive strength becomes unbalanced at larger sizes, or biased acquisition of *A. nasuta* colonies by *G. histrio* among juveniles that have settled to small coral colonies and subsequently need to search for larger coral colonies that can support a breeding pair (Hobbs and Munday 2004). At this stage the superior competitor, *G. histrio* may secure available colonies of *A. nasuta*, whereas *G. erythrospilus* is forced to use more *A. spathulata*. Post-settlement movement is not yet well understood for coral-dwelling gobies, despite the fact that single adults appear to move more than juveniles and breeding pairs (Wall and Herler 2009).

Given the lottery for space at settlement combined with a competitive hierarchy in adults that favours *G. histrio*, the question arises; How does the inferior competitor *Gobiodon erythrospilus* persist? As predicted, *G. erythrospilus* suffered less of a decline in growth by occupying non-preferred habitat, *A. spathulata,* compared with the dominant competitor *G. histrio* in that habitat. Consequently, *G. erythrospilus* appears better able to maintain growth performance in the alternative habitat that it is forced to occupy in greater proportion than *G. histrio* as a result of competition between the two species. Furthermore, *G. erythrospilus* is still able to maintain some access to the preferred coral, presumably because body size and priority effects prevent *G. histrio* from evicting larger resident *G. erythrospilus* from preferred habitat (Munday et al. 2001). Previous removal experiments of both species at Lizard Island (Munday 2004) found that removal of adult *G. histrio* from *A. nasuta* had a greater effect on recruitment of *G. erythrospilus* than the other way around, which supports the notion that *G. erythrospilus,* maintains adequate reproductive capacity despite frequent use of the less preferred coral. The differences in a fitness-associated trait (growth) detected between adults of the two goby species occupying preferred and non-preferred habitat is consistent with theoretical predictions; *G. histrio* had higher performance than *G. erythrospilus* on the preferred coral, *A. nasuta*, but suffered a greater decline in performance on the alternative habitat. These differences in performance on the two habitats can explain both why *G. histrio* is the dominant competitor for *A. nasuta* and how the two species coexist through niche partitioning despite the similar preference of *G. erythrospilus* for *A. nasuta*.

Although *G. histrio* suffered a larger decline in growth rate in the non-preferred coral compared with *G. erythrospilus*, it still achieved a similar growth rate to *G. erythrospilus* in the non-preferred coral. Thus, *G. histro* could potentially have a higher overall fitness compared with *G. erythrospilus* when both coral species are considered. However, we have only compared growth rates here, and not their reproductive performance. It is possible that *G. erythrospilus* has a higher reproductive output than *G. histro* on the non-preferred coral, which would help balance their relative fitness. Indeed, Munday (2004) observed that settlement of *G. erythrospilus* and *G. histrio* was proportional to the relative abundance of adults of these two species, indicating that *G. erythrospilus* is able to maintain sufficient reproductive output despite using a lower proportion of the preferred habitat.

Coral colony size also played a minor role in resource partitioning between *G. histrio* and *G. erythrospilus*. *Gobiodon erythrospilus* tends to use large and medium colonies whilst *Gobiodon histrio* uses smaller ones. Patterns of habitat use by the two species differed little among reefs from wind exposure regimes, indicating that niche partitioning occurred similarly on all reef types. This suggests that fitness differences between habitats were similar among reef types for the two *Gobiodon* species. If one species was a stronger competitor on a particular reef type, leading to greater use of the preferred coral on those reefs, we would have expected reef type to explain more variance in the data. Nevertheless, minor differences in habitat use in regard to coral colony size and wind exposure could potentially enhance the ability of the inferior adult competitor (*G. erythrospilus*) to persist in the presence of the superior adult competitor (*G. histrio*).

The ontogenetic shift from a lottery for space at settlement to niche-partitioning in adults that we observed in the two species of fish studied here is consistent with the continuum model of coexistence explored by Gravel et al. (2006). In that model, individuals recruit into limited space through a lottery, but then exhibit niche differentiation and their probability of surviving to reproduce is a species-specific function of an environmental factor. Here we demonstrate that there is a competitive lottery for space at settlement, there is niche-differentiation by adults between coral habitats, and that there is a species-specific fitness-related (growth) function associated with access to different coral habitats. In the continuum model, the coexistence of each species in the community and their relative abundance is determined by the distribution of environmental conditions and the amount of immigration from the metacommunity. This suggests that variation in the distribution of the coral species occupied by the two goby species, *A. nasuta* and *A. spathulata*, along with regular immigration and connectivity among reefs though the pelagic larval stage is probably crucial to the coexistence of these two species of fish at a local scale.

In one of the only other studies to empirically test the role of both lottery and niche-based processes in marine organisms, Shinen and Navarrete (2014) examined the processes responsible for the distribution and abundance of barnacles on rocky shorelines in Chile. They concluded that a lottery for space occurs at settlement and that this largely determines species' distributions within and among sites. Despite some differences in the spatial distribution of two barnacle species on the shore profile (vertical overlap of approximately 75%, which is similar to the niche-partitioning we observed among adult gobies) they found no evidence for differences in competitive ability or fitness trade-offs that could explain distribution patterns. Unlike our study, they did not detect significant differences in vital rates, such as growth, that could account for any slight differences in species distributions. Consequently, the two barnacle species examined in their study appear to be closer to the neutral end of the continuum than the two species of gobies in our study.

Plant communities are another place that a mix of lottery and niche-partitioning might be expected. Plants are good candidates for the presence of a lottery for space because of their life histories and mechanisms of dispersal, and indeed, much of the support to date for competitive lotteries comes from plant communities (e.g. Fagerström 1988; Aarssen 1992; Bengtsson et al. 1994; Kubo and Iwasa 1996; Iwata et al. 2007). Fagerström (1988) proposed that no interspecific differences are required for coexistence of plants provided the system is of finite size and spatially heterogeneous (e.g. evident variation in the biotic or abiotic environment, such as humidity and temperature) so variations are at least to some extent asynchronous. Niche-partitioning also occurs among plants (Kielland 1994; Mamolos et al., 1995; McKane et al. 2002) and it is known that plants segregate along different environmental niche axes; including gradients of light, soil moisture and roots depth that are likely to facilitate coexistence (Silvertown 2004). Consequently, just as observed for the goby species studied here, it seems that aspects of both neutral and niche-models may operate in plant communities (Adler et al. 2007). The life history attributes of perennial plants with a dispersive reproductive phase that will colonize vacant space stochastically (i.e. by lottery) could be potentially compared with reef fishes with a pelagic larval phase. Thus, ontogenetic changes in the mechanisms of competitive coexistence might also be observed in further research on plants communities.

Ecology has progressed from a focus on single ecological processes to a multifactorial perspective of the processes and mechanisms that govern population dynamics and community structure (Jones 1991, Caley et al. 1996 Hixon et al. 2002; Johnson and Stinchcombe 2007; Wiens et al. 2010). In this context, it is not surprising that the same ecological process might operate in different ways among interacting species. Competition is one of the most important ecological processes in natural communities (Connell 1983; Tilman 1994; Chesson 2000; Amarasekare 2004), yet few empirical studies have tested whether alternative mechanisms of competitive coexistence might co-occur in the same communities. Our results empirically demonstrate ontogenetic changes in the mechanisms of competitive coexistence and suggest that it could be relevant for taxa other than reef fishes. Just as marine ecologists have embraced the idea that multiple ecological processes (predation, competition, dispersal) are responsible for the maintenance of populations and communities (e.g. Jones 1991, Caley et al. 1996 Hixon et al. 2002), our study suggests the need to recognise that a variety of mechanisms within each of these processes may be responsible for the maintenance of biodiversity of coral reefs.

Chapter 3: Influence of resource availability on competition among coral-dwelling fishes

This chapter is submitted to Oecologia. Authors: PHC Pereira, PL Munday and GF Jones.

3.1 Summary

Ecologically similar goby species compete for access to preferred habitat; however, the mechanism of competitive coexistence changes from a lottery to niche-partitioning with ontogeny. Here, we explore how variation in the abundance of *A. nasuta* coral colonies, the preferred habitat of *Gobiodon histrio* and *G. erythrospilus*, influences the outcome of competitive interactions between these two fish species. First, we compared the relative abundance and patterns of habitat use of the two goby species among sites that varied in the absolute and relative abundance of their preferred habitat. We then used a recolonization experiment to test the prediction that the effects of competition are greatest where preferred habitat is relatively less abundant. Both gobies had similar relative abundance among sites; however, similarity in habitat use was closely correlated with the abundance of their preferred habitat. The proportional occupancy of *A. nasuta* by the superior competitor, *G. histrio*, increased as the relative abundance of *A. nasuta* declined. In the recolonization experiment the effects of preferred coral availability differed between juveniles and adults. For juveniles, where a competitive lottery operates, the proportional use of preferred coral was the same for the two species, regardless of the relative abundance of *A. nasuta.* In contrast, for adults niche-partitioning was greater at locations that had a lower relative abundance of *A. nasuta.* Our results show that changes in the relative abundance of preferred resources can influence competitive interactions between reef fishes, but the effects differ depending on the mechanisms of competitive coexistence.

3.2 Introduction

Competition is a fundamental ecological process structuring natural communities in a range of different environments, including tropical rainforests (Wright 2002), savannas (Dohn et al. 2013), rocky shores (Connell 1978) and coral reefs (McCook et al. 2001; Connell et al. 2004; Connolly et al. 2014). Competition occurs when vital resources such as food and shelter are in limited supply causing individuals of the same or different species to come into conflict and have deleterious effects on one another. However, resource availability is rarely static and temporal and spatial fluctuation in resource availability can modify the intensity of competitive interactions (Holling 1973; Abrams 2000; Holt et al., 2008; Pekkonen et at. 2013). When resources are abundant, individuals have greater access to preferred resources and thus competitive effects may be negligible. Conversely, when resources become scarce, competition for these resources may be intense, affecting fundamental demographic traits, such as growth, survival and reproduction (Robertson 1996; Dyer and Rice 1999; Pollitt et al. 2011). However, few studies have assessed the levels of competition over the natural range of resource levels.

The mechanisms by which competing species coexist will influence how different species respond to variation in resource availability and their relative fitness. Niche theory predicts that competition between species leads to resource partitioning, with species using a different range of resources in the presence of a competitor than they do in the absence of the competitor (Colwell and Fuentes 1975; Schoener 1982; Grant 1986). If this model applies, changes in resource use may occur for both species, or may be greater in one species than the other (Colwell and Fuentes 1975). A common feature of competitive interactions is that some species are stronger competitor than others. In a competitive hierarchy, changes in resource availability could affect patterns of resource use and relative fitness among species because superior competitors should gain greater access to preferred resources when they are scarce, whereas subordinate competitors are forced to use inferior resources.

Outcomes will differ if species interactions conform more with the lottery hypothesis, (Sale 1977, 1978) or neutral models (Bell 2000, Hubbell 2001), which assume that ecologically similar species have identical competitive abilities and coexist through demographic stochasticity at one or more life-stages. In a competitive lottery (Sale 1977, 1978), where species are competitive equivalents and resources are used on a first-come-first-served basis, changes in resource availability may affect individual fitness, but should not alter relative fitness between species. Changes in resource availability may affect population sizes, but not the relative performance of different species, because each species will still have an equivalent chance to use remaining resources. Hence, to understand the consequences of interactions between the intensity of competition and resource availability, the mechanism of coexistence is critical.

Coral reef fishes are often assumed to exhibit competition for living space, although this has been a particularly controversial topic (Jones 1991; Forrester 2015; Bonin et al. *in press*). Early researchers assumed that competition for space was universal, but were divided over whether competition led to changes in resource use by niche-portioning (Smith and Tyler 1972, 1975; Robertson and Lassig 1980) or whether reef fish were competitive equivalents, successfully exploiting the same limited resources by the lottery mechanism (Sale 1977, 1978). Subsequent hypotheses, proposed that space was not a limiting factor and that similarities or differences in resource use had little to do with the availability of those resources. According to the recruitment limitation hypothesis (Doherty 1983), larval mortality of reef fishes is so high, and subsequently settlement so low, that local populations of juveniles and adults never reach abundances where they compete for space or other resources. However, laboratory and field experiments have since demonstrated that space is a limiting factor for at least some reef fishes (Clarke 1992; Munday et al. 2001; Holbrook and Schmitt 2002; Munday 2004; Forrester et al. 2006; Bonin 2009) and that competition for space can affect demographic traits such as growth and survival (Shulman 1984; Robertson 1996; Munday 2001). While the majority of studies suggest the presence of competitive hierarchies and niche partitioning among competing species (Robertson and Gaines 1986; Clarke 1989; Munday et al. 2001; Geange et al. 2013), there is also evidence for competitive lotteries in some reef fish taxa (Munday 2004; Pereira et al. 2015).

Coral-dwelling gobies (genus *Gobiodon*) are small fishes that use *Acropora* coral colonies as a vital resource for shelter, breeding and nutrition (Munday 2001; Dirnwoeber and Herler 2007; Brooker et al. 2010). *Acropora* coral colonies are a limited resource and competition among gobies for preferred coral colonies influences both abundance and patterns of habitat use (Munday et al. 2001; Hobbs and Munday 2004). Previous studies indicate that gobies coexist by a variety of mechanisms. There is a clear competitive hierarchy and niche partitioning among some species, whereas other species appear to be competitively equivalent and coexist by a lottery for space (Munday et al. 2001; Munday 2004).

Furthermore, both niche partitioning and lottery mechanisms may be involved in some competitive interactions. For example, *Gobiodon histrio* and *Gobiodon erythrospilus* are two ecologically similar species that compete for access of their preferred habitat, *A. nasuta.* The two species have equivalent competitive ability at settlement and access to vacant habitat space is determined by a lottery at this life stage (Munday 2004; Pereira et al. 2015). However, *G. histrio* becomes a superior competitor in later life stages and gains greater access to the preferred coral habitat (Pereira et al. *in press*).

Gobiodon histrio and *Gobiodon erythrospilus* provide a unique opportunity to test how resource availability influences the outcome of competition for habitat space under different mechanisms of competitive coexistence. We predicted that adult *G. histrio* (superior competitor) would become relatively more abundant, or gain greater proportion of preferred corals as the relative abundance of preferred corals diminishes. In contrast, adult *G. erythrospilus* (subordinate competitor) should become relatively less abundant, or have reduced access to preferred coral, as the relative abundance of preferred corals declines. Furthermore, the ontogenetic change in the competitive mechanism should lead to differences in patterns of relative abundance and patterns of habitat use among life phases. If a lottery for space operates at settlement, then juveniles of both species should use the preferred resource (*A. nasuta*) in the same proportion, regardless of the relative abundance of the preferred habitat. However, as a competitive hierarchy is established in older life stages, the superior competitor (*Gobiodon histrio)* could gain access to an increased proportion of the preferred habitat. To test these predictions we first compared the relative abundance and patterns of habitat use of the two goby species among sites with different absolute and relative abundances of *A. nasuta*, the preferred habitat for both species. We then conducted a recolonization experiment at the same sites where abundance surveys were conducted to test if different mechanisms of competitive coexistence influence the relationship between resource availability and the relative abundance of the two species in juvenile and adult life stages. Due to the ontogenetic shift in the mechanism of competition, we predicted that there would initially be equivalent recolonization of *A. nasuta* colonies by juveniles of both goby species regardless of the relative abundance of the preferred coral (i.e. recolonization would be a lottery based on chance arrival to vacant habitat). However, through time, when individuals reached larger size classes and a competitive hierarchy develops, we predicted that *G. histrio* should gain greater proportional accesses to *A. nasuta* at sites with a lower abundance of preferred habitat.

3.3 Methods

Study species and location

Gobiodon histrio and *G. erythrospilus* (Figure 3.1A) are ecologically similar sister species (Duchene et al. 2013) that overlap broadly in their geographical distributions. At Lizard Island on the northern Great Barrier Reef, Australia, they occur in similar abundances and exhibit similar patterns of habitat use (Munday 2004; Pereira et al. 2015). Both species prefer to inhabit colonies of *A. nasuta*; however, the mechanism of competitive coexistence changes with ontogeny. A lottery for living space occurs at settlement, whereas a competitive hierarchy and niche partitioning occurs in the adult stage (Pereira et al. 2015).

