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THE RELATIONSHIP BETWEEN HABITAT USE AND THE POPULATION ECOLOGY OF CORAL-DWELLING FISHES (GENUS *GOBIODON*)

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Philip L. Munday

ABSTRACT

The role of resource availability and competition in determining the distributions and abundances of species remains one of the most controversial subjects in ecology. In particular, the spatial scales over which these factors influence patterns of distribution and abundance is unclear. In this thesis I examine the effects of habitat selection, habitat availability and competition for space on the distribution and abundance of obligate coral-dwelling gobies (genus *Gobiodon*) at multiple spatial scales. I also examine the link between habitat specialisation and competitive ability, and assess the fitness consequences of inhabiting different species of coral. To achieve this I used a combination of comparative studies and manipulative experiments within and among four geographic locations, extending from the southern Great Barrier Reef to northern Papua New Guinea.

In a broad sense, all species of *Gobiodon* included in this study were found to be habitat specialists. However, some species inhabited only one or two species of coral and exhibited very conservative patterns of habitat use at all spatial scales examined. Other species exhibited a more flexible pattern of habitat use, particularly among geographic locations. Variation in the abundance of most species of *Gobiodon*, within and among locations, was closely associated with variation in the abundance of the corals they usually inhabit. Therefore, habitat availability appears to play a major role in determining the abundances of *Gobiodon* species at both local and regional scales. However, abundances were also correlated with reef zones, reef types and geographic locations, independently to coral availability. Therefore, as spatial scales increase a variety of other factors influence patterns of distribution and abundance of coral-dwelling gobies. A multiscale model of *Gobiodon* distribution and abundance is presented that includes: 1. Geographical differences in abundance, 2. Broad scale habitat selection of reefs within locations, 3. Finer scale habitat selection for reef zones and then individual coral colonies within zones and, 4. Competition for space within reef zones.

In laboratory experiments, species of *Gobiodon* differed in their ability to compete for preferred corals. Body size and prior residency of coral colonies also had a significant effect on competitive ability. A competitor removal experiment in the field demonstrated that some species of *Gobiodon* compete for space. Following the removal of a dominant competitor (*G. histrio*) from replicate patches of reef at Lizard Island (Great Barrier Reef), the abundances of two species, *G. axillaris* and *G. brochus*, significantly increased in abundance. Moreover, there was a very close relationship between the change in abundance of *G. histrio* and the change in abundance of *G. axillaris* and *G. brochus* combined. *G. axillaris* and *G. histrio* inhabit and compete directly for the same species of corals in the field but exhibit habitat partitioning at larger spatial scales (reef zones and reef types). *G. brochus* is apparently forced to use an inferior species of coral as a result of competition with *G. histrio*. Three other species of *Gobiodon* did not compete for space with *G. histrio*, either because they inhabit different species of coral or are able to co-habit coral colonies with *G. histrio*. The results of the competitor removal experiment were largely predictable from knowledge of overlap in habitat use and an understanding of these species' competitive abilities. Experiments at other geographic locations indicate that the intensity of competition appears to decline in locations where the relative abundance of preferred corals is high.

Transplant experiments demonstrated significant differences in growth and survival of fish inhabiting different species of coral. Furthermore, estimated lifetime reproductive success differed by more than an order of magnitude for fish inhabiting different species of coral. Habitat related differences in fitness might explain habitat preferences of *Gobiodon* species and the intense competition for some species of coral. Differences in habitat structure between species of coral may be the mechanism underlying habitat related differences in fitness. The consequences of inhabiting different species of coral were similar at two locations on the Great Barrier Reef (Lizard Island and One Tree Island) and, therefore, habitat related differences in fitness appear to have general relevance to habitat preferences and competition among species of *Gobiodon*. For at least some species of *Gobiodon*, the degree of habitat specialisation exhibited appears to be linked to their competitive abilities and the fitness consequences of inhabiting different species of corals.

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STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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CHAPTER 1: GENERAL INTRODUCTION

Resource limitation and interspecific competition have played central roles in ecological theory (Diamond 1978, Brown 1981, Roughgarden 1983). In particular, competition for limited resources has been considered a significant force acting on species niches (Brown and Wilson 1956, MacArthur and Levins 1964, 1967, May 1975, Abrams 1983), species coexistence and spatial distributions (Gause 1934, Hutchinson 1959, Schoener 1974, Diamond 1975), and population sizes (MacArthur 1960, 1970, Tilman 1980, 1982). Empirical observations and manipulative experiments have provided support for some of this theory and shown that interspecific competition can influence the distribution, abundance, and fitness of many types of organisms (reviews by Connell 1978, 1983, Schoener 1974, 1983, Roughgarden 1986, 1989, also Moulton and Pimm 1986). In many other cases, however, resources may not be limiting and competition does not appear to influence the structure of communities, the distribution and abundance of populations or the fitness of individuals (eg Nilsson 1969, Conner and Simberloff 1979, Lawton and Strong 1981, Lawton 1982, 1984, Schoener 1982, Underwood et al. 1983, Weins 1984, 1986). Consequently, the role of competition in structuring animal communities remains controversial.