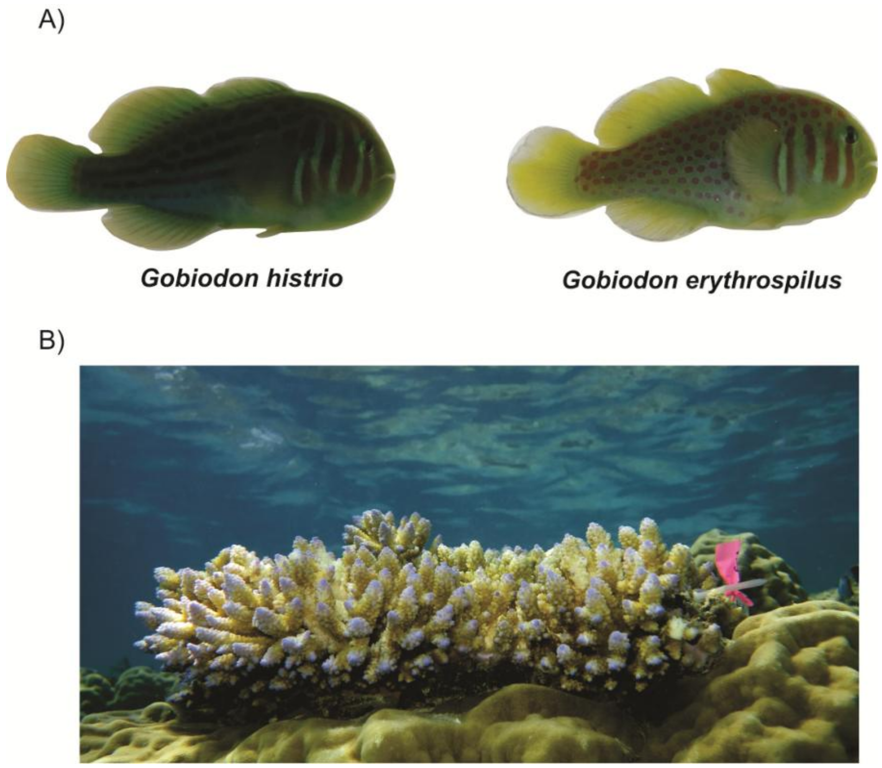

Figure 3.1 – *Gobiodon histrio* and *Gobiodon erythrospilus*, the two goby species investigated in this study (A) and tagged *Acropora nasuta* coral colonies used during the recolonization experiment (B).

Field surveys and a recolonization experiment were conducted in October 2013 and January 2014 on reefs at Lizard Island (14° 38'S - 145° 26'E). To examine how variation in availability of preferred coral habitat influences competitive interactions between coral dwelling gobies we took advantage of the natural variation in the relative abundance of the preferred coral species (*A. nasuta*) on reefs around the Lizard Island. Preliminary surveys showed that Loomis Reef was a site with high relative abundance of *A. nasuta*, Horseshoe Reef had a moderate relative abundance and North Point had a low relative abundance of *A. nasuta* (Figure 3.2).

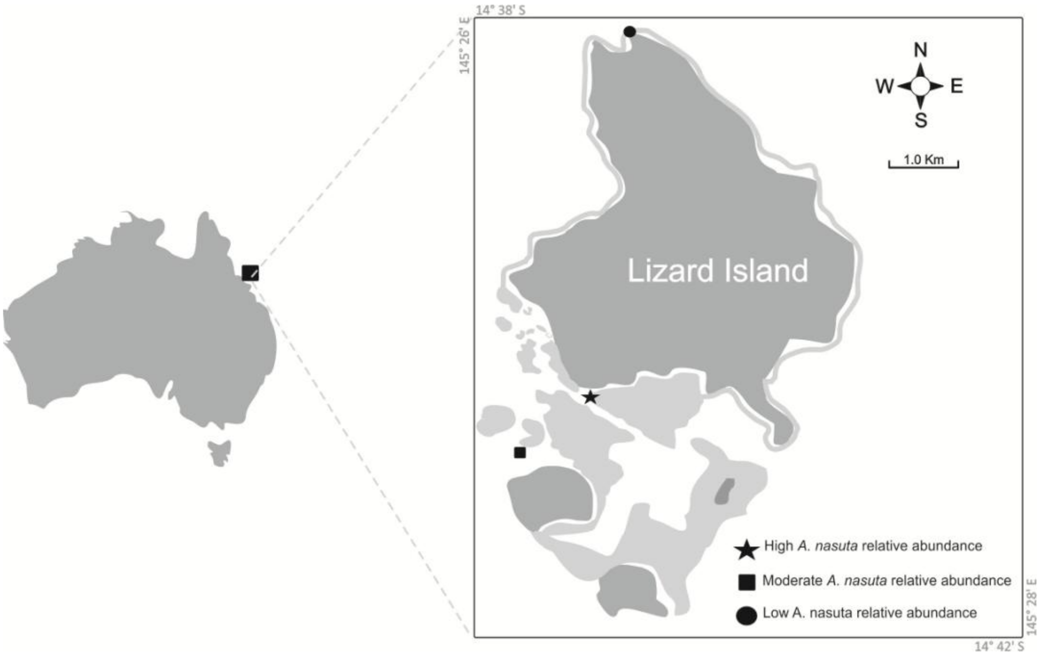

Figure 3.2 - Map of study area (Lizard Island - Northeast Australia) showing the surveyed sites and highlighting the relative abundance of the preferred habitat (*Acropora nasuta*).

Surveys of coral and goby abundance

The abundance of the two goby species, *G. histrio* and *G. erythrospilus*, and their preferred habitat *A. nasuta* were surveyed in 10 replicate belt transects (25 X 2 m) on the reef flat at each of the three sites that differed in the relative abundance of *A. nasuta*. For each transect, the total number of all suitable *Acropora* coral colonies (including the preferred habitat - *A. nasuta*) and the total number of *G. histrio* and *G. erythrospilus* (excluding recruits and small juveniles) were recorded.

A Kruskal–Wallis test was used to compare mean abundance of *A. nasuta* and mean abundance of gobies among the three sites. Analysis of covariance (ANCOVA) was then used to test if changes in the total number of coral colonies within and among sites affected the relative abundance of *G. histrio* and *G. erythrospilus* in the same way. This analysis tested for homogeneity of regression slopes of the total number of gobies of each species versus the total number of coral colonies. Finally, linear regressions were used to compare the percentage similarity of the habitat use between *G. histrio* and *G. erythrospilus* with the relative abundance of the preferred habitat (*A. nasuta*). In this analysis, percent similarity of the habitat use by the two species was calculated using the percent similarity index (Wolda, 1981), the following formula: $PS = \sum \min(p_{1i}, p_{2i})$ where p_{ji} is the proportion of species i in sample J being $J = \frac{n_{ji}}{N_j}$ and n_{ji}= the number of individuals of species i in sample j and N_j= the number of individuals in sample j.

All analyses were conducted using Statistica 10 (StatSoft Inc. 2011).

Recolonization experiment

Pereira et al. (2015) found that competition between *G. histrio* and *G. erythrospilus* shifts from a lottery at settlement to a competitive hierarchy and niche-partitioning among adults. If a lottery for space occurs at settlement, we predicted that similar proportions of the two goby species should recolonise vacant *A. nasuta* colonies at settlement, regardless of the relative abundance of the preferred coral. In other words, the relative abundance of the two goby species in the preferred habitat should not be affected by the abundance of that habitat if they coexist through a lottery for space. In contrast, if a competitive hierarchy develops among adults, we predicted that *G. histrio* would gain greater proportional accesses to the preferred habitat as the abundance of that preferred habitat diminishes. Furthermore, we predicted that over time we should observe a shift from newly-settled juveniles of the two species that exhibited similar proportional use of *A. nasuta*, to larger individuals and adults that exhibited a gradient in proportional use of *A. nasuta* depending on the availability of the preferred habitat. Accordingly, we surveyed the recolonization experiment at two different timeframes: monitoring corals every day for a week after initially establishing the experiment (short-term) and then again after 3 months (long-term).

A total of 40 colonies of *A. nasuta* were numbered and tagged with cable ties at each of three sites (120 colonies in total) (Figure 3.1B). All resident gobies were removed from those colonies using clove oil (Munday and Wilson 1997) in October 2013. Empty coral colonies were monitored daily for seven days and any gobies colonizing the corals were removed and identified. Coral colonies were then left for 3 months and surveyed again in January 2014.

A chi-square test of independence was used to compare the frequency with which juveniles and adults of *G. histrio* and *G. erythrospilus* recolonized *A. nasuta* coral colonies among the three sites. Juveniles and adults were analysed separately because of the predicted differences in patterns of relative abundance among sites. Additionally, short and long term surveys were analysed separately. For the short term survey, the cumulative number of recruits and adults observed over the week of monitoring was used in the analysis. Analyses were conducted in Statistica 10 (StatSoft Inc. 2011).

3.4 Results

Relative abundance of preferred coral habitat

There was a significant difference in the relative abundance of the preferred coral, *A. nasuta*, among the three sites ($H = 21.36$; $df = 2$, $p < 0.05$). The percentage of *A. nasuta* compared to the total number of coral colonies per transect was 32.27 ± 5.08% at Loomis Reef, 20.40 ± 3.53% at Horseshoe Reef and 14.6 ± 3.11% at North Point. There was a negative relationship between the total number of coral colonies and the percentage of *A. nasuta* per transect ($R^2 = 0.67$; $p = 0.009$) (Figure 3.3).

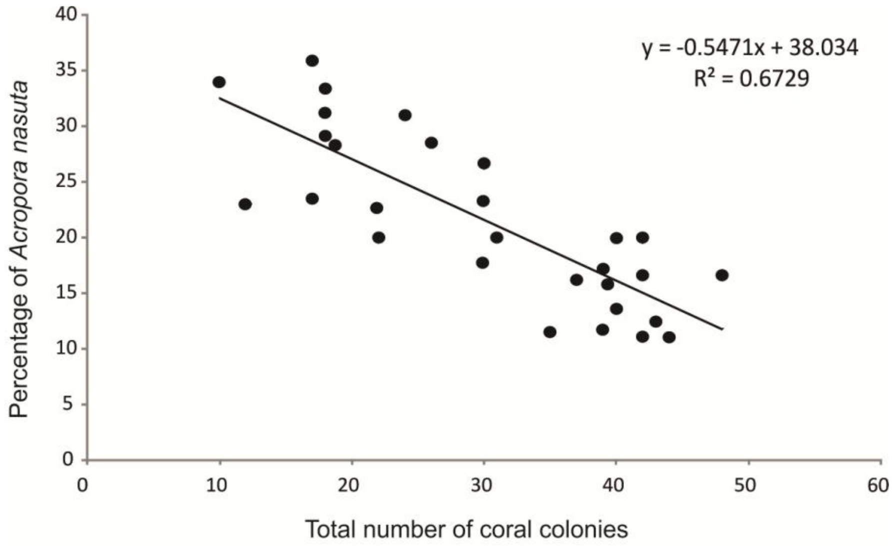

Figure 3.3 – Linear regression of the percentage of *A. nasuta* colonies compared with the total number of coral colonies per transect. Each point represents a belt transect.

Relative abundance of coral gobies and patterns of habitat use

The relative abundance of adult *G. histrio* and *G. erythrospilus* was similar among the three sites (H = 19.72; df = 2, $p = 0.5$), despite the substantial difference in the relative abundance of preferred habitat. Relative abundances were 50.6% for *G. histrio* and 49.3% for *G. erythrospilus* at Loomis Reef (high *A. nasuta* relative abundance), 52.3% for *G. histrio* and 47.7% for *G. erythrospilus* at Horseshoe Reef (moderate relative abundance), and 54.6% for *G. histrio* and 45.4% for *G. erythrospilus* at North Point (low relative abundance).

The total abundance of adult *G. histrio* ($R^2 = 0.60$; $p < 0.05$) and *G. erythrospilus* ($R^2 = 0.70$; $p < 0.05$) increased with the total number of coral colonies per transect. However, there was no difference in the relative abundance of the two species as indicated by the similar regression slopes ($F_{1,29} = 7.76$, $p = 0.9$), emphasizing that changes in the total number of *Acropora* coral colonies affected the abundance of *G. histrio* and *G. erythrospilus* in the same way (Figure 3.4).

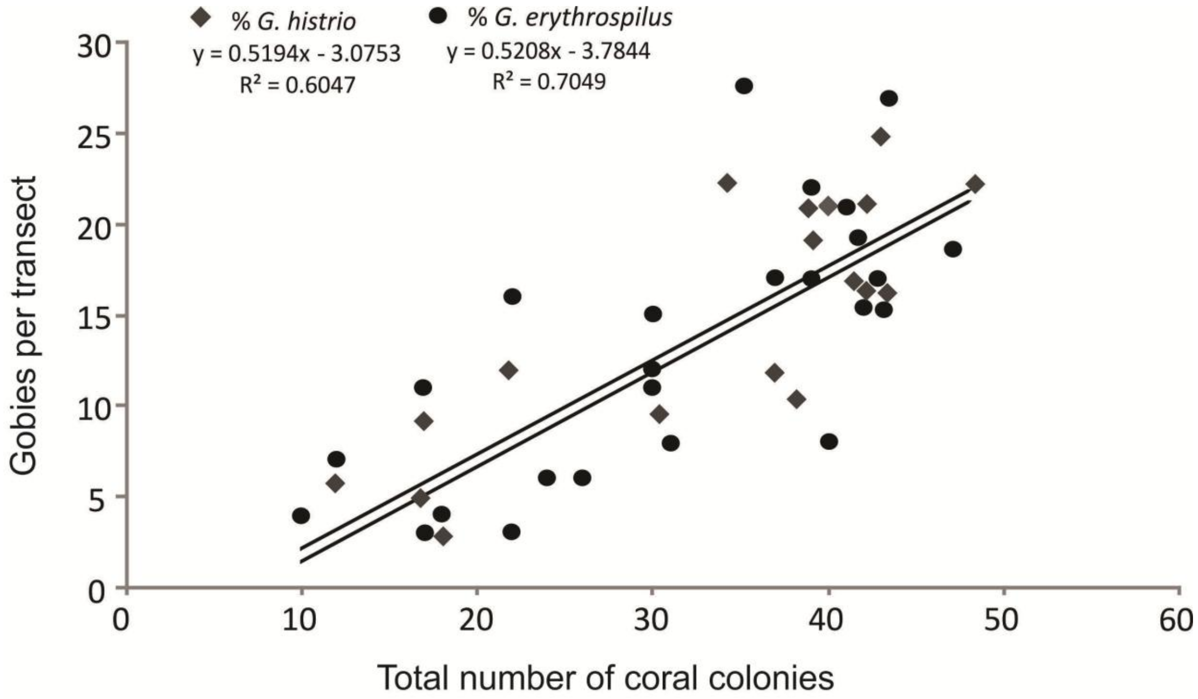

Figure 3.4 - Analysis of covariance of the number of *G. histrio* and *G. erythrospilus* compared with the total number of coral colonies. Each point represents a belt transect.

Percentage similarity of habitat use between *G. histrio* and *G. erythrospilus* was closely correlated with the relative abundance of preferred habitat ($R^2 = 0.703$; $p < 0.05$) (Figure 3.5). The two species exhibited more similar patterns of habitat use (>50%) where the relative abundance of *A. nasuta* was high compared with transects where the relative abundance of *A. nasuta* was low. For instance, where the relative abundance of *A. nasuta* was very low (15% of the total number of coral colonies), the similarity in habitat use was around 20%. In contrast, where *A. nasuta* relative abundance was high (35% of the total number of colonies) the similarity in habitat use increased to approximately 70% (Figure 3.5).

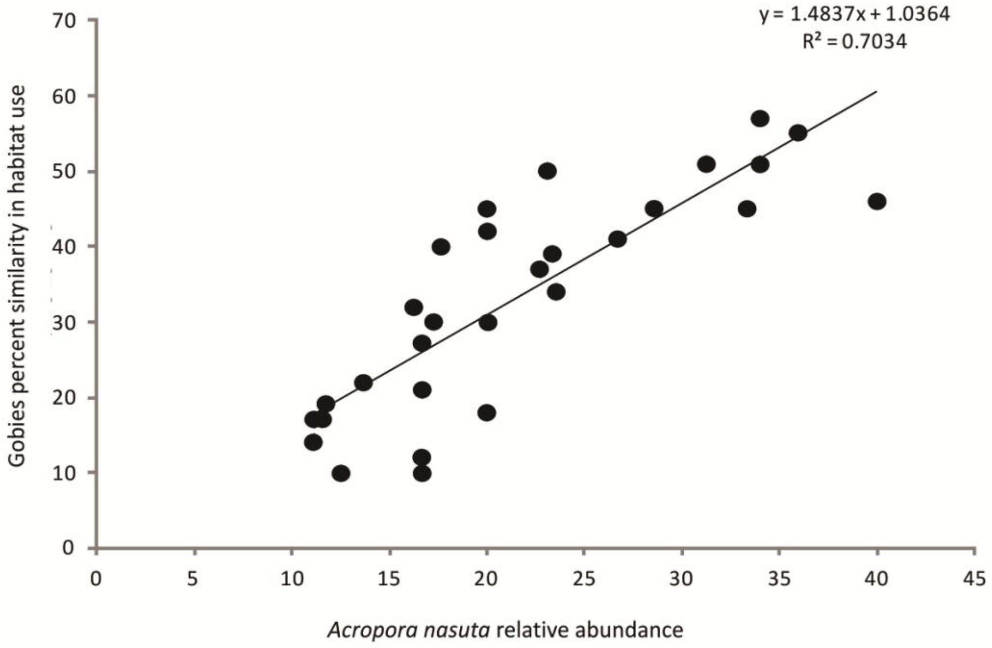

Figure 3.5 – Percent similarity of the habitat use by *Gobiodon histrio* and *Gobiodon erythrospilus* compared to the relative abundance of the preferred habitat (*Acropora nasuta*) per transect.

Recolonization experiment

A total of 283 *Gobiodon* individuals were recorded during the recolonization experiment conducted in October 2013 (short-term) and 192 in January 2014 (long-term) (Figure 3.6 A-B). During the short term monitoring, juveniles of the two species exhibited nearly identical patterns of recolonization to *A. nasuta* coral colonies (chi-square = 0.56, df = 2, *p* = 0.75) regardless of the difference in the relative abundance of the preferred coral (*A. nasuta*) among sites (Figure 3.6A). In contrast, adults of the two species exhibited significant differences in the recolonization process (chi-square = 9.54, df = 2, *p* = 0.008) (Figure 3.6A). Adults of the superior competitor (*G. histrio*) used proportionally more preferred coral colonies at sites where *A. nasuta* was less abundant (Figure 3.6A). Specifically, occupancy of *A. nasuta* by adult *G. histrio* was 51% for high relative abundance, 67% for moderate and 77% for low *A. nasuta* relative abundance. In contrast, occupancy of *A. nasuta* by adult *G. erythrospilus* was 49% for high relative abundance, 33% for moderate and 23% for low *A. nasuta* relative abundance (Figure 3.6A).

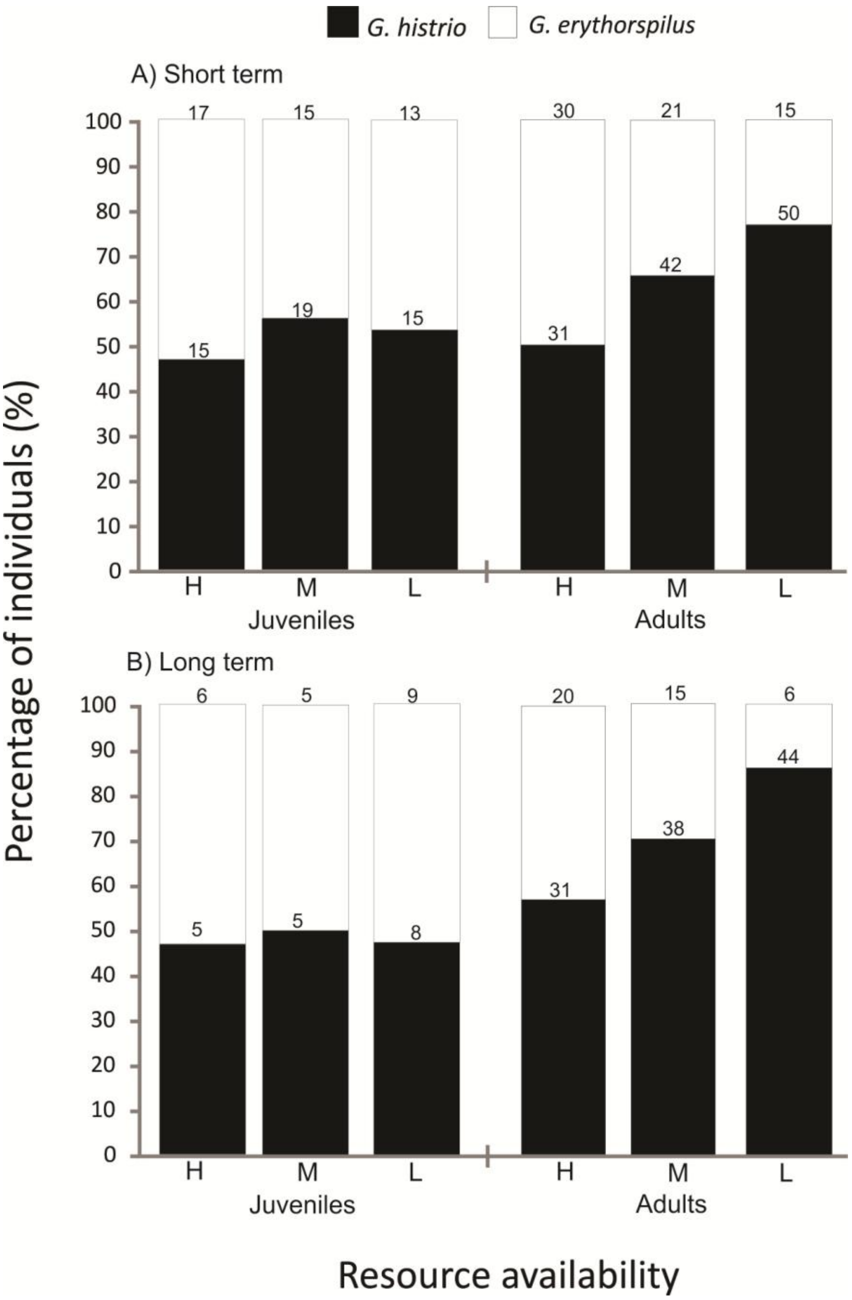

Figure 3.6 – Results of short term (A) and long term monitoring (B) of the field removal experiment. H = High *A. nasuta* relative abundance, M = Moderate *A. nasuta* relative abundance, Low = High *A. nasuta* relative abundance. Numbers above bars indicate the total number of individuals.

As expected, there were fewer juveniles of both species on the coral colonies after three months. Nevertheless, juveniles of *G. histrio* and *G. erythrospilus* were still present in equal proportions (chi-square = 0.45, df = 2, p = 0.97) (Figure 3.6B). As predicted for adults, the proportional abundance of *G. histrio* using the preferred habitat increased as the relative abundance of *A. nasuta* declined (chi-square = 9.68, df = 2, *p* = 0.007). Specifically, occupancy of *A. nasuta* by adult *G. histrio* was 61% for high relative abundance, 71% for moderate and 88% for low *A. nasuta* relative abundance. In contrast, occupancy of *A. nasuta* by adult *G. erythrospilus* was 39% for high relative abundance, 29% for moderate and 12% for low *A. nasuta* relative abundance (Figure 3.6B).

3.5 Discussion

Our results show that variation in resource availability influences the outcome of competitive interactions between coral reef fishes, and also that the outcome of competitive interactions directly depends on the mechanisms of competitive coexistence. As predicted for juveniles, where a lottery for space operates, variation in the relative abundance of preferred habitat had no effect on patterns of resource use by the two coral-dwelling gobies. However, for adults, where a competitive hierarchy occurs, the superior competitor *G. histrio* used an increasingly greater proportion of the preferred habitat as the abundance of that habitat declined, both in the field surveys and recolonization experiment. For adults, both goby species occurred in similar relative abundance at the sites surveyed around Lizard Island, but their patterns of habitat use diverged as the the relative abundance of the preferred coral decreased. Similarly, in the recolonization experiment the two species used the preferred coral in approximately equal proportion where it was abundant, but adult G. *histrio*, gained greater proportional access to this habitat in locations where the relative abundance of the preferred habitat was low. These results indicate that the availability of preferred habitat does not affect the relative abundance of these two species, but it does influence competition for preferred habitat, and thus patterns of habitat use.

Our results add further evidence to the conclusion that a competitive lottery for space operates between *G. histrio* and *G. erythrospilus* at settlement and in the juvenile phase, as suggested by Munday (2004) and Pereira et al. (2015) Predictions of the lottery hypothesis were supported in the field recolonization experiment. During daily monitoring of vacant coral colonies, the abundance of juveniles of both species recolonizing *A. nasuta* was very similar, regardless of the availability of the preferred coral in different sites. This pattern of recruitment is consistent with the lottery hypothesis, which assumes that species have similar competitive abilities and space is occupied on a first-come-first-served basis (Sale 1977, 1978). As expected, the total abundance of juveniles was less in the recolonization experiment after 3 months, probably due to habitat exclusion by larger individuals (Hobbs and Munday, 2004). However, the relative proportion of juveniles of the two species remained approximately equal throughout the experiment, as would be expected if a competitive lottery is operating.

While a lottery for space occurs at settlement, there is a shift to a competitive hierarchy between *G. histrio* and *G. erythrospilus* in adults. Field surveys at nine sites around Lizard Island during a previous study showed that juvenile *G. histrio* and *G. erythrospilus* used *Acropora* coral species in a similar proportion, but habitat use diverged in adults (Pereira et al. 2015). Here we found that the relative proportion of *A. nasuta* used by the two species depends on its relative abundance in the coral community. The two fish species had over 70% similarity in habitat use where *A. nasuta* was relatively abundant, but this dropped to approximately 20% where the relative abundance of *A. nasuta* was low. Importantly, the superior competitor *G. histrio* gained a greater proportional access to the preferred habitat as the relative abundance of that habitat declined. Consequently, the subordinate competitor, *G. erythrospilus* was forced to use a greater proportion on non-preferred habitat as the relative abundance of the preferred habitat declined, with potential effects on individual fitness.

Competitive hierarchies have been shown to influence patterns of resource use in other reef fishes (Robertson 1996; Munday et al. 2001; Geange et al. 2013). For example, following the removal of the superior competitor (*Stegastes planifrons*) in a damselfish assemblage, adult *S. partitus*, which are less aggressive and half the size of *S. planifrons*, doubled in number and expanded their range into a microhabitat previously used almost exclusively by *S. planifrons* (Robertson 1996). A third species, *S. variabilis*, which is less aggressive and 20% smaller than *S. planifrons*, also increased in abundance following the removal of *S. planifrons*. By contrast, removal of *S. planifrons* had no effect on the abundances and patterns of resource use of *S. diencaeus* and *S. leucostictus* because these two species use different microhabitats to *S. planifrons* and thus do not compete directly (Robertson 1996). Similarly, Munday et al. (2001) found that the presence of a superior competitor influenced habitat use of subordinate species of coral-dwelling gobies. Following the removal of a superior competitor, *G histrio*, the subordinate competitor, *G. brochus*, increased its use of the preferred coral *A. nasuta*, where it has faster growth, increased survival, and reaches a larger maximum size and thus has higher fecundity (Munday 2001; Herler et al. 2011). In the present study we found that the proportional use of *A. nasuta* by adult *G. histio* and *G. erythrospilus* changed in relation to habitat availability, with the superior competitor having greater proportional access to preferred habitat as that habitat became less abundant. Consequently, a reduction in the availability of preferred resources may intensify competition, with significant consequences to the subordinate species (Griffis and Jaeger 1998, Orrock and Watling 2010).

Cryptic density-dependence (Shima and Osenberg 2003) is another concept that deals with the correlation of site quality, species abundance and competition outcomes. This hypothesis argues that if sites differ spatially and temporally in quality (*e.g.* supply of a limited resource) then species abundance will become positively correlated with resource availability. The cryptic density-dependence phenomenon has been described for site-attached reef fishes (Overholtzer-McLeod 2004; Schmitt and Holbrook 2007), crabs (Donahue 2006) and aphids (Helms and Hunter 2005). Heterogeneity in site quality can affect species recruitment, causing species abundance to become positively correlated with resource availability. However, the connection between the strength of density dependence and resources availability can the "cryptic" giving the false idea that all sites have the same capability of support similar populations. Because survival is density dependent, habitat quality masks the deleterious effects of density. Although cryptic density-dependence is associated with variation in habitat quality, it is not relevant to our study system because goby density is not higher in preferred habitats. A maximum of two adult fishes (breeding pairs) colonize preferred habitats, regardless of habitat size or quality (Hobbs and Munday 2004). Instead, preferred habitat provides benefits to individual fitness (Munday 2001; Pereira et al. 2015) rather than population density.

Given the competitive advantage of adult *G. histrio* when preferred habitat is scarce, the question that arises is how does *G. erythrospilus* persist? It is known that growth, survival and reproductive output of coral-dwelling gobies are enhanced by access to preferred coral habitat (Munday 2001, Caley and Munday 2003; Herler et al. 2011). Therefore, we might expect that *G. histrio* will have a fitness advantage and might produce more larvae than *G. erythrospilus*. As vacant space is colonized by a lottery at settlement, *G. histrio* would effectively have more "*winning tickets*" in the lottery and should gain a numerical advantage at settlement. A numerical advantage at settlement could flow through to the adult population, eventually leading to the exclusion of *G. erythrospilus*. However, our data suggests that *G. histrio* does not gain a numerical advantage at settlement. In fact, we observed that the two species settled in nearly identical number during the recolonization experiment. Furthermore, Munday (2004) observed a numerical bias toward settlement of *G. erythrospilus*. It seems that *G. erythrospilus* is able to produce sufficient offspring to compete with *G. histrio* at settlement, despite using a greater proportion of non-preferred corals. In some years, *G. erythrospilus* might be even able to outcompete *G. histrio* with the number of larvae available to occupy vacant space, as observed by Munday (2004), which would help buffer their populations through the storage effect (Chesson and Warner 1981). Additionally, Pereira et al. (2015) found that *G. erythrospilus* suffered less of a fitness loss when occupying the non-preferred coral (*A. spathulata*) compared with *G. histrio*, which could explain its ability to maintain adequate larval supply to compete with *G. histrio*. Even though *G. histrio* prefers to occupy *A. nasuta*, some individuals occupy other corals, such as *A. spathulata*, where they may have lower reproductive success compared with *G. erythrospilus*. Consequently, *G. erythrospilus* appears to be better able to maintain performance in the alternative habitat; therefore, ensuring its coexistence with *G. histrio*.

Spatial and temporal variation in resource availability can also facilitate competitive coexistence (Stewart and Levin 1973) and may help explain how *G. erythrospilus* and *G. histrio* coexist. Coral community structure varies both spatially and temporally, especially for fast growing *Acropora* species (Alvarez-Filip et al. 2011; Edmunds 2013). As a result there will always be some reefs with a high abundance of *A. nasuta* where both goby species are able to use their preferred habitat in similar relative abundance, and some other reefs with a low abundance of *A. nasuta* where *G. histrio* can only access low quality coral habitat. Indeed, Pereira et al. *in press* found a considerable number of adult individuals of *G. histrio* inhabiting *A. spathulata* coral colonies in sites around Lizard Island. In these locations, *G. histrio* is likely to have lower relative fitness by using non-preferred habitats compared to *G. erythrospilus*. Therefore, spatiotemporal variation in coral community structure is likely to produce spatial and temporal variation in the production of offspring by *G. histrio* or *G. erythrospilus,* which would favour species coexistence.

Coral cover is declining on reefs all around the world (Gardner et al. 2003; Bruno and Selig 2007; De’ath et al. 2012). However, the effects of competition on reef fish communities following coral loss and habitat degradation are poorly understood. Boström-Einarsson et al. (2014) showed that reduced habitat quality can have such a profound effect on reef fish competition that it eliminates density dependent mortality and competitive dominance hierarchies. Additionally, McCormick et al. (2013) showed that habitat degradation caused major changes in the interspecific competition among damselfishes. Our results show that the composition of the remaining coral community will also directly influence competition among reef fishes. If there is a relationship between overall coral cover and the relative abundance of preferred habitats, then coral loss could have disproportionate effects on subordinate competitors. Alternatively, superior competitors that specialize on the preferred resource could also be affected once the abundance of this specific resource diminishes. Inferior competitors and more generalist species could become more abundant in the future if they attain better fitness outcomes in alternative habitats. Our results suggest that will be critical to understand the mechanisms of competition between fish species to better predict how reef fish communities will respond to habitat degradation.

Chapter 4: Habitat size and complexity as a determinant factor on habitat use and fitness of coral reef fishes

This chapter is submitted to Marine Ecology Progress Series (MEPS). Authors: PHC Pereira and PL Munday.

4.1 Summary

Competition for space affects patterns of habitat use and individual performance of coral-dwelling fishes; however, the physical attributes of corals that influence habitat preferences are poorly known. In this study we investigated the influence of coral colony size and branching structure on habitat use and growth rate of two coral gobies, *Gobiodon histrio* and *Gobiodon erythrospilus.* First, we examined two key aspects of coral colony structure, interbranch depth and interbranch width that may influence habitat preferences. We then used laboratory and field-based experiments to test the effects of coral species, coral colony size and branching structure on habitat preference and growth rates of *G. histrio* and *G. erythrospilus.* The preferred coral species, *A. nasuta* had smaller interbranch width than *A. spathulata*. A binary-choice laboratory experiment demonstrated that both gobies preferred coral colonies with smaller interbranch width, except when they had the opportunity to occupy *A. nasuta* over *A. spathulata*. A field transplant experiment showed that both goby species grew faster on larger coral colonies and in colonies with smaller interbranch width. *G. erythrospilus* grew faster than *G. histrio* on *A. spathulata*, indicating that it suffers less of a fitness loss occupying this alternative habitat. Our results show that coral physical attributes are important factors driving habitat preference of coral-dwelling gobies; however, there must also be additional factors that influence their habitat use. Declining average coral size and reduced habitat complexity on coral reefs could have significant impacts on the performance of fishes, affecting ecological processes such as competition.

4.2 Introduction

Habitat characteristics have a profound influence on the distribution, abundance and diversity of animals associated with complex habitats, such as rainforests (McIntyre 1995) and coral reefs (Friedlander & Parrish 1998, Jones & Syms 1998). Habitat quality, patch size, location and structural complexity can all be important predictors of species diversity and influence ecological interactions among resident species (Crowder & Cooper 1982, Grabowski 2004, Kovalenko et al. 2012, Fabricius et al. 2014). Species are expected to selected habitat types that benefit individual fitness and may compete for access to these habitats (Adler & Gordon 2003, Wakefield et al. 2011). However, competitive interactions are often asymmetric, such that superior competitors gain greater access to preferred habitats and inferior competitors are forced to use suboptimal habitat, regardless of their natural preference, with consequences for growth, survival and reproduction (Gibb 2011, Carrington 2014, Bonin et al. 2015).