Competition for space was ascribed a primary role in early models of community structure and population dynamics of coral-reef fishes (Smith and Tyler 1972, Roughgarden 1974, Sale 1974, 1977). However, rigorous experimental studies that have examined the potential for effects of interspecific competition on important demographic parameters have not always supported this. In pairwise comparisons of closely related and ecologically similar species, there is often very little evidence of interspecific competition when properly controlled density manipulations are carried out (Doherty 1982, 1983, Jones 1987a, 1988, Roberts 1987). More recently, theory and empirical data have highlighted the importance of variable recruitment (Doherty and Williams 1988, Doherty 1991, Doherty and Fowler 1994, Booth and Brosnan 1995) and predation (Hixon 1991, Hixon and Beets 1993, Caley 1993, 1995a, Caley and St. John 1996) on the population dynamics of reef fishes. A multi-factorial perspective of population dynamics in reef fish has now developed and it is widely recognised that a variety of process such as larval supply, settlement choices, habitat availability, predation and competition can influence the population dynamics of coral-reef fishes (Warner and Hughes 1988, Forrester 1990, Hixon 1991, Jones, 1991, Caley et al. 1996). The questions now focus on the spatial and temporal scales at which these processes act and the fundamental differences among species that determine which processes are most likely to influence patterns of distribution and abundance.

Coral-reef fish have characteristic habitats in which they are found but the importance of these habitats in determining patterns of distribution and abundance is still poorly understood (Jones 1991, Sale 1991a). Local-scale abundances of coral-reef fishes have been correlated with coral cover (Bell and Galzin 1984, Bouchon-Navaro et al. 1985, Bouchon-Navaro and Bouchon 1989, Jennings et al 1996, Munday et al. 1997), availability of shelter holes (Roberts and Ormond 1987), structural complexity (Luckhurst and Luckhurst 1978, Carpenter et al. 1981, Friedlander and Parish 1998, Ohman and Rajasuriya 1998) and microhabitat heterogeneity (Kaufman and Ebersole 1984). Experimental studies using artificial habitats have also demonstrated close associations between habitat structure and the abundance of reef fishes (Shulman 1984, Hixon and Beets 1989, Caley and St. John 1996). Although these results do not demonstrate that habitat is a limited resource, they are consistent with the notion that habitat availability influences local abundances. In contrast, other studies have found that the local-scale abundances of coral-reef fishes are not closely related to microhabitat characteristics (Robertson and Sheldon 1979, Wellington 1992, Sale et al. 1994, Green 1996). Furthermore, disturbances that reduce habitat availability have been associated with changes in abundance of some reef fishes (Williams 1986, Sano et al. 1987, Clarke 1996, Munday et al. 1997) but not others (Wellington and Victor 1985, Williams 1986, Sano et al. 1987) while Chabanet et al. (1997) only detected strong correlations between habitat variables and the total abundance of fish at disturbed sites where coral diversity was low. Overall, it is clear that the influence of habitat availability on the abundance of coral-reef fishes varies considerably.

Relationships between habitat availability and patterns of distribution and abundance may be strongest among small, habitat-specialist species of reef fish (Munday and Jones 1998). Many of the positive correlations between habitat characteristics and the abundance of fish described above involve small sedentary species or obligate corallivores. In other studies, Fricke (1980) correlated coral colony size with group size for *Dascyllus marginatus* and Sale (1972) found that *Dascyllus aruanus* populations were related to coral colony size at some sites. However, where branching corals were more abundant, there was no such relationship. For anemonefishes, where social interactions limit the number of adults per colony, the availability of suitable habitat appears to limit abundance (Ross 1978, Fricke 1979). At Lizard Island on the Great Barrier Reef, Munday et al. (1997) found that the abundances of some coral-dwelling gobies (genus *Gobiodon*) were correlated with the abundance of preferred coral species across reef zones. Furthermore, *Gobiodon* numbers declined significantly when the abundance of suitable corals declined following a crown-of-thorns starfish outbreak, but were not affected at sites where coral numbers did not decline. Similar relationships between habitat availability and population abundances have been reported for coral gobies from the genus *Paragobiodon* in Japan (Kuwamura et al. 1994). Therefore, it appears that the population dynamics of coral-dwelling gobies are closely linked to the dynamics of their host corals. For another small, habitat specialist, *Acanthemblemaria spinosa*, Buchheim and Hixon (1992) experimentally demonstrated that living space is a limited resource. In contrast, Robertson and Sheldon (1979) found that *Thalassoma bifasciatum* defended shelter holes but failed to find any evidence that nocturnal shelter sites were limiting for *T. bifasciatum* or *Stegastes planifrons*. In this case it appears that shelter defence probably reduces time exposed to predation rather than being a response to limited resources.