Coral reefs are well known for their astonishing diversity of fishes (Sale 1977). A range of habitat-associated variables such as coral cover, coral diversity and structural complexity can influence the community structure and population dynamics of reef fish (Messmer et al. 2011, Coker et al. 2012, Komyacova et al. 2013). Habitat characteristics may be especially important for species that have a close association with live coral habitat; influencing recruitment, survival, group size and individual growth (e.g. Kuwamura et al. 1994, Holbrook & Schmitt 2003, Thompson et al. 2007, Schiemer et al. 2009, Noonan et al. 2012). The complex architecture of coral colonies created by their branching structure constitutes the living space for many small reef fishes (Coker et al. 2014). Coral species differ greatly in their structural complexity and this may influence the diversity and abundance of coral-associated fishes (Messmer et al. 2011). Furthermore, many coral species exhibit substantial intraspecific morphological variation (Veron & Pichon 1976, Vytopil & Willis 2001, Schiemer et al. 2009), which may influence the quality of shelter they provide for fish (Untersteggaber et al. 2014). Variation in habitat quality and structural complexity can influence ecological interactions among reef fishes, such as competition and predation (Beukers & Jones 1997, Almany 2004; Harborne et al. 2011). Consequently, variation in coral colony physical characteristics is likely to play an important role in determining the population dynamics of coral-associated fishes.

Gobies in the genus *Gobiodon* are obligate coral-dwelling fishes that live among the branches of *Acropora* coral colonies. Some goby species are highly specialized, inhabiting just one or two species of *Acropora*, whereas other species are more generalist and will use a variety of *Acropora* species (Munday et al. 1997, Dirnwoeber & Herler 2007). Coral-dwelling gobies compete for access to preferred coral colonies (Munday et al. 2001, Hobbs & Munday 2004, Pereira et al. 2015) and utilization of different coral species has significant effects on individual performance (Munday 2001, Caley & Munday 2003). However, the physical attributes of coral colonies (*e.g.* coral size, branching structure) that drive habitat preferences and competition for different *Acropora* species, is unknown. If coral colony structure influences the risk of predation we expect that coral species with greater interbranch depth and smaller interbranch width will be preferred as they will provide more protection against predators. Interbranch spacing could also influence foraging efficiency through an interaction between predation risk and ease of access to food resources. Consequently, we expect that growth and survival rates of coral-dwelling gobies will be associated with coral interbranch spacing. Coral-dwelling gobies also prefer larger coral colonies (Hobbs & Munday 2004, Schiemer et al. 2009), possibly because they enhance growth and survival. Several studies have explored the relationship between coral colony structure and the body shape of coral-dwelling gobies (Wehrberger & Herler 2014, Untersteggaber et al. 2014), but the inter-relationships among coral colony structure, habitat preferences, and the individual performance of coral-dwelling gobies, has not been tested.

Gobiodon histrio and *Gobiodon erythrospilus* are ecologically similar goby species that compete for access to their preferred habitat, *Acropora nasuta* (Munday 2004; Pereira et al. 2015). Previous studies have shown that both niche-partitioning and lottery mechanisms of competition influence habitat use and abundance of these two goby species, and that the relative importance of these competitive mechanisms changes with ontogeny (Pereira et al. 2015). Furthermore, the two species have similar patterns of habitat use when *A. nasuta* is abundant, but the subordinate competitor, *G. erythrospilus*, is forced to use disproportionately more of an alternative coral host, *Acropora spathulata* when *A. nasuta* is scarce (Pereira et al., 2015 *in prep*.). While competitive interactions between these two goby species have been studied in detail, the characteristics of coral colonies that drive habitat preferences and differences in individual performance for fish inhabiting the two coral species remain unknown. Coral interbranch space appears to have influenced the evolution of body shapes among *Gobiodon* species (Wehrberger & Herler 2014); therefore, the physical attributes of coral colonies are likely to be determinants of habitat use and fitness of coral-dwelling fishes.

This study aimed to better understand the physical characteristics of coral colonies driving habitat preference and competition in coral-dwelling gobies. First, we compared key aspects of coral colony branching structure (interbranch depth and interbranch width) between *Acropora nasuta* and *Acropora spathulata*. We then used binary-choice laboratory experiments to test the preference of *G. histrio* and *G. erythrospilus* for *A. nasuta* and *A. spathulata* colonies with either wide or narrow branching structure. Finally, we transplanted gobies to colonies of *A. nasuta* and *A. spathulata* in the field and correlated growth rates with coral species, coral colony size and branching structure. We predicted higher growth rates of both goby species when inhabiting the preferred habitat (*A. nasuta*) compared with the alternative habitat (*A. spathulata*), and also an increase in growth rate with increasing coral colony size and increasing structural complexity. Furthermore, for individuals inhabiting the alternative habitat, we expect a greater cost to growth rate for the superior competitor (*G. histrio*) compared with the subordinate competitor (*G. erythrospilus*).

4.3 Material and Methods

Study location

Field surveys and a transplant experiment were conducted in October 2013 and January 2014 on reefs at Lizard Island in the northern Great Barrier Reef, Australia (14° 38'S - 145° 26'E).

Coral interbranch space

Interbranch depth (ID) and interbranch width (IW) are key parameters associated with the body shape of coral-dwelling gobies and have been implicated in difference in growth rate of gobies (Wehrberger & Herler 2014, Untersteggaber et al. 2014). ID and IW were measured in a total of 50 colonies of *A. nasuta* and 50 colonies of *A. spathulata*. Only colonies inhabited by one or more *G. histrio* or *G. erythrospilus* were measured. To control for a possible correlation between coral colony size and interbranch space, the size of coral colonies was standardized between 20-30 cm at their longest axis. The relationship between coral colony size and interbranch space for *A. nasuta* and *A. spathulata* was later tested using coral colonies in the field transplant experiment (below). An underwater calliper was used to precisely measure ID and IW with a total of 10 measurements of each variable taken at haphazard locations on each coral colony. The average of the 10 measurements was calculated for each coral colony.

A t-test was used to compare mean ID and IW between similar sized colonies of the two coral species. Analysis of covariance (ANCOVA) was then applied to coral data collected during the field transplant experiment to test if coral colony size, within and among species, influences the IW of *A. nasuta* and *A. spathulata*. This analysis tested for homogeneity of regression slopes of IW on coral colony size for the two coral species, and for a significant relationship between IW and coral colony size.

Coral complexity binary-choice experiment

A binary-choice experiment was used to test the preference of *G. histrio* and *G. erythrospilus* for colonies of different IW. Colonies (15–20 cm diameter) of *A. nasuta* and *A. spathulata* were carefully removed from the reef, transported alive to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). Colonies were visually characterized as having a wide or narrow IW. Subsequently, at the end of the experiment, the volume and IW of each colony was measured. The water-displacement method (Herler & Dirnwöber 2011) was used to estimate the total volume and average IW was calculated by the mean of ten measurements of IW per coral colony.

Four different combinations of coral species and IW were used to test the preference of *G. histrio* and *G. erythrospilus* for colonies of each coral species and with either wide or narrow IW: (1) *A. nasuta* with wide IW *vs. A. nasuta* with narrow IW, (2) *A. spathulata* with wide IW *vs. A. spathulata* with narrow IW, (3) *A. spathulata* with wide IW *vs. A. nasuta* with narrow IW and (4) *A. nasuta* with wide IW *vs. A. spathulata* with narrow IW. One colony of each coral species (approximately equal volume), was placed at opposite ends of a glass aquarium (50 x 30 x 30 cm). The position of each coral species on either the left or right side of each aquarium was changed regularly during the experiment and coral colonies were replaced if their condition visibly deteriorated. Gobies were collected from the field by lightly anesthetizing them with clove oil (Munday & Wilson 1997). A single individual of *G. histrio* or *G. erythrospilus* (ranging from 1.5 to 3.8 cm) was released between 18:00 and 19:00 in the middle of glass aquarium and their choice of *A. nasuta* or *A. spathulata* recorded between 06:00 and 07:00 the following morning (Munday et al. 2001; Pereira et al. 2015). Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 h. Habitat preference were tested for 24 individuals of each species in each of the four coral combinations.

A chi-square goodness of fit test was used to test for non-random habitat preference for *G. histrio* and *G. erythrospilus* in each of the four combinations.

Field transplant experiment

A transplant experiment was used to test if growth rates of *G. histrio* and *G. erythrospilus* were influenced by coral colony size and IW. Specifically, we predicted that growth of the two goby species would be positively correlated with coral size and negatively correlated with IW. In other words, we predicted that both species of goby would grow faster in larger coral colonies with narrower interbranch width. Further, we predicted that growth of the subordinate competitor *G. erythrospilus* would be higher compared with the superior competitor, *G. histrio,* when occupying an alternative habitat, *A. spathulata* and that IW and coral colony size could directly influence this relationship.

Growth rates of *G. erythrospilus* and *G. histrio* on the preferred (*A. nasuta*), and alternative coral species (*A. spathulata*), were determined in a three month period between January and April 2014. A total of 50 individuals of both goby species were collected from *A. nasuta* by lightly anesthetizing them with clove oil. Collected fishes were transported to the laboratory, measured (SL to 0.1 mm) and individually marked with a small fluorescent-elastomer tag injected into the dorsal musculature (Munday 2001). Tagged fishes were held for 24 hours in aquaria to ensure recovery. Fishes were then transported to the reef and released on coral colonies of *A. nasuta* and *A. spathulata*. A total of 25 individuals of each goby species were transplanted to each of the two coral species. Coral colonies were tagged for subsequent identification and any resident fishes present were removed before a goby was released onto a coral colony. After three months, all the remaining fishes were collected from marked coral colonies and the SL of each tagged fish was measured in the laboratory to determine the increase in size. The size and IW of each coral colony were measured as described above.

Linear mixed effects models (LME) were used to compare the growth of both goby species in both coral species (*A. nasuta* and *A. spathulata*), while accounting for interbranch width and coral colony size. In the LME model the fixed effects were goby species and coral species and the random effects were coral colony size and interbranch width. Individual goby growth was the dependant variable. Interactions between fixed and random effects and the growth rates of *G. erythrospilus* and *G. histrio* were also tested. If the effects of coral colony size and interbranch width on goby growth differ between coral species we expected to find a significant interaction between IW and coral species, and also coral colony size and coral species. LME was performed in R using the package nLme.

4.4 Results

Coral interbranch space

A. nasuta had a mean ID of 81.37 ± 14.01 mm and *A. spathulata* had a mean ID of 72.53 ± 15.12 mm, which was not significantly different (t = 10.76, df = 1, $p = 0.1$). However, there was a significant difference in IW between the two coral species (t = 6.19, df = 1, $p = 0.001$). *A. nasuta* had a mean IW of 16.078 ± 4.12 mm and *A. spathulata* had a mean IW of 23.84 ± 4.82 mm (Figure 4.1). The IW of *A. nasuta* ($R^2 = 0.01$; $p = 0.3$) and *A. spathulata* ($R^2 = 0.09$; $p = 0.2$) tended to increase with coral colony size. However, there was no difference in the relationship between coral colony size and IW for the two coral species as indicated by the homogeneity of slopes ($F_{1,29} = 3.63$, $p = 0.5$). Consequently, coral colony size was associated with interbranch width in the same way for *A. nasuta* and *A. spathulata* (Figure 4.2).

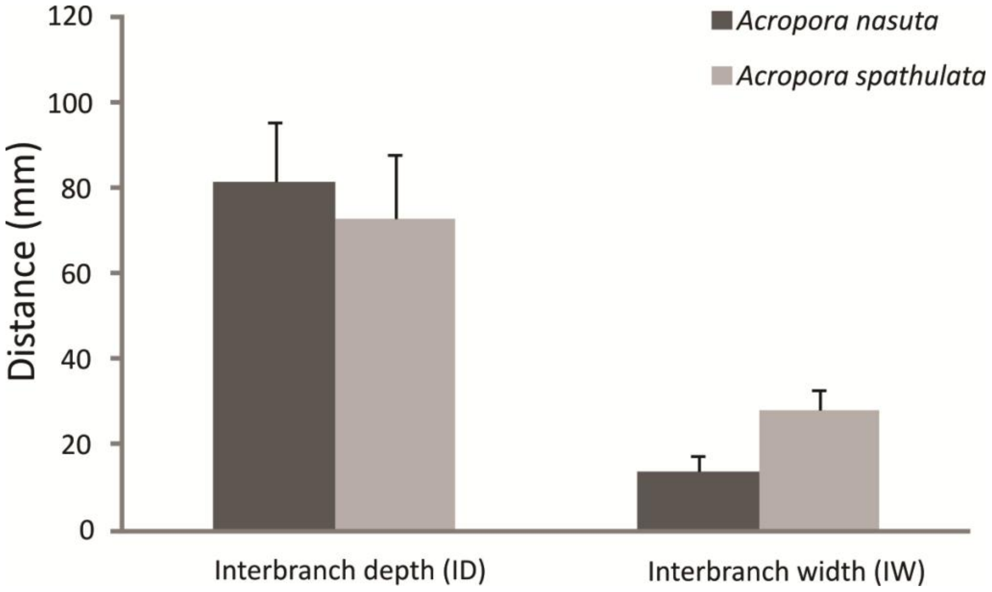

Figure 4.1 – Interbranch space of *A. nasuta* and *A. spathulata* coral colonies. N = 50 for each coral species.

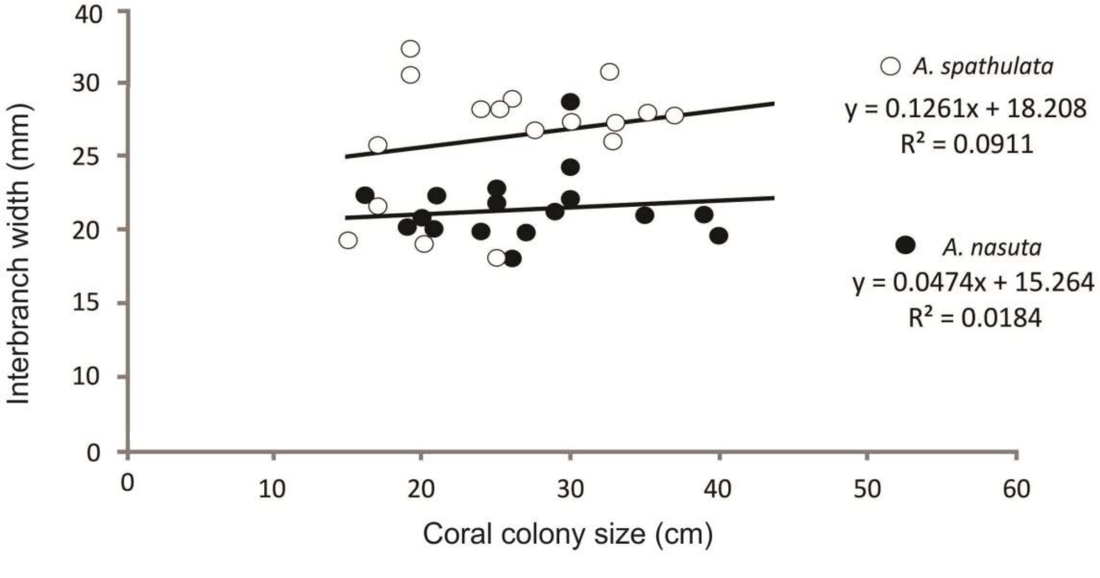

Figure 4.2 – Relationship between interbranch width and coral colony size of *A. spathulata* (open circles) and *A. nasuta* (closed circles) using corals from transplant experiment.

Coral complexity binary-choice experiment

Both gobies exhibited a strong preference for coral colonies with narrow IW, both for *A. nasuta* (*G. histrio* = $\chi^2 = 5.93$, df = 1, $p = 0.001$; *G. erythrospilus* = $\chi^2 = 6.03$, df = 1, $p =$

0.001) and *A. spathulata* (*G. histrio* = χ^2 = 5.59, df = 1, *p* = 0.001; *G. erythrospilus* = χ^2 = 5.59, df = 1, *p* = 0.001) (Figure 4.3A-B). Both gobies also exhibited a strong preference for *A. nasuta* when given the choice of *A. spathulata* with wide IW or *A. nasuta* with narrow IW (*G. histrio* = χ^2 = 4.13, df = 1, *p* = 0.001; *G. erythrospilus* = χ^2 = 3.56, df = 1, *p* = 0.001) (Figure 4.3C). However, they did not prefer the coral colony with narrow IW in the reverse combination. Both goby species preferred coral colonies of *A. nasuta* with wide IW over a colony of *A. spathulata* with narrow IW (*G. histrio* = χ^2 = 3.72, df = 1, *p* = 0.001; *G. erythrospilus* = χ^2 = 2.91, df = 1, *p* = 0.001) (Figure 4.3D).

Field transplant experiment

The average size of transplanted fishes at the beginning of the experiment was 27.4 mm SL for *G. histrio* and 27.7 mm for *G. erythrospilus,* and there was no difference in the size of the transplanted gobies between the two species (t = 0.28, df = 48, *p* = 0.77).

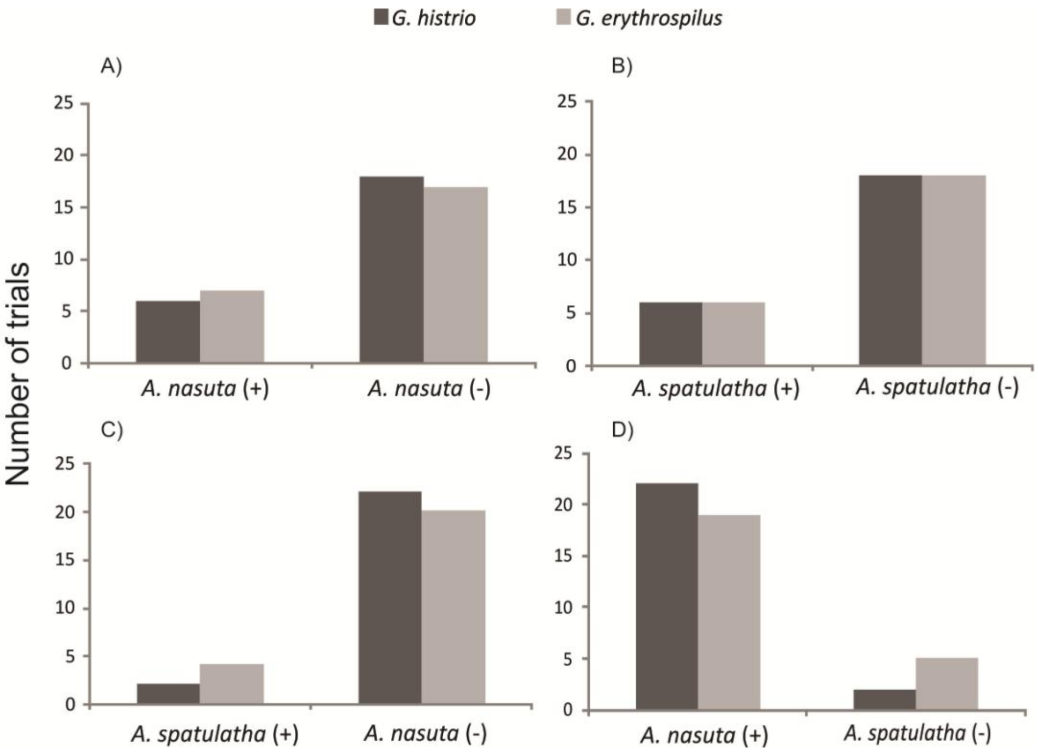

Figure 4.3 – Preference of *G. histrio* and *G. erythrospilus* for colonies of *A. nasuta* and *A. spathulata* with either a wide (+) or narrow (-) interbranch width in the binary choice experiment. N = 24 for each species in combination.

LME revealed a significant effect of coral species on growth of fish transplanted to colonies of *A. nasuta* and *A. spathulata* (Table 4.1). Additionally, there were significant interactions between IW and coral species, and colony size and coral species, on the growth of gobies (Table 4.1). In general, both *G. histrio* and *G. erythrospilus* grew faster on larger coral colonies with smaller IW (Figures 4.4 and 4.5). There was a negative relationship between IW and growth of *G. erythrospilus* and *G. histrio*; however the effect was stronger for fish inhabiting *A. spathulata* coral colonies compared to *A. nasuta* (Figure 4.4). Gobies grew faster on larger coral colonies, but there was an interaction with coral species, such that growth tended to increase faster with coral colony size in *A. spathulata* compared with *A. nasuta* (Figure 4.5).

While interactions between goby growth and: 1) IW and goby spp., 2) colony size and goby spp. and 3) coral spp. and goby spp. were not statistical significant (p = 0.06-0.07; Table 1), there were clear trends in the data. Most notably, *G. histrio* tended to grow faster on *A. nasuta* compared with *G. erythrospilus*, whereas *G. erythrospilus* maintained similar growth on both coral species (Figures 4.4 and 4.5).

Table 4.1 – Linear mixed effects model comparing growth rates of *G. erythrospilus* and *G. histrio* transplanted to *A. nasuta* or *A. spathulata* with covariance of interbranch width and coral size.

	Value	**SE**	***df***	**t-value**	**p-value**
Intercept	16.6840	11.3210	28	1.47	0.15
Goby spp.	-1.7136	5.0544	28	-1.34	0.73
Coral spp.	- 8.5414	4.9010	28	-0.47	0.03
Colony size	-0.2011	0.4234	28	-1.74	0.63
Interbranch width (IW)	-0.9400	0.6980	28	-0.33	0.18
IW * Colony size	0.0265	0.0255	28	1.03	0.30
IW * Coral spp.	0.7581	0.2816	28	2.69	0.01
IW * Goby spp.	-0.1110	0.2788	28	-0.39	0.06
Colony size * Coral spp.	-0.2992	0.1861	28	- 1.60	0.02
Colony size * Goby spp.	0.2666	0.1216	28	2.19	0.06
Coral spp. * Goby spp.	-4.5829	2.0556	28	-2.22	0.07

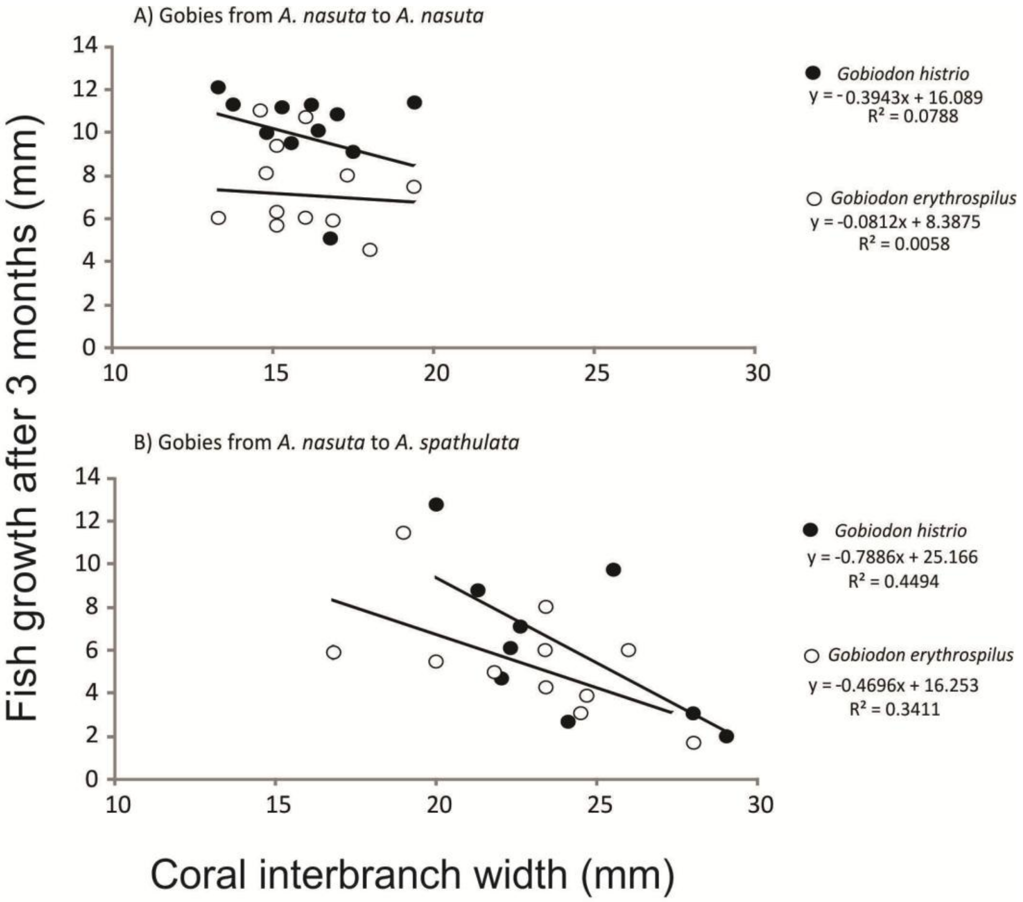

Figure 4.4 – Relationship between coral interbranch width (mm) and growth (mm) of *G. histrio* (closed circles) and *G. erythrospilus* (open circles) transplanted to colonies of *A. nasuta* (top) and *A. spathulata* (bottom).

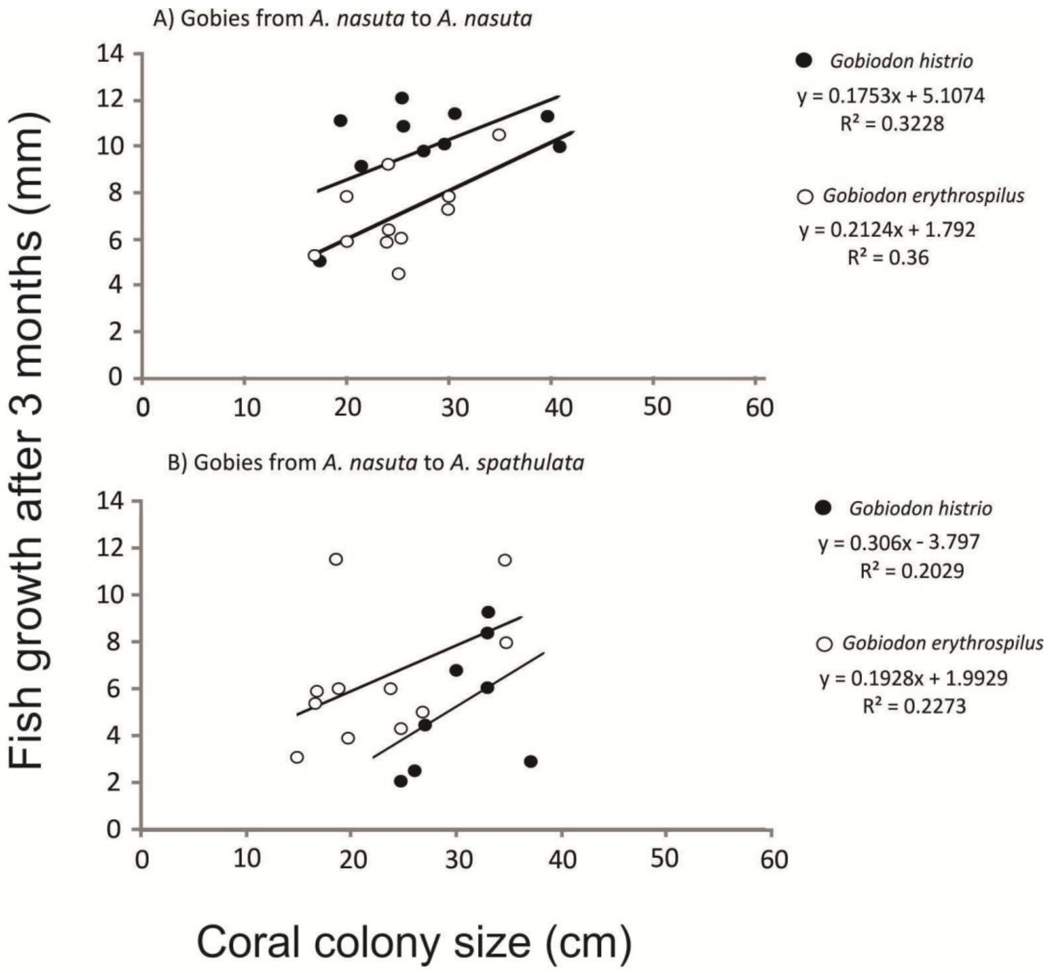

Figure 4.5 – Relationship between coral colony size (cm) and growth (mm) of *G. histrio* (closed circles) and *G. erythrospilus* (open circles) transplanted to colonies of *A. nasuta* (top) and *A. spathulata* (bottom).

4.5 Discussion

Our results empirically demonstrate that coral colony size and branching structure directly influence habitat use and growth of coral-dwelling fishes. When considering coral colonies with the same habitat volume, both gobies preferred corals with smaller interbranch width, supporting the hypothesis that coral complexity is an important component of habitat selection for these fishes. However, gobies still preferred *A. nasuta* over *A. spathulata* when they had the opportunity to occupy it, suggesting that there must also be other factors (*e.g.* coral nutritional quality) that determine the preference of one coral species over another. Additionally, a field transplant experiment demonstrated a negative correlation between coral interbranch width and growth, which can explain the preference of gobies for coral colonies with narrow interbranch space. Furthermore, there was a positive correlation between coral colony size and growth rates of *G. histrio* and *G. erythrospilus,* with both species growing faster on larger coral colonies. Yet, goby growth was also influenced by interactions between interbranch width, coral colony size and coral species, indicating that the effects the physical characteristics of coral colonies have on goby growth rates differed between coral species.

Habitat patch size is often a good predictor of abundance and species richness in natural communities (Gaston & Blackburn 1996, Robles & Ciudad 2012; Leal et al. 2015). On coral reefs it also seems that habitat patch size could influence the fitness-associated traits (*e.g.* growth and survival) of reef fishes (Noonan et al. 2012). During the present study we found that gobies grew faster in larger coral colonies. Coral-dwelling gobies usually tend to exclude other fishes from their coral habitat and defend corals from corallivorous predators (Dirnwöber & Herler 2013). Just one breeding pair normally occupies each coral colony; therefore, it is likely that larger coral colonies could require more time and energy to defend, but overall are probably optimal habitats because they provide larger feeding areas. The concept of economic defensibility (Brown 1964) is widely used to explain territorial behaviour in reef fishes (Mumby & Wabnitz 2002). It predicts the development of territorial behaviour if the benefits derived from exclusivity of access to a particular resource are greater than the cost of defending it. Therefore, it is likely that the growth benefits that gobies attain from access to larger coral colonies outweigh any additional cost of defense. A similar trend was observed for damselfishes occupying fire-coral on Brazilian reefs, where regardless of an increase in *Stegastes fuscus* aggressive behaviour, larger *Millepora* spp. coral colonies were still preferred (Leal et al. 2015).

Habitat complexity can influence the distribution and abundance of coral reef fishes on a variety of spatial scales (Friedlander et al. 2003, Coker et al. 2013, Komyakova et al. 2013). Specifically, for coral-dwelling fishes, attributes of coral colony branching structure are likely to be important variables in determining individual fitness. For example, Wehrberger & Herler (2014) showed that coral architecture influences the size, shape and growth of coral-associated fishes. We found that *G. histrio* and *G. erythrospilus* both exhibited a preference toward and grew faster on coral colonies with narrow interbranch width. Factors such as protection for predators and superior nesting sites seem to be the most important variables driving habitat preference of coral-associated fishes. For example, Holbrook & Schmitt

(2002) showed that juvenile coral specialists are more likely to be eaten by predators that were closer to their own body size than larger ones; therefore even subtle differences in branching structure could influence predation rates on coral-dwelling gobies.

As observed in previous studies (Pereira et al. 2015), we found that *G. histrio* and *G. erythrospilus* preferred colonies of *A. nasuta* over *A. spathulata*. Interbranch width differed among the two coral species, and growth rates of the gobies was directly correlated with interbranch width, suggesting that coral branching structure is possibly one of the most important factors influencing goby habitat preference and subsequent fitness. However, both goby species still exhibited a strong preference for *A. nasuta* when it had a wider interbranch width than *A. spathulata*. This indicates that factors other than interbranch width must influence habitat selection by coral-dwelling gobies. *Acropora nasuta* is the preferred habitat for a number of *Gobiodon* species, including the two species studied here (Munday 2001; Pereira et al. 2015) and must provide additional resources above-and-beyond suitable habitat structure. The additional benefits of inhabiting *A. nasuta* are unknown, but could be associated with nutrition or breeding sites. Coral-dwelling gobies attain part of their nutritional resources from their host corals (Brooker et al. 2010) and *A. nasuta* might have a higher nutritional status. Future studies could examine lipids levels in coral tissue to test this hypothesis. Alternatively, regardless of differences in branching structure, *A. nasuta* colonies might offer superior locations for nesting due other aspects of coral morphology.

Interactions between interbranch width and coral species, and also colony size and coral species influenced goby growth in the field experiment. These interactions demonstrate that a complex set of coral colony physical characteristics define optimal habitat for coral-dwelling fishes. Goby growth was lowest on *A. spathulata* colonies with wide interbranch width (*i.e.* less complex habitats) and highest on *A. nasuta* colonies with narrow interbranch width. Colony size also interacted significantly with coral species. *G. histrio* and *G. erythrospilus* inhabiting larger *A. nasuta* coral colonies exhibited higher growth rates compared to gobies living on *A. spathulata*. Additionally, as a general trend both species grew faster on *A. nasuta* compared with *A. spathulata*. The interactions observed in our field-based experiment highlight the fact that combinations of different coral physical attributes influence the growth of coral-dwelling fishes, but these relationships are not identical for fish occupying different coral species. The diet of coral-dwelling gobies is composed of a mix of macrofauna, zooplankton invertebrates and coral tissue (Riedlecker & Herler 2008, Brooker et al. 2010).

Therefore, variations in the abundance and diversity of coral-associated invertebrates due to changes in coral complexity (Vytopil & Willis 2001, Stella et al. 2011), and also ontogenetic changes in the nutritional quality of *Acropora* species *per se* (Pratchett 2007) are likely to influence the performance of coral-dwelling gobies. If the availability of food resources is unequal on different coral species with different size and branching structure, this could potentially explain the interaction between interbranch width and coral species, and also colony size and coral species on goby growth.