Where habitat space is limiting, we might expect interspecific competition to occur. However, only a few studies have demonstrated significant effects of competition on the habitat use, abundance or fitness of coral-reef fishes (Jones 1991). Clarke (1992) found that sympatric species of hole-dwelling blennies compete for space in artificial habitats. *Acanthemblemaria spinosa*, with a higher metabolic rate, out competed *A. aspera* for preferred spaces. However, *A. aspera* was able to persist in locations with lower food abundance due to lower metabolic demands. When *A. spinosa* was not present, *A. aspera* preferentially occupied holes usually occupied by *A. spinosa*. The natural distributions of these two species reflect this competitive interaction (Clarke 1989, 1994). Recently, Clarke (1996) has shown that the abundance of both species track changes in habitat availability in the wild. Furthermore, following a dramatic decline in habitats suitable for use by *A. spinosa*, the relative abundances of the two species changed in accordance with predictions of the laboratory experiments.

In addition to hole-dwelling blennies, interspecific interactions are known to influence patterns of habitat use and/or abundances of some surgeonfishes (Robertson and Gaines 1986) and some damselfishes (Ebersole 1985, Robertson 1995, 1996, Schmitt and Holbrook 1999). For example, in a comprehensive examination of the interactions among 7 sympatric species of damselfishes in the Caribbean, Robertson (1984, 1995, 1996) has shown that interspecific competition helps determine patterns of habitat use and species abundances and that the effects of competition are largely dependent on body size. Robertson (1995) concluded that the largest species of *Stegastes, S. diencaeus,* was competitively dominant and that space holding ability among *Stegastes* species was size dependent. Larger individuals of *S. diencaeus* and *S. dorsopunicans* frequently evicted smaller conspecific and heterospecifics when their territory size was constrained (Robertson 1995). Neither species, however, was able to evict larger heterospecific or conspecific neighbours. Following removals of the most abundant, and second largest species, *S. planifrons*, the abundance of smaller and less aggressive species increased (Robertson 1996). Furthermore, there was a strong correlation between the prior density of *S. planifrons* on individual reefs and the combined increase in density of the less aggressive species (Robertson 1996). In an earlier study, Robertson (1984) found that the largest damselfish in the assemblage, *Microspathodon chrysurus*, aggressively dominates and has a negative effect on the body mass and fat deposits of *Stegastes planifrons*. Clearly, size related competitive asymmetries influence patterns of habitat use, abundance and individual fitness of the damselfishes in this assemblage.

In anemonefishes, another group of small, habitat-specialists, it appears that distributions of species among host anemones are controlled by a variety of factors including imprinting of larvae on their host anemone before they enter the pelagic environment (Arvedlund and Nielsen 1996), learned host preferences, competition for limited space and stochastic processes (Fautin 1986, 1992). The competitive dominant, *Premnas biaculeatus*, occurs with only one actinian species (Fautin 1986). Other species occur with more actinian species in decreasing order of competitive dominance (Fautin 1986). In field and laboratory experiments Fautin (1986) found that a combinations of size, species and prior residence were important in determining competitive superiority.

Advantages to the individual fitness (growth, survival, reproduction) of fish using particular habitats might explain many of the patterns of habitat use and competitive interactions described above. Selection of habitats where individual fitness is high is frequently observed in animals (Pulliam 1989, Rosenzweig 1991) and may occur at several spatial scales (Morris 1987, Orians and Wittenberger 1991). Habitat selection by coral-reef fish at settlement is know to occur among locations on the reef (Doherty et al. 1996, Sponaugle and Cowen 1996) among reef zones (Wellington 1992) and among microhabitats (Williams and Sale 1981, Sale et al. 1984, Eckert 1985, Booth 1992, Elliott et al. 1995, Tolimieri 1995, Danilowicz 1996, Gutiérrez 1998, Ohman et al. 1998). Corresponding with these patterns of habitat selection, it is known that survivorship and/or growth of reef fishes can be influenced by factors such as location on the reef (Thresher 1983a,b, Aldenhoven 1986, Jones 1986, 1997, Forrester 1990), coral type (Jones 1988, Tolimieri 1995), habitat structure (Hixon and Beets 1993, Caley and St John 1996), and the presence of conspecifics (Doherty 1982, Jones 1987a,b, 1988, Forrester 1990) or heterospecifics (Thresher 1983a, Jones 1988). Selection for these physical and biotic features would favour individual fitness of reef fish. Therefore, these are the spatial scales (ie 10's-100's of metres) where relationships between habitat availability and the abundance of reef fishes are most likely to be observed. These are also the scales where strong interactions between individuals that might influence patterns of habitat use and abundance are expected to occur (Doherty and Williams 1988, Caley et al. 1996).

Reef fish have open populations where the relatively sedentary juveniles and adults live on patches of reef which are linked to populations on other reefs by a dispersive larval phase (Sale 1991b). Processes that affect the distribution and abundance of larvae among reefs, such as currents and tides, can dominate spatial and temporal patterns of abundance at large spatial scales (Roughgarden et al. 1988). Therefore, variability in recruitment at large spatial scales might obscure patterns of distribution and abundance generated by habitat selection and competitive interactions at small spatial scales (Doherty 1991, Sale 1991a, Caley et al. 1996). Whether habitat availability influences the distribution and abundance of coral-reef fishes at larger spatial scales is poorly understood (Fowler et al. 1992). Very few studies have compared habitat use of coral-reef fish at multiple locations or explicitly included spatial scale in studies of habitat use by reef fish. There is some indication that the importance of habitat associations in determining the distribution and abundance of coral-reef fishes may decline with increasing spatial scale (Tolimieri 1995, Caselle and Warner 1996). However, the importance of habitat availability in determining distributions and abundances of coral-reef fishes at regional or geographical scales (100s -1000s km) is largely unknown.

Because identical studies of habitat use by coral-reef fish have rarely been conducted at more than one location it is not know whether habitat availability and competition for space influence the abundances of reef fishes in similar ways at different locations. Furthermore, it is not known whether patterns of habitat use tend to be conservative feature of each species biology or whether they change in relation to variations in habitat availability among locations. These alternatives have implications for patterns of distribution and abundance of reef fish among locations (Brown 1984, Foster and Endler 1998). Conservative patterns of habitat use might limit distributions to locations where preferred habitats are available. Also, if habitats are a limited resource then conservative patterns of habitat use might result in strong relationships between habitat availability and abundances of fish among locations. In contrast, plasticity in habitat use might provide greater opportunities for widespread distributions. Also, because a variety of habitats might be used, plasticity in habitat use might result in weaker relationships between habitat availability and abundances of fish among locations.

Some of the most habitat specific fishes on coral reefs are obligate coral-dwelling gobies from the genus *Gobiodon* (Munday et al. 1997, 1999). These small fish (< 60mm total length) live among the branches of coral colonies, mostly of the genus *Acropora* (Munday et al. 1997, 1999) and usually only a single individual or a breeding pair inhabits each coral colony (Munday et al. 1998). Because of their obligate association with specific coral species and their simple social structures these fish might be expected to exhibit strong relationships between local abundances the abundance of their preferred corals. Also, if these species exhibit conservative patterns of habitat use among locations then habitat associations might influence abundances in similar and predictable ways at different locations. Furthermore, if interspecific competition for space can influence abundance or other demographic parameters of coral-reef fishes then it might be apparent among these habitat specialist fishes.

Coral-dwelling gobies have widespread distributions and are common on reefs throughout the Australasian region (Munday et al. 1999). Also, the coral species inhabited by these fish form small discrete colonies which can be easily censused for the presence of gobies with the aid of a bright lamp (Munday et al. 1997). Therefore, coral-dwelling gobies are an ideal group in which to examine relationships between habitat use and patterns of distribution and abundance at both local and geographical spatial scales. Moreover, because of their small size and highly sedentary nature, these fish are well suited for use in manipulative experiments which aim to examine the effects of habitat selection and competition on patterns of habitat use, abundance, growth, survival and reproductive fitness.

In this thesis I investigate the relationships between habitat use and the distribution and abundance of coral-dwelling gobies at multiple spatial scales. This research programme embraces the concept of incorporating both comparative and experimental studies, conducted at different spatial scales, in order to better understand the complexity of ecological systems (Ricklefs and Schluter 1993, Maurer 1999). Firstly, I investigate patterns of habitat use of coral-dwelling gobies at one geographic location (Chapter 2). Using a fully orthogonal sampling design I examine patterns of habitat use and then determine the relationships between habitat availability and the abundances of coral gobies among reef zones and among reef types. I then expand my investigation of habitat use to include multiple locations spanning several thousand kilometers, from the southern Great Barrier Reef to northern Papua New Guinea (Chapter 3). Here I determine whether patterns of habitat use exhibited by coral dwelling gobies are conservative features of their biology or whether they change in accordance with the availability of different coral species within and among geographic locations. I then investigate the relationships between habitat availability and the abundances of coral dwelling gobies within and among these widely separated locations. In order to examine habitat use of coral-dwelling gobies on multiple spatial-scales I have introduced statistical techniques that have not previously been used to investigate habitat use of fishes (log-linear modeling and resource selection functions) (Chapters 2 and 3). I have also used multiple regression techniques, but with the inclusion of categorical variables such as reef zones, reef locations and geographic locations, to consider how processes acting at these spatial scales might influence the distribution and abundances of coral-dwelling gobies, independently of habitat availability (Chapters 2 and 3).