Preferred habitat is a limited resource for coral-dwelling gobies (Munday et al. 2001), with up to 98.0% of all colonies of *A. nasuta* occupied (Hobbs & Munday 2004). Our results indicate that both *G. histrio* and *G. erythrospilus* are likely to prefer larger and structurally complex *A. nasuta* coral colonies. However, these habitat preferences are altered by competition between species. Coral-dwelling gobies coexist by a range of mechanisms, including niche partitioning and lotteries (Munday et al. 2001; Pereira et al 2015). Even though innate preferences exist, it seems that larger individuals of *G. histrio* are the superior competitors and thus have greater access to preferred habitat. As a result, *G. erythrospilus* is often forced to use the alternative habitat, *A. spathulata*. The ability of *G. erythrospilus* to maintain its performance on *A. spathulata* coral colonies appears to be critical in enabling it to coexist with *G. histrio* (Pereira et al. 2015). Our transplant experiment demonstrated that *G. erythrospilus* suffered much less of a fitness loss when occupying the non-preferred coral, compared with *G. histrio*, which could explain its ability to persist when displaced by the superior competitor.

Coral reef habitat is being degraded by the combined effects of storms, crown of thorns starfish outbreaks, coral bleaching and diseases (Gardner et al. 2003, De'ath et al. 2012). Loss of habitat structure has a major effect on reef fish communities. For example, loss of reef structural complexity by cyclones has a larger impact on reef fish communities than an outbreak of the coral-eating sea star *Acanthaster*, which cause widespread coral mortality, but leave the physical structure of the reef intact in the short term (Adam et al. 2014). Likewise, the average size of coral colonies is declining due to the increasing frequency of disturbances that cause partial or whole colony mortality (Baird & Marshall, 2002, Nugues & Roberts 2003; McClanahan et al. 2008). Our results suggest that a decrease in average the size and structural complexity of coral colonies, caused by ongoing disturbances, may affect patterns of habitat use and subsequent fitness of coral associated fishes. Furthermore, a decrease in coral architectural complexity may affect recruitment and competition within reef fish communities. Competition could be increased as the availability of large and complex coral colonies diminishes, with consequences for the populations of fishes that depend on coral habitat for their survival.

Chapter 5: Benthic composition influences habitat use and toxicity of coral-dwelling fishes

This chapter is in under preparation for submission at Coral Reefs. Author: PHC Pereira.

5.1 Summary

The distribution and abundance of habitat specialists is often associated with the availability of preferred habitat; however, other environmental features can also influence habitat selection. Coral-dwelling gobies are habitat specialist fishes that depend on the availability of a few key species of coral for their survival and also rely on skin toxins to reduce predation risk. This study investigated the influence of benthic substratum around coral colonies on patterns of habitat use and toxicity of two species of coral-dwelling gobies (*Gobiodon erythrospilus* and *Gobiodon histrio*) that compete for access to the coral, *Acropora nasuta*. Field surveys demonstrated that the benthic substratum around colonies of *A. nasuta* differed between colonies occupied by *G. histrio* and *G. erythrospilus*. Juvenile, single adult and breeding pairs of *G. erythrospilus* mostly inhabited *A. nasuta* colonies surrounded by branching corals. In contrast, juvenile and single adult *G. histrio* associated with *A. nasuta* coral colonies that had adjacent epilithic algal matrix and *G. histrio* breeding pairs inhabited colonies surrounded by sand/rubble. Habitat-choice experiments showed that both goby species prefer *A. nasuta* coral colonies with benthic substratum mainly composed by epilithic algal matrix and sand; suggesting that competition for coral colonies in preferred locations could influence patterns of habitat use observed in the field. The substratum around preferred coral colonies also influenced the toxicity levels of the associated fishes. Gobies inhabiting *A. nasuta* coral colonies surrounded by epilithic algal matrix and sand showed higher levels of toxicity than gobies collected from colonies surrounded by branching corals. Given the potential for toxicity level to reduce the risk of predation, this could explain why gobies would compete for access to colonies of the preferred coral species surrounded by epilithic algal matrix and sand. These results show that the habitat use of coral habitat specialist fishes can be affect by the benthic composition around preferred coral colonies and demonstrate how competition for important secondary resources can influence patterns of habitat use.

5.2 Introduction

Organisms interact with the environment along multiple biotic and abiotic niche dimensions (Hutchinson 1957). The distribution and abundance of multiple resources is therefore likely to influence the distribution and abundance of most species (Schemske et al. 1991; Devictor et al. 2008). However, the relative importance of different resources in determining patterns of distribution and abundance will likely depend on the level of specialisation exhibited along the different niche axes. The distribution and abundance of generalist species may be only weakly associated with any particular resources, whereas the distribution and abundance of specialist species is expected to be closely linked to the availability of just one or a few preferred resources (McNally 1995). Furthermore, while one resource axes may be of primary importance, especially for specialist species, other resources axes can also play a role in shaping patterns of distribution and abundance. For instance, the distribution of a habitat specialist arboreal folivore, the koala, is directly dependent on the presence of preferred tree species; however the distance of these trees from water courses is also an important determinant in some areas (Smith et al. 2013). Therefore, a holistic analysis of multiple biotic and abiotic niche dimensions is critical to better understand patterns of distribution and abundance of habitat specialists.

Coral reefs provide essential resources for many habitat specialist reef fishes (Sale 1977; Munday et al. 2001; Coker et al. 2014). To date, most of the research analysing habitat use of coral-dwelling fishes has focused on aspects of the coral habitat, such as coral species identity, coral colony size and physical structure (Friedlander and Parrish 1998; Feary et al. 2007; Holbrook et al. 2015; Pereira and Munday 2015 *in prep.*). Much less is known about how the benthic substratum around coral colonies influences the distribution and abundance of coral-dwelling fishes. Wen et al. (2013) observed that the recruits of three predator reef fishes (*Plectropomus maculatus, Lutjanus carponotatus* and *Epinephelus quoyanus*) were mostly associated with *Acropora* coral colonies located over sand substratum. Similarly, Chase et al. (2014) found that the abundance of a habitat specialist damselfish, *Dascyllus aruanus* was directly correlated with the presence of the preferred habitat *Pocillopora damicornis* with a sandy substratum. Consequently, there is evidence that the benthic composition around preferred coral colonies could directly influence the habitat use of habitat specialist reef fishes; however, this assumption has not been adequately tested.

Coral-dwelling gobies from the genus *Gobiodon* are among the most specialized fishes on coral reefs. These fishes compete for and associate almost exclusively with corals from the genus *Acropora*, using them as shelter, food and breeding sites (Munday et al. 1997; Hobbs and Munday 2004; Brooker et al. 2010). The distribution of coral gobies is primarily associated with the availability of their preferred coral species (Munday 2004; Dirnwoeber and Herler 2007). Furthermore, coral colony size has been shown to influence the distribution and abundance of gobies (Schiemer et al. 2009). Habitat preference and individual performance of coral-dwelling gobies is also correlated with coral structural complexity. For instance, habitat use and goby growth is correlated with coral colony branching structure (Munday 2001; Untersteggaber et al. 2014; Pereira and Munday *in prep.*). However, if coral colony location on the reef, and the benthic substratum surrounding coral, influences habitat preference and individual performance is unknown.

Gobiodon histrio and *Gobiodon erythrospilus* are ecologically similar sister species (Duchene et al. 2013) that overlap broadly in their geographical distribution. These species occur in similar abundances and have broadly similar patterns of habitat use (Munday 2004) with a strong preference for *Acropora nasuta* coral colonies during their entire life (Pereira et al. 2015). However, patterns of habitat use of these two species are regulated by competitive interactions (Munday et al. 2001; Pereira et al. 2015). Previous studies have shown that adults of the superior competitor, *G. histrio,* gain increased access to the preferred coral habitat, *A. nasuta*, forcing the inferior competitor, *G. erythrospilus*, to use a greater proportion of an alternative coral habitat, *Acropora spathulata* (Pereira et al. 2015). Habitat partitioning of these two goby species has been correlated with coral species, colony size and branching structure (Munday et al. 2001; Hobbs and Munday 2004; Pereira and Munday 2015 *in prep.*). Nevertheless, sublet differences on the benthic composition around preferred coral species could be influencing habitat partitioning of these gobies during different life phases and social status (juveniles, single adults or breeding pairs).

In addition to habitat use, benthic substratum around preferred habitat may also affect the likelihood of predation for some resource specialists due to changes in toxicity levels. Biological toxins have been described in sponges, echinoderms, cnidarians (Halstead 1978; Bakus 1981; Cuiping et al. 2012) as well as some fishes (Schubert et al. 2003; Gratzer et al. 2013). About 50 species of 13 fish families have been reported to be toxic (Cameron and Endean 1973) and some of these species are normally avoided by predators, suggesting a deterrent function (Cameron and Endean 1973; Gratzer et al. 2013). Previous studies have shown that coral gobies (*Gobiodon* spp.) have strong toxins that are likely to reduce their predation risk (Schubert et al. 2003; Gratzer et al. 2013). Toxicity level varies among species (Schubert et al. 2003) and geographic range (Gratzer et al. 2013). Furthermore, gobies become more toxic after consuming toxic seaweed (*Chlorodesmis fastigiata*) during a mutualistic interaction with *Acropora* coral colonies (Dixson and Hay 2012). Consequently, gobies could be sequestrating their toxin from benthic resources such as epilithic algal matrix. However, if the benthic composition around preferred coral species influences the toxicity levels on coral gobies has not been tested. If the benthic substratum around coral colonies influences the toxicity levels of coral gobies, and this in turn influences their risk of predation, then it might be expected that gobies will compete for access to coral colonies in locations that enhance their toxicity.

The present study aims to analyse, for the first time, the effects of benthic substratum around preferred coral colonies on the habitat use and toxicity of obligate coral specialists. First, I analysed patterns of habitat use in the field by *G. histrio* and *G. erythrospilus* at different life-stage categories (juveniles, single adults or breeding pairs) relative to different types of benthic substratum (epilithic algal matrix, sand and branching corals) around *A. nasuta* coral colonies. Then, I experimentally tested the preference of both goby species for coral colonies situated on different benthic substratum. Finally, I used a bioassay to assess the influence of epilithic algal matrix, sand and branching corals around *A. nasuta* coral colonies on the toxicity levels of *G. histrio* and *G. erythrospilus.* Specifically, I predicted that different resources around coral colonies could affect the toxicity levels of coral gobies and consequently influence both their habitat preferences and competition for these preferred resources.

5.3 Material and Methods

This study was conducted in October 2010, January and September 2014 on reefs at Lizard Island in the northern Great Barrier Reef, Australia (14° 38'S - 145° 26'E) (Figure 5.1).

Influence of benthic substratum on habitat use

Patterns of habitat use of *G. histrio* and *G. erythrospilus* were examined in three reef zones, based on their exposure to the prevailing south easterly trade winds; (1) sheltered lagoon, (2) leeward side of island, and (3) windward side of island (Johansen 2014). Three replicate sites were selected within each zone (Figure 5.1). Habitat use of 50 haphazardly selected individuals of *G. histrio* and 50 individuals of *G. erythrospilus* was recorded at each site. To do this, a diver conducted a haphazard swim in the depth range where suitable *Acropora* corals are most abundant (0-10m). All sighted *Acropora* coral colonies were inspected and the coral species identity and coral colony size was recorded for each coral colony containing one or more individual of *G. histrio* or *G. erythrospilus*. Gobies were recorded by life-stage categories (juveniles, single adults or breeding pairs) using criteria stipulated by Munday et al. (1997). *Acropora* coral colonies were identified to species level according to Wallace (1999) and Veron (2000). Any colonies with doubtful identification were photographed for further identification. Among all the inhabited corals colonies only data from *A. nasuta* (the preferred coral of *G. histrio* and *G. erythrospilus)* was considered. Also, to control for a possible correlation between coral colony size and patterns of habitat use, only coral colonies between 20-30 cm at their longest axis were considered. In order to record the benthic substratum around each *A. nasuta* coral colony, eight equally-spaced points around the colony (i.e. 45° apart) were selected at a maximum of 5 cm away from the edge of the colony and the benthic composition quantified at these specific points. The benthic substratum at each point was classified as: epilithic algae matrix, sand/rubble, massive coral, soft coral and branching coral (Figure 5.2).

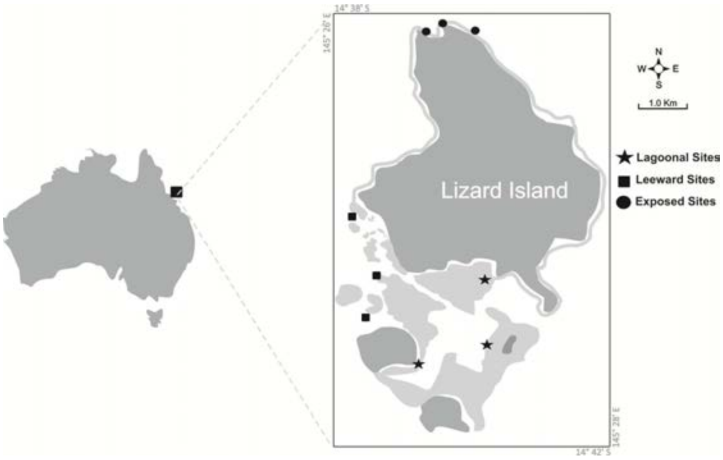

Figure 5.1 - Map of study area (Lizard Island - Northeast Australia) showing the sites surveyed for gobies

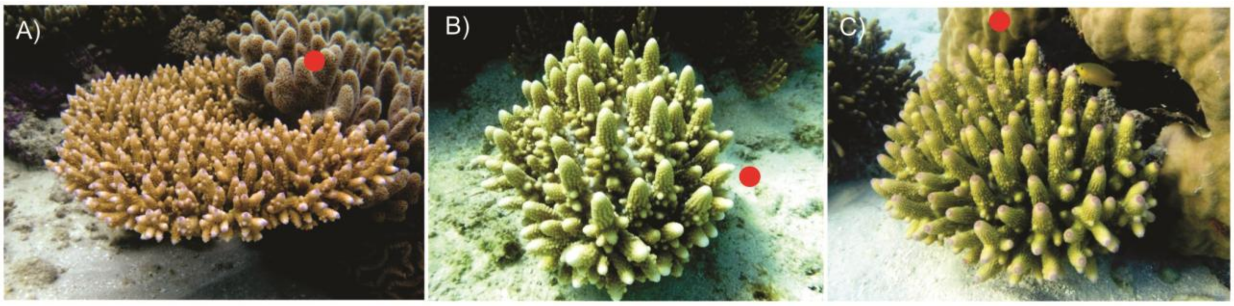

Figure 5.2 – Differences in the substratum around *Acropora* coral colonies from A) Soft coral, B) Sand/rubble and C) Hard coral. Red dots indicate the main substratum category around coral colonies.

Principal component analysis (PCA) by life phase and social status (juveniles, single adults and breeding pairs) was used to investigate the relationship between *G. histrio* and *G. erythrospilus* and the benthic composition around *A. nasuta* coral colonies. Habitat use data was log-transformed prior to multivariate analyses. PCA was performed using Primer-e 6 PERMANOVA+1.0 software (Ver. 6.1.14)

Benthic habitat preference experiment

In order to better understand the natural preference of *G. histrio* and *G. erythrospilus* for colonies of their preferred coral, the two species were offered *A. nasuta* colonies situated on different benthic substratum during a habitat choice laboratory experiment. Gobies had three different options during the preference experiment: (1) *A. nasuta* coral colonies surrounded by epilithic algal matrix; (2) *A. nasuta* coral colonies surrounded by sand and (3) *A. nasuta* coral colonies surrounded by branching corals. The experiment was repeated for gobies on three different life stage: juveniles, single adults, breeding pairs.

Small colonies (15–20 cm diameter) of the preferred coral, *A. nasuta*, were carefully removed from the reef, transported alive to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). A similar volume (around 10 L) of the three different benthic substratum types (epilithic algal matrix, sand and branching corals) were also collected from the field. A water-displacement method was used to estimate an equal volume of the benthic substratum types. An equal volume of epilithic algal matrix, sand and branching corals was placed in a symmetrical arrangement in the base of a large round tank (200 x 200 x 75 cm). One colony of *A. nasuta* was then place in the center of each patch of benthic substratum (Figure 5.3).