Having detected strong relationships between habitat availability and the abundances of some species of *Gobiodon* (Chapters 2 and 3), I then use laboratory and field experiments to determine whether interspecific competition influences patterns of habitat use and/or abundances of coral-dwelling gobies (Chapter 4). Firstly, I use experiments in the laboratory to determine the competitive ability of each species of *Gobiodon* and to determine the influence of body size and prior residency on the outcome of competitive interactions for preferred habitats. I then use a traditional competitive exclusion experiment in the field to determine how the presence of a superior competitor influences the abundances of other species of *Gobiodon*. In addition, I use the results of the laboratory experiments and observations of habitat overlap to predict the outcome of competitive interactions in the field experiment.

Next I consider the fitness consequences of habitat selection and competition for habitats (Chapter 5). Here I use transplant experiments in the field to determine the consequences on growth, mortality and fecundity of inhabiting different coral species. These experiments focus on two key species of *Gobiodon*, one that is a competitive dominant and exhibits strong habitat selection and one that is an inferior competitor whose patterns of habitat use and abundance are affected by the presence of the superior competitor. I then combine the results of these experiments with data on the reproductive biology of coral-dwelling gobies to estimate the reproductive success of fish inhabiting different species of coral. These calculations demonstrate the fitness consequences of competition for habitats and indicate a potential trade-off between competitive ability and fitness in different habitats.

Having established that habitat use can influence abundances and individual fitness of *Gobiodon* at one location (Chapters 4 and 5), I examine the potential for habitat use to influence the abundances and fitness of *Gobiodon* species in a similar way at different geographical locations (Chapter 6). First, I examine patterns of recolonisation to vacant corals by competitively superior and subordinate species of *Gobiodon* to compare the importance of interspecific competition for preferred habitats at three widely separated locations. I then use reciprocal transplant experiments in the field to determine whether inhabiting different coral species has similar consequences for the growth of *Gobiodon* species at each of these widespread locations. Finally, I investigate the relationship between habitat structure and the growth of individuals inhabiting different species of coral at each location, to determine whether habitat structure might be the mechanism underlying habitat related differences in growth.

Although coral-dwelling gobies have many characteristics favourable for conducting observational and experimental studies on habitat use, the taxonomic status of many species is not well established. To investigate habitat use by coral-dwelling gobies it was necessary to establish a sound taxonomic framework during the early stages of this research. To do this I made extensive collections of *Gobiodon* at each of the geographic locations studied here and liaised closely with Dr. A. Harold and Dr. R. Winterbottom regarding the taxonomic status of species in these collections. As a consequence of this collaboration we have established a uniform framework for the current nomenclature of *Gobiodon* species and developed a guide to coral-dwelling gobies of the Australasian region (Munday et al. 1999). This paper is included as Appendix 1. Other papers published during my PhD and relevant to this thesis are included in subsequent appendices.

CHAPTER 2: INTERACTIONS BETWEEN HABITAT USE AND PATTERNS OF ABUNDANCE IN CORAL-DWELLING FISHES

2.1. ABSTRACT

Coral-dwelling fish from the genus *Gobiodon* are some of the most habitat specialised fishes on coral reefs. Consequently, we might expect that their population dynamics will be closely associated with the abundance of host corals. I used a combination of log-linear modelling and resource selection ratios to examine patterns of habitat use among eight species of *Gobiodon* in Kimbe Bay, Papua New Guinea. I then used multiple regression analysis to investigate relationships between the abundance of each species of *Gobiodon* and the abundance of the corals they inhabited. Each species of *Gobiodon* used one or more species of coral more frequently than expected by chance. The pattern of habitat use exhibited by each species of *Gobiodon* did not vary among reef zones or among reefs with different exposures to prevailing winds, despite changes in the relative abundances of corals among reef zones. This consistency in habitat use might be expected if the coral species inhabited confer considerable fitness advantages and, therefore, are strongly preferred. For most species of *Gobiodon*, abundances among reef zones and exposure regimes were correlated with the abundance of the coral species usually inhabited. Therefore, it appears that habitat availability helps determine abundances of most species of *Gobiodon* in Kimbe Bay. In addition to correlations with habitat availability, the abundances of *G. histrio*, *G. quinquestrigatus* and *G. rivulatus* (dark form) were also associated with particular reef zones and exposure regimes. Therefore, in these species, reef type appears to influence patterns of abundance independently of coral availability. In contrast to other species of *Gobiodon*, the abundance of the most specialised species, *Gobiodon* spA, was not closely associated with the abundance of the only coral species it inhabited. This study demonstrates that even for habitat specialised species, the relationship between habitat availability and abundance varies widely and is multiscalar.

2.2. INTRODUCTION

Studies of habitat use by animals can be divided into those that investigate patterns of habitat use and the processes determining these patterns and those that consider the importance of habitat use to patterns of abundance and population dynamics. Particular emphasis has been placed on investigating relationships between habitat use and population dynamics in studies of coral-reef fishes (Jones 1991). Many coral-reef fishes associate with particular microhabitats (Sale 1991a), however, the importance of these microhabitat associations in determining larger-scale patterns of distribution and abundance appears to vary widely among species. The strongest correlations between habitat availability and the abundance of coral-reef fishes have come from species of obligate coral-dwellers (Kuwamura et al. 1994, Munday et al. 1997), coral feeders (Bell and Galzin 1984, Bouchon-Navaro et al. 1985, Bouchon-Navaro and Bouchon 1989, Jennings et al 1996), or species with specific shelter requirements (Roberts and Ormond 1987, Buchheim and Hixon 1992, Clarke 1996). Even for these species, however, factors other than habitat availability are likely to influence patterns of abundance (Caley et al. 1996) and the relationship between abundance and habitat characteristics may vary from place to place (Sweatman 1985, Caley 1995a, Munday et al. 1997). There is also evidence that relationships between habitat availability and the abundance of coral-reef fishes become weaker with increasing spatial scale (Tolimieri 1995, 1998, Caselle and Warner 1996). Therefore, the relationship between habitat availability and the abundance of reef fish is likely to be multiscalar and to vary among species.

For species with a dispersive larval phase such as coral-reef fishes, there is likely to be considerable variability among locations in the types of habitats available when settling to the benthic environment. Due to the patchiness of the reef environment there may also be limited potential for movement to a more suitable location following settlement (Warner 1991). Therefore, these species might benefit from the ability to change their patterns of habitat use, depending on the types and abundances of habitats available at settlement. Patterns of habitat use might also change from place to place, depending on the intensity of interactions with other species (Werner et al. 1983). A variety of other factors, such as reef types or environmental parameters, can also interact with habitat associations to influence patterns of distribution and abundance (Wellington 1992, Gutiérrez 1998). If species change their patterns of habitat use among locations it will be necessary to consider these differences when examining relationships between abundance and habitat availability.

The degree of habitat specialisation and consistency of habitat use among locations are also predicted to have implications for patterns of commonness and rarity in animal assemblages (Gaston 1994). Because habitat specialist species use fewer habitats than generalist species their local abundances are more likely to be limited by habitat availability (Brown 1984). Habitat specialist are expected to dominate the best habitats but if these habitat tend to be rare then specialist species will nearly always be less abundant than generalist species (Rosenzweig and Lomolino 1997). The relationship between habitat specialisation and patterns of relative abundance have received little attention for reef fishes.

Species of *Gobiodon* (Gobiidae) are some of the most habitat specialised fishes on coral-reefs (Munday et al. 1999). These small fish live among the branches of living corals and have specific associations with one or more species of coral, mostly from the genus *Acropora* (Munday et al. 1997, 1999). Because of their obligate association with live corals, we might expect that the abundance of these fish will be closely related to the availability of suitable coral species. Despite close associations with particular coral species, Munday et al. (1997) found that the relationship between the abundance of some species of *Gobiodon* and coral availability was more consistent across reef zones within a site (10's meters apart) than among sites with different exposures to prevailing winds (km's apart). Therefore, it appears that the abundance of coral-dwelling gobies might be influenced by factors other than habitat availability and that the relationship between abundance and habitat availability may change with increasing spatial scale. In this study, I examine patterns of habitat use by species of *Gobiodon* and determine whether these patterns of habitat use change among reef zones or among reefs with different exposures to prevailing winds. I then examine the relationship between the abundance of each species of *Gobiodon* and the abundance of its host corals and consider how reef zones, exposure regimes and degree of habitat specialisation may interact with habitat availability to influence patterns of abundance.

Patterns of habitat use have been analysed with a multitude of techniques (Manly et al. 1993), however, many of these techniques cannot incorporate a range of independent variables in the analysis. Here I use a combination of log-linear modelling and resource selection ratios to investigate habitat use of coral-dwelling gobies. Log-linear analysis enables multiple independent variables to be considered (Heisey 1985). Therefore, it is possible to determine how different reef zones or exposure regimes influence patterns of habitat use among species of *Gobiodon*. Selection ratios (Manly et al. 1993) can then be used to determine the particular habitats that are favoured or avoided. Resource selection ratios are preferred over a range of electivity indices that are commonly used because they are amenable to statistical testing and are more robust to decisions made about which habitats to include in the analysis (Manly et al. 1993).