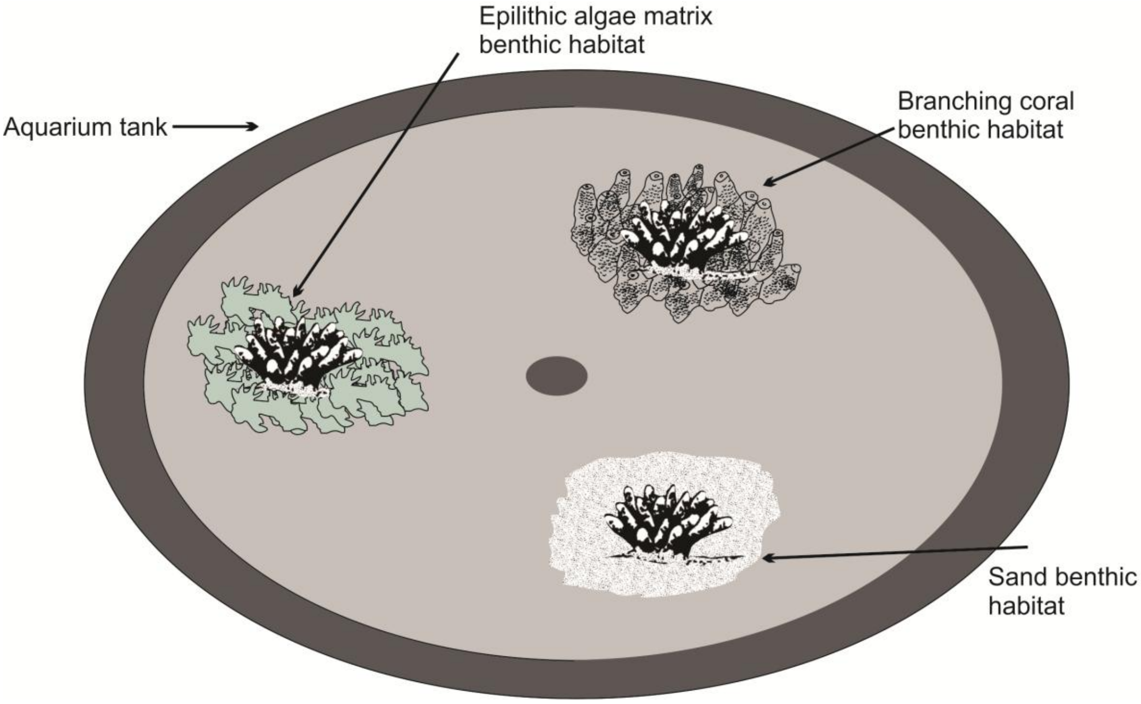

Figure 5.3 – Illustration of habitat choice preference experiment. Three different choices were offered to gobies in the preference experiment: (1) *A. nasuta* coral colonies surrounded by epilithic algal matrix; (2) *A. nasuta* coral colonies surrounded by sand and (3) *A. nasuta* coral colonies surrounded by branching corals.

Gobies were collected from the field by lightly anesthetizing them with clove oil (Munday and Wilson 1997) and transported to the laboratory where they were kept in aquariums with a constant flow of fresh seawater. An individual of *G. histrio* or *G. erythrospilus* from one of the three life-stage categories (juveniles, single adults or breeding pairs) was released between 1800 and 1900 in the middle of the tank and their habitat choice recorded between 0600 and 0700 the following morning. Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 h. Habitat preference was tested for 12 individuals of each species in each of the three life-stage categories.

Log-linear models were used to examine the frequency each patch of benthic substratum was selected in relation to goby species and different life-stages. In this approach a succession of increasingly complex models (Table 5.1) are fitted to the observed data until there is no significant improvement in the goodness-of fit statistic (maximum likelihood X^2) from one model to the next. Analysis was performed using Statistica 10. The method of testing patterns of habitat use follows Munday et al. (2001).

Benthic composition and goby toxicity

Gobiodon species have toxins that can reduce their risk of predation (Schubert et al. 2003; Gratzer et al. 2013). In bioassays these toxins cause loss of equilibrium, and eventually death, of other reef fishes (Hashimoto et al. 1974, Lassig 1981, Schubert et al. 2003).

I used a bioassay to analyse the influence of benthic habitat (epilithic algal matrix, sand and branching corals) surrounding *A. nasuta* coral colonies on the toxicity levels of *G. histrio* and *G. erythrospilus*. Standard toxicological protocol involves exposing the toxin to a bioassay organism for which individuals have been standardised for size, condition and life history (Parrish 1985; Schubert et al. 2003). I chose as the bioassay organism a small planktiverous fish, *Chromis viridis*, which was available in large schools of roughly uniformly sized individuals on the inshore reefs around Lizard Island. The small size of *C. viridis* (<5 cm total length) made it amenable to replicated laboratory experiments and the uniform size among individuals in the same school of fish ensured that the skin secretions could be tested on similar-sized individuals with a similar life history since settlement to the reef.

Chromis viridis were collected by lightly anaesthetising them with a 1:30 clove oil/alcohol solution (Munday and Wilson 1997) so they could be easily captured with hand nets. Bioassays fishes were held in large outdoor aquaria supplied with a continuous flow of fresh seawater and used within two days of capture. Gobies were also caught by anaesthetising them with clove oil/alcohol solution and held in outdoor aquaria with a continuous flow of fresh seawater. All gobies were collected from their preferred coral species, *A. nasuta*. In order to analyze the effects of benthic habitat around *A. nasuta* coral colonies on the toxicity levels of *G. histrio* and *G. erythrospilus* gobies were collected from coral colonies with different composition of benthic substratum around them. The benthic substratum around *A. nasuta* coral colonies was recorded at eight points (distant 45° each other) around each coral colony. Corals were then categorized as being situated around epilithic algal matrix, sand or branching corals levels, based on the benthic substratum around them. A minimum of 60% of one specific benthic community was necessary to include a corals in that habitat category.

To compare toxicity levels of gobies from corals situated on different benthic substratum, the toxin had to be presented to the bioassay fishes. These gobies secreted frothy white secretion from the skin (mucus) when aggravated. This mucus causes rapid disorientation and loss of equilibrium in the bioassay species (Schubert et al. 2003). Loss of equilibrium is an unambiguous indicator of locomotory control in fish and is widely used in toxicological investigations (e.g. Munday and Wilson 1997). To collect the mucus for use in bioassays, a single goby was placed in a small plastic bag with 10 ml of seawater. The fish was agitated for ten seconds by gently rubbing the plastic over its skin. The mucus produced was washed from the goby and from the plastic bag into a small beaker using 90 ml of seawater, giving a final volume of 100 ml. Each goby was used only once to produce mucus and then returned to the field.

At the start of each bioassay trial, a single *C. viridis* individual was placed in a beaker containing 200 ml of fresh seawater. The 100 ml of water containing the mucus of one goby was then tipped into the beaker. Time to loss of equilibrium, when fish were no longer able to maintain horizontal or vertical orientation, was used to provide an estimate of the toxins' effect on the bioassay fish. Time to loss of equilibrium was recorded using a stopwatch started when the mucus was added to the beaker containing a *C. viridis* individual.

This bioassay procedure was replicated 20 times for each goby species collected from *A. nasuta* coral colonies surrounded primarily by 1) epilithic algal matrix, 2) sand and 3) branching corals. Thus a total of 60 bioassay trials were performed for each goby species, *G. histrio* and *G. erythrospilus.*

Two-way analysis of variance (ANOVA) was used to compare mean time to loss of equilibrium in *C. viridis.* Goby species and benthic substratum were the main effects. A Tukey *a posteriori* test was the pairwise comparison method. All analyses were conducted using Statistica 10 (StatSoft Inc. 2011).

5.4 Results

Influence of benthic substratum on habitat use

G. histrio and *G. erythrospilus* showed different patterns of habitat use in relation to the benthic substratum around the preferred coral *A. nasuta*. *G. histrio* juveniles and single adults were closely associated with corals surrounded by epilithic algal matrix; while breeding pairs of *G. histrio* preferred coral colonies with more sand/rubble around them. In contrast, juveniles, single adults and breeding pairs of *G. erythrospilus* were closely associated with *A. nasuta* surrounded by another branching corals. Principal component analysis (PCA) explained 79.5% of the total variability in habitat use for both *G. histrio* and *G. erythrospilus*, with 56.3% of the variability explained by PC1 (Eigenvalue 918) and 23.2% by PC2 (Eigenvalue 506) (Figure 5.4).

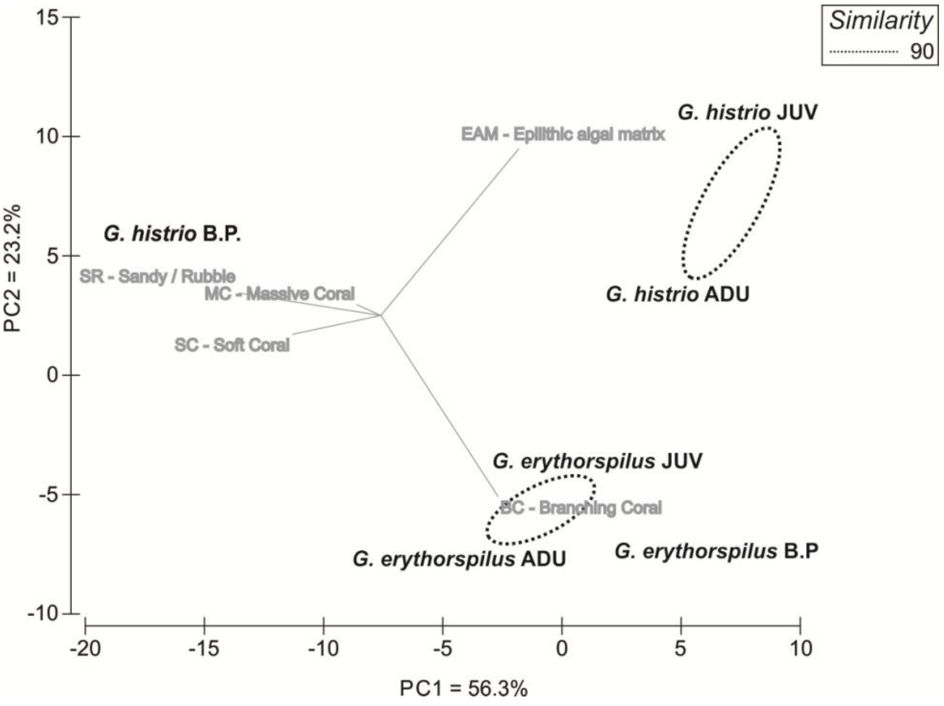

Figure 5.4 – Principal component analyses (PCA) of habitat use of *Gobiodon histrio* and *Gobiodon erythrospilus* from different life phases and social status (juveniles, single adults or breeding pairs) in relation to benthic substratum around preferred coral habitat.

Benthic habitat preference experiment

G. histrio and *G. erythrospilus* at different life phases and social status exhibited a strong preference for *A. nasuta* coral colonies situated on benthic substratum composed primarily of epilithic algal matrix and sand (Figure 5.5). The best-fitting log-linear model contains the term habitat, but no interaction between habitat and life-stage or goby species (Model 5 – Table 5.1). This model indicates that gobies exhibited habitat selection, but it did not differ between life-stage or species. The frequency of choice shows habitat selection for epilithic algal matrix by both gobies species at all life-stages (Figure 5.5).

Table 5.1 - Log-linear models used to test patterns of habitat use in benthic habitat preference experiment. Models were tested sequentially until there was no further improvement in the fit of the model to the observed data.

	Model	**Maximum Likelihood X^2**	**df**	***p***
1	S x L x H	0	-	-
2	S x L + S x H + L x H	1.988	4	0.737
3	S x L + L x H	2.461	6	0.873
4	S x L + S x H	3.184	8	0.923
5	S x L + H	3.657	10	0.962
6	S x L	27.926	12	0.005

S = Species of goby (*G. erythrospilus* and *G. histrio*), L = Life-stage categories (juveniles, single adults or breeding pairs) and H = Habitat (epilithic algal matrix, sand and branching corals).

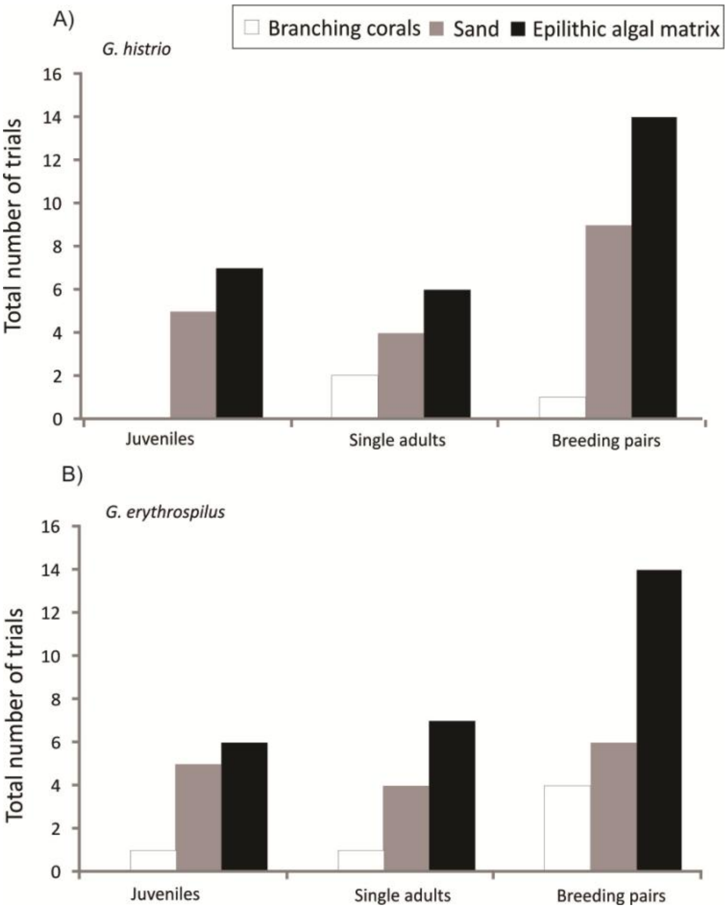

Figure 5.5 - Outcomes of preference experiments of *Gobiodon histrio* (A) and *Gobiodon erythrospilus* (B) for *A. nasuta* coral colonies surrounded by epilithic algal matrix, sand or branching corals.

Benthic composition and goby toxicity

The mucus of *G. histrio* individuals caused equilibrium loss in *C. viridis* in a mean time of 187 ± 44.3 seconds for individuals collected from corals that predominantly had branching corals around them, 131 ± 35.1 for sand and 90 ± 43.3 for epilithic algal matrix (Figure 5.6) (ANOVA = *F* = 17.21; df = 5; *p* = 0.001). Specifically, there was a faster loss of equilibrium induced by toxins from *G. histrio* individuals inhabiting coral colonies near sand and epilithic algal matrix compared with branching coral, but no significant difference between sand and epilithic algal matrix around (Figure 5.6). By comparison, *G. erythrospilus* individuals caused equilibrium loss in *C. viridis* in a mean time of 199 ± 39.5 seconds from individuals collected from corals that predominantly had branching corals around them, 110 ± 33.5 for sand and 99 ± 33.8 for epilithic algal matrix (Fig. 6) (ANOVA = *F* = 11.13; df = 5; *p* = 0.002). Specifically, there was a faster loss of equilibrium induced by toxins from *G.*

erythrospilus individuals inhabiting coral colonies near sand and epilithic algal matrix compared with branching coral, but no significant difference between sand and epilithic algal matrix around (Figure 5.6).

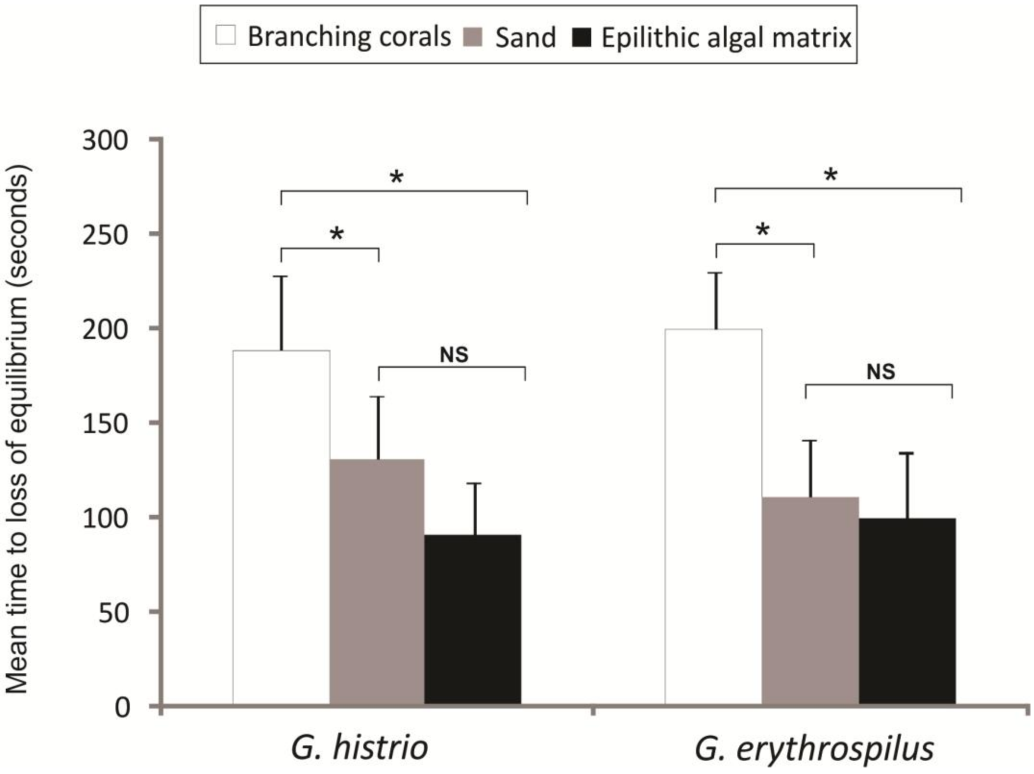

Figure 5.6 - Outcome of bioassays experiment analysing the influence of benthic habitat around *A. nasuta* coral colonies (epilithic algal matrix, sand or branching corals) on the toxicity levels of *G. histrio* or *G. erythrospilus*. * = $p < 0.05$.