Log-linear models and resource selection ratios compare the frequency distribution of habitat occupancy to the proportional availability of these habitats. These methods provide no information on the relationship between the absolute abundance of coral gobies and the absolute abundances of the corals sampled at different spatial scales. Therefore, I then use multiple regression analysis, with the incorporation of categorical variables, to examine the relationship between habitat availability and the abundance of each species of *Gobiodon*. This method enables me to consider how different reef zones and exposures to prevailing winds might influence the abundance of coral-dwelling gobies independently to the availability of corals.

2.3. METHODS

Study location and species

This study was conducted in Kimbe Bay (5^0 15' S; 150^0 15' E) on the north coast of New Britain, Papua New Guinea (Fig. 2.1) between August 1996 and May 1997. Reefs within the bay can be categorised as (1) lagoonal reefs, (2) inner-bay reefs, (3) mid-bay reefs, and (4) outer-bay reefs (Holthus and Maragos 1996). Coral communities (Holthus and Maragos 1996) and fish communities (Allen and Munday 1996) are predictably distributed among these reef types. Furthermore, these categories correspond with increasing exposure to winds from the inner bay to the outer bay. Kimbe Bay has one of the highest recorded diversities of scleractinian corals (Holthus and Maragos 1996) including 72 species of *Acropora* (Wallace and Wolstenholme pers com) which are the primary habitat of fishes in the genus *Gobiodon.*

Gobiodon are small (< 60 mm total length) obligate coral-dwelling gobies (family Gobiidae) that live among the branches of corymbose and digitate corals mostly from the genus *Acropora* (Munday et al. 1997). Species are easily identified by body colour in life and identification is covered in detail by Munday et al. (1999). Here I consider 6 species of *Gobiodon* that are common in Kimbe Bay; *G. axillaris*, *G. histrio*, *G. quinquestrigatus*, *G. rivulatus* (light and dark forms), *Gobiodon* sp A, and *Gobiodon* sp D (Munday et al. 1999). Munday et al. (1999) note that *G. rivulatus* as currently recognised might consist of more than one species, therefore, the two forms of *G. rivulatus* were considered separately until the taxonomy is resolved.

Sampling design

The species of corals inhabited by species of *Gobiodon* were compared among reef zones (flat, crest, slope) and among reefs with different exposures to prevailing winds (sheltered, moderate, exposed). The gradient in exposure to prevailing winds across Kimbe Bay was used to segregate reefs by exposure. Outer-bay reefs are exposed to the prevailing trade winds, mid-bay reefs are moderately exposed to prevailing winds, and inner-bay reefs are relatively sheltered. Three representative sites were selected within each of these exposure regimes (Fig. 2.1). I then censused *Gobiodon* in all coral colonies of *Acropora* species used by *Gobiodon*, within five, 10m x 1m belt transects on the reef flat, reef crest and reef slope at each site. Each transects was oriented parallel to the reef crest and the starting position was haphazardly selected. A 10m tape was placed along the centre of the transect and a 1m plastic measuring bar was used to measure the transect width. Each colony of an acroporid species used by *Gobiodon,* located at least half within the transect and with a diameter greater than 5 cm, was carefully searched for *Gobiodon* with the aid of a small underwater light. Gobies remained within coral colonies during the census and, therefore, corals could be repeatedly censused if there was uncertainty about the accuracy of any count. In addition to comparing patterns of habitat use among exposures and zones, this sampling design enabled me to examine variation in the abundance of each species of *Gobiodon* among exposures and zones.

Analysis of habitat use

Log-linear models were used to determine if, (1) each species of *Gobiodon* used particular corals disproportionately to their availability on the reef and, (2) whether patterns of habitat use were consistent among exposures and reef zones. Resource selection ratios were then used to determine the particular species of corals that were used more frequently than expected by each species of *Gobiodon*.

A series of log-linear models were used to examine the frequency that corals were used by each species of *Gobiodon* in relation to the proportional availability of these corals at each exposure level and reef zone. In this approach a succession of increasingly complex models (Table 2.1) are fitted to the observed data until there is no significant improvement in the goodness-of-fit statistic (likelihood ratio chi-square) from one model to the next. Analysis was performed using SPSS for windows version 7.0. This method of testing patterns of habitat use follows Heisey (1985) and Manly et al. (1993), who provide detailed accounts of constructing and testing log-linear models.

All species of *Acropora* used by *Gobiodon*, and with a combined abundance exceeding 10 colonies, were used in the log-linear analyses. These corals were *Acropora anthocercis, A. cerealis, A. digitifera, A. divaricata, A. gemmifera, A. humilis, A. millepora, A. microclados, A. nasuta, A. secale, A. selago, A. solitaryensis, A. tenuis, A. valida* and one undescribed species. Application of log-linear modelling to analysis of habitat use requires that observations are independent (Manly et al. 1993). Aggregations of *Gobiodon* individuals from the same species within coral colonies would violate this assumption if total abundance data were used. Therefore, as recommended by Thomas and Taylor (1990), the presence or absence of each *Gobiodon* species per colony was used to ensure independence of habitat use observations. Rarely were more than two individuals of any species of *Gobiodon* found in a coral colony, therefore, the use of presence – absence data did not bias estimates of habitat use among coral species. Transect were then pooled within zones at each exposure level to provide adequate cell counts for reliable analysis.

Where log-linear modelling indicated that a species of *Gobiodon* used corals disproportionately to their availability, resource selection ratios were used to determine the particular corals that each species of *Gobiodon* used more or less frequently than expected. Selection ratios (w_i) were estimated using the formula:

$$w_i = o_i/a_i$$

where o_i is the proportion of all coral colonies occupied by a species of *Gobiodon* which were coral species *i* and a_i is the proportion of total available coral colonies which were coral species *i*. A Bonferroni corrected 95% confidence interval was estimated for each selection ratio, using the formula:

$$Z_{\alpha/2k}\sqrt{\left\{o_i\left(1-o_i\right)/\left(u_+a_i^{\,2}\right)\right\}}$$

where $z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $\alpha/2k$, $\alpha = 0.05$, k = the total number of corals species, o_i is the proportion of all coral colonies occupied by a species of *Gobiodon* which belong to coral species *i*, u_+ is the total number of coral colonies of all species occupied by that species of *Gobiodon*, and a_i is the proportion of total available coral colonies which were coral species *i*. The use of a coral species was considered to be proportional to its availability where the 95% confidence interval of the selection ratio encompassed 1 (Manly et al. 1993).

Analysis of habitat heterogeneity

Because patterns of habitat use could be associated with changes in the relative abundances of coral species among zones or exposure regime, I examined the heterogeneity of coral community structure among zones and exposures. Transects were pooled within each combination of site and zone in order to analyse habitat heterogeneity at the same scale as the habitat use of the fish. Heterogeneity was then estimated for the 15 coral species used in previous analyses, using the Shannon-Weiner Index;

$$H = \Sigma\,(p_i)(\log p_i)$$

Where p_i is the proportion of the total number of corals belonging to species i sampled at each site. A split-plot ANOVA without replication was used to examine variation in heterogeneity (Shannon-Weiner Index) among zones and exposures.

Analysis of abundance

Log-linear models and selection ratios only examine the frequency distribution of the habitats used in relation to the proportion available, they do not provide information on the relationship between the absolute abundance of coral gobies and the absolute abundances of the corals at the different spatial scales sampled. Stepwise multiple regression using a forward-backward stepping algorithm ($p = 0.05$ to enter and remove) was used to examine the relationship between the abundance of each species of *Gobiodon*, the abundance of each coral species, exposure level and reef zone. If the availability of preferred corals were the main variables influencing the abundances of gobies then those coral species should be the only significant variables retained in the regression model. However, if exposure regime helps determine variation in goby abundances, independently of coral availability, then one or more levels of exposure (exposed, moderate, sheltered) will be a significant factor in the regression model. Similarly, if reef zones significantly influence abundances then one or more zones (flat, crest, slope) will be retained in the regression model.

The inclusion of categorical variables, such as exposure regime and reef zones, requires the use of contrast groups (Aiken and West 1991). Exposure levels (exposed, moderate, sheltered) and reef zones (flat, crest, slope) were coded as dummy variables. Exposed reefs and reef slope were arbitrarily selected as the contrast groups. The influence of each exposure level and reef zone was compared to these contrast groups when interpreting each analysis. For each comparison the magnitude of the regression coefficient is a direct indicator of the difference between the variable of interest and it's contrast group. These coefficients are partial effects provided that each of the categorical variables is present in the regression equation (Aiken and West 1991). Where only one of each pair of categorical variables (sheltered/moderate or crest/slope) was retained in the final regression equation the partial coefficient was obtained by re-running the analysis with both variables included. Abundances of fish and corals per transect were transformed [log(x +1)] to improve the distribution of residuals.

2.4. RESULTS

Habitat use

A total of 1539 coral colonies of the 15 *Acropora* species used by *Gobiodon* were censused (Fig. 2.2). Within these coral colonies a total of 2257 *Gobiodon* were observed (Fig. 2.3). Species of *Gobiodon* differed in the range of corals species occupied (Fig. 2.3), however, no species occupied corals in proportion to availability (Table 2.2). Log-linear models revealed that the patterns of habitat use exhibited by each species of *Gobiodon* were consistent among zones and exposures (Table 2.2). These conservative patterns of habitat use occurred despite significant changes in the relative abundances of the 15 species of *Acropora* among reef zones (Table 2.3).

The degree of habitat specialisation differed among the species of *Gobiodon* examined. *Gobiodon* species A and *Gobiodon* species D exhibited