Discussion

This study demonstrates that the benthic composition around preferred coral habitat can have a major influence on the habitat use and toxicity of coral-dwelling fishes. Habitat use of *G. histrio* and *G. erythrospilus* was directly influenced by the benthic substratum around the preferred coral, *A. nasuta*, with laboratory experiments confirming that both gobies prefer coral colonies with benthic substratum mainly composed by epilithic algal matrix and sand. Benthic substratum around preferred coral also influenced the toxicity levels of the associated fishes. Gobies inhabiting corals with more epilithic algal matrix and sand had higher levels of toxicity that caused equilibrium loss in bioassay fishes quicker than fishes collected from *A. nasuta* surrounded by branching corals. Given the likely role of toxins in reducing predation, this correlation between toxicity and benthic composition could explain the preference of both goby species for coral colonies with a high percentage of epilithic algal matrix in the surrounding benthic substratum.

Previous studies have categorized *G. histrio* and *G. erythrospilus* as having the same habitat preference, with resource partitioning explained largely by competition (Pereira et al. 2015). Here my findings show resource partitioning among goby species due to variation in the substratum around inhabited corals as well as life-history stage. Juveniles, single adults and breeding pairs of *G. erythorspilus* primarily inhabited colonies surrounded by branching corals. In contrast, *G. histrio* juveniles and single adults were mostly observed associated with coral with epilithic algal matrix, whilst *G. histrio* breeding pairs inhabited *A. nasuta* colonies surrounded by sand/rubble. Habitat partitioning by coral gobies has previously been correlated with coral species, colony size and wave exposure (Munday et al., 2001; Schiemer et al. 2009) and is strongly influenced by a competitive hierarchy for preferred coral species (Munday et al., 2001; Pereira et al. 2015). Here I uniquely demonstrate a relationship between habitat use by coral gobies and the substratum around preferred coral colonies, where the benthic composition around corals could potentially provide different resources for these habitat specialist reef fishes.

Habitat structural complexity is often a strong predictor of reef fish habitat use and fitness (Munday 2001; Noonan et al. 2012), but the understanding of the underlying mechanism during this process is rarely known. Surprisingly, in this study gobies seemed to avoid coral colonies in close proximity to other branching corals. The laboratory preference experiments demonstrated that both *G. histrio* and *G. erythrospilus* from different life-stages and social status preferred corals surrounded mostly by sand and epilithic algae matrix. One potential explanation is that the presence of branching corals in close proximity to inhabited coral colonies could allow predators to shelter in nearby habitat. Alternatively, my results suggest that gobies prefer colonies mostly surrounded by sand and epilithic algal matrix because it increases their toxicity, and thus reduce their palatability to predators.

Coral colonies surrounded by sand were the second most preferred habitat by coral gobies. According to Wen et al. (2013) sand could provide extra dietary resources for some coral reef fishes. Similarly, the preference for coral colonies surrounded mostly by epilithic algal matrix could also be due to the availability of food resources (*i.e.* associated invertebrates). Epilithic algal matrix is an important component of the diet of some coral reefs fishes (Wilson et al., 2003; Kramer et al., 2012). Coral-dwelling gobies ingest a high percentage of amorphous material and detritus (Brooker et al., 2010) that could originate from epilithic algal matrix.

During laboratory experiments both goby species showed similar preference for *A. nasuta* coral colonies mostly surrounded by epilithic algal matrix and sand. However, field surveys demonstrated different patterns of habitat use for *G. histrio* and *G. erythrospilus* related to benthic composition around preferred corals. Previous studies have shown that *G. histrio* is the superior competitor and tends to exclude subordinate competitors for alternative habitats (Munday et al., 2001; Pereira et al., 2015). Therefore, the different habitat use observed for *G. erythrospilus* in the field suggests that it is displaced or outcompeted by *G. histrio.* In summary, both goby species prefer corals mostly surrounded by epilithic algal matrix and sand but due to competition *G. histrio* have preferred access for this resource. Size-based interspecific competition on coral gobies is also very likely as suggested by (Hobbs and Munday 2004). This is a strong explanation for the distinct patterns of habitat use observed in the field for *G. histrio* individuals on different life-stage categories (juveniles, single adults or breeding).

Toxicity of coral-gobies appears to be an important chemical defense against predation (Schubert et al. 2003; Gratzer et al. 2013). Yet, the origin of these toxins is not clear as well as the extent of variation among different goby species and habitat types. My results suggest that the benthic composition around preferred coral influences toxicity levels in these gobies. *G. histrio* and *G. erythrospilus* individuals inhabiting corals with epilithic algal matrix and sand around presented higher levels of toxicity and caused equilibrium loss in bioassay fishes more quickly than fishes collected from *A. nasuta* surrounded by branching corals. Feeding behaviour has been suggested to influence the intensity of coral gobies toxicity (Dixson and Hay 2012) supporting our findings that different resources available around coral colonies could influence toxicity levels in coral-dwelling gobies. However, further physiological and biochemical research is necessary to better understand the sequestration process and also the role of toxins in habitat selection and competitive interactions.

Fishes inhabiting coral colonies are known to potentially enhance coral growth through defence from coral predators, aeration of coral tissue and nutrient provision (Goldshmid et al. 2004; Holbrook et al. 2008; Gochfeld 2010; Chase et al. 2014). However, the extent to which the cost-benefits of this interaction are positive seems to vary with local environmental variation (Sachs and Simms 2006; Kiers et al. 2010; Chase et al. 2014). Previous studies have shown that the presence of toxic gobies is likely to be positive for the hosting *Acropora* coral colonies. Dirnwoeber and Herler (2013) found that the presence of coral-dwelling gobies could reduce predation by butterflyfishes on coral colonies. Additionally, a mutualistic relationship seems to be established which allows corals to chemically cue symbiotic goby fishes to remove toxic seaweeds, thereby dramatically reducing coral damage (Dixson and Hay 2012). Therefore, it seems that goby presence could be potentially positive for coral colony fitness and the benthic substratum around colonies directly influences gobies toxicity levels.

In conclusion, this study has shown that benthic composition around coral colonies can influence habitat use and toxicity levels of coral associated fishes. To date, factors such as coral identity, colony size and complexity have been considered the main variables driving gobies habitat selection. However, my findings demonstrate, for the first time, that the location of coral colonies on different benthic substratum can also be an important variable for coral-dwelling fishes. Hence, benthic composition around coral colonies should be included when considering habitat partitioning of coral specialist fishes. Furthermore, the protection and management of resource specialists may require more than the mere availability of primarily resources.

Chapter 6: General Discussion

Determining how ecologically similar species coexist is central to understanding the function of natural communities. This knowledge is especially relevant in this era of increasing anthropogenic disturbances. Habitat degradation is a major threat to high diversity ecosystems, such as tropical rainforests and coral reefs, and it is critical to access how coexistence and competitive interactions will be influenced by this change. This thesis addressed key questions about the mechanisms of coexistence in coral-dwelling fishes and the influence of resource availability on competitive interactions. It uniquely shows that the mechanisms of competitive coexistence can change with ontogeny and that these mechanisms, in turn, influence how variation in resource availability affects individual fitness. This thesis also shows that both the species identity and structural characteristics of coral colonies influence habitat use and fitness of coral-dwelling fishes. Lastly, the benthic composition around preferred coral habitat appears to influence habitat preference of these fishes and could therefore influence competitive interactions and coexistence.

6.1. Mechanisms of competitive coexistence and the interaction with resource availability

My research suggests that different mechanisms of competitive coexistence (i.e. lottery and niche partitioning) are not mutually exclusive as previously thought and that both could operate in different life phases of ecologically similar species (Chapter 2). Just as observed for the goby species studied here, it seems that aspects of both neutral and niche-models also operate in plant communities (Adler et al. 2007). The life history attributes of perennial plants, which include a dispersive reproductive phase that can stochastically colonize vacant space (i.e. by lottery) could be potentially compared with the pelagic larval phase of reef fishes. Once colonization occurs, plants are sedentary and competitive hierarchies predominate. Thus, ontogenetic changes in the mechanisms of competitive coexistence might also be observed in further research in plant communities and in other taxa with similar life histories. Marine ecologists have embraced the idea that multiple ecological processes (predation, competition, dispersal) are responsible for the maintenance of populations and communities (e.g. Jones 1991, Caley et al. 1996; Hixon et al. 2002). My findings suggests the need to recognise that a variety of mechanisms within each of these processes may be simultaneous responsible for the maintenance of biodiversity in high diversity ecosystems such as coral reefs.

Preferred resources vary in space and time for most species in nature. The findings of this study demonstrate that the effects of such variation on population size and patterns of resource use will depend on the mechanisms of competitive coexistence (Chapter 3). Where a lottery for space operates, a decline in preferred resources could affect individual performance, but not relative fitness compared with other species. Therefore, all species would suffer proportionally the same. In contrast, where there is a competitive hierarchy, subordinate species may be forced to use a greater proportion of inferior resources, which could alter their relative fitness. If a lottery for space operates (e.g. settlement of coral dwelling fishes and perennial plants) a decline in resource availability is likely to influence population sizes, but not alter community structure. In contrast, where niche-partitioning and competitive hierarchies are predominant, a reduction on the availability of preferred resource could affect the relative fitness among species and thus both population sizes and community structure. Critically, if competitive processes change through ontogeny it will be important to understand at what life stages resources are limiting and the mechanisms by which species compete if we are to make reliable predictions about how habitat degradation and other changes in resources availability will affect coral reef fish communities. More generally, understanding the complexity of competitive processes could be an important for accessing and managing natural communities during periods of significant change in resource availability.

6.2. Influence of anthropogenic disturbance on reef fish competition and habitat use

Coral cover is declining on reefs around the world (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). Climate change and ocean acidification could affect competition in coral reef fishes, either indirectly through changes in the availability of habitat or other resources, or more directly by altering the competitive ability of individuals. However, the effects of competition on reef fish communities following coral loss and habitat degradation are still poorly understood (Bonin et al. 2015). Despite the obvious potential for the degradation of coral reef habitat to alter or exacerbate competition among reef fishes, only two studies to date have tested this hypothesis. Boström-Einarsson et al. (2014) demonstrated that habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes. A reduction in habitat quality overwhelmed the effects of both intra- and interspecific competition and eliminated competitive hierarchies on two competition species, *Chrysiptera parasema* and *Dascyllus melanurus* (Boström-Einarsson et al. 2014). In contrast, McCormick (2012) observed that mortality of a subordinate competitor, the damselfish *Pomacentrus moluccensis*, was higher on bleached and dead coral compared with healthy coral in the presence of a dominant damselfish competitor *P. amboinensis*. This suggests that habitat degradation intensified the effects of competition on the subordinate species. The contrasting results of these two studies demonstrates that how competitive interactions in reef fish communities will be altered by the widespread anthropogenic disturbances occurring on coral reefs is still to be determined. More empirical research is necessary analysing the outcomes of competitive interactions under different levels of habitat degradation as well as future projections of water temperature and acidification. Additionally, the concept of ontogenetic changes on competitive mechanisms suggested here should be considered in future studies to better understand the effects of changing resource availability reef fish populations and communities.

The findings presented in this thesis suggest that the composition of degraded coral communities will influence the outcome of competitive interactions among reef fishes. If there is a relationship between overall coral cover and the relative abundance of preferred habitats, then coral loss could have disproportionate effects on subordinate competitors. Alternatively, superior competitors that specialize on the preferred resource could also be affected once the abundance of this specific resource diminishes. However, inferior competitors and more generalist species could become more abundant in the future if they attain better fitness outcomes in alternative habitats. Understanding the mechanisms of competition between fish species could thus improve our ability to predict how reef fish communities will respond to habitat degradation.

6.3. Future research questions

Despite decades of research, the mechanisms that enable ecologically similar species to coexist in species-rich communities is still debated (Schoener 1983; Goldberg and Barton 1992; Amarasekare 2003; Ben-Hur et al. 2012). One limitation to understanding the role of competition in structuring ecological communities is that theoretical explanations for competitive coexistence have generally advanced more rapidly than empirical investigations (Amarasekare 2003; Siepielski and McPeek 2010; Shinen and Navarrete 2010; Hixon 2011). My thesis has empirically demonstrated ontogenetic changes in the mechanisms of competitive coexistence on reef fish communities. Similar changes may occur in other natural communities and this should be investigated, especially in taxa with similar life history traits to coral reef fishes.

Ecological and life history changes through ontogeny could affect both the fitness consequences of resource use and the potential competitive mechanisms involved. Ontogenetic shifts in habitat (Dahlgren and Eggleston 2000) and food preference (Schmitt and Holbrook 1984; Pereira and Ferreira 2013) could potentially alter the degree of resource overlap between species and their competitive abilities. Additionally, it is well known that the strength of competitive effects can be stage-dependent (Werner 1994; Callaway and Walker 1997; Connolly and Muko 2003). Hence, further investigation is necessary to focus on understand when, how and why ontogenetic changes on the mechanisms of competitive coexistent are operating and their relationship with the maintenance of biological diversity on natural communities. For instance, Loreau and Ebenhoh (1994) suggested that resource differentiation between life stages can make coexistence between species easier. Moreover, species with complex life cycles, such as holometabolous insects and amphibians with extreme metamorphosis, have a competitive advantage over other species due to ontogenetic changes on resource use as well as morphological and behavioural changes throughout life history (Wilbur 1980; Loreau and Ebenhoh 1994; Werner and Anhold 1996). Ontogenetic changes in physiology, morphology or behavior of competing species may be relevant for ontogenetic changes in the mechanisms of competitive coexistence and therefore maintenance of biodiversity on natural communities.

The close relationship between coral-dwelling fishes and a limiting resource (coral colonies) make them ideal models for testing hypotheses about competition and habitat selection in natural communities. Additionally, results obtained using gobies as models can be extrapolated for other reef fishes and reef fish communities. However, to better use coral gobies as models in future studies some ecological and biological data regarding the genus *Gobiodon* as well as their coral habitat still needs to be elucidated: (1) A few studies have attempted to determine the diet of coral-dwelling gobies (Patton, 1994; Brooker et al. 2010), but the extent and reliance of corallivory is unknown Understanding the reliance of these fishes on coral tissue as a dietary resource could help establish why they prefer particular coral species and why “species identity” influences individual performance. Coral complexity is an important determinant of gobies habitat use and fitness; however, preferences for specific *Acropora* species could be driven by nutritional quality of the corals. Further laboratory analysis must be performed examining levels of proteins and lipids on coral tissues.

My research suggests that the benthic substratum around coral colonies is an important additional component of habitat selection in coral-dwelling fishes. Therefore, the protection and management of resource specialists may require more than ensuring just the availability of primarily resources. The ontogenetic changes in preferredbenthic substratum around preferred colonies for coral gobies also suggests more frequent post-settlement movement for these species than previously thought. Previous studies suggested that single adult coral-dwelling gobies appear to move more than juveniles and breeding pairs (Wall and Herler 2009), possibly to locate breeding partners or to locate habitat that is more suitable for breeding. Yet, this has never been empirically tested and field-based studies using motion sensor cameras could be performed to investigate the movement patterns of goby species in relation to life phase and various aspects of habitat quality, including coral species, coral colony size, branching complexity and surrounding benthic substratum.

Overall, my thesis demonstrates ontogenetic changes in the mechanisms of competition and the importance of resource availability in shaping the outcome of competitive interactions. This thesis answered some fundamental questions about the mechanisms of competition in animal communities, but these results also have broader implications for predicting the effects of climate change and other anthropogenic disturbances on natural communities. Understanding how fluctuations in resource availability can influence the intensity of competition is vital to predicting the effects of these changes on species performance and population size and ultimately manage natural communities.

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Appendix 1: Publication list

A1.1. Publications derived from the thesis

Pereira PHC, Munday PL, Jones GP. 2015. Mechanisms of competitive coexistence change with ontogeny in coral-dwelling gobies. Ecology 96: 3090–3101.

Pereira PHC, Munday PL, Jones GP (2015) Influence of resource availability on competition among coral-dwelling fishes. *Oecologia*

Pereira PHC, Munday PL, (2015) Habitat size and complexity as a determinant factor on habitat use and fitness of coral reef fishes. *Marine Ecology Progress Series*

Pereira PHC. Effects of secondary resources on habitat use and toxicity levels of habitat specialist coral reef fishes. *Coral Reefs*

A1.2. Additional publications during PhD. candidature

Barros B, Sakai Y, **Pereira PHC**, Gasset E, Buchet V, Maamaatuaiahutapu M, Ready JS, Oliveira Y, Giarrizzo T, Vallinoto M (2015). Comparative allometric growth of the mimetic ephippid reef fishes *Chaetodipterusfaber* and *Platax orbicularis*. *Plos One. in press.*

Pereira PHC, Leal ICS, Araujo ME (2015) Observer presence may alter the behaviour of reef fishes associated with coral colonies**.** *Marine Ecology. in press.*

Leal ICS, Araujo ME, Cunha SR, **Pereira PHC** (2015) The influence of fire-coral colony size and agonistic behaviour of territorial damselfish on associated coral reef fish communities. *Marine Environmental Research*. **108,** 45–54.

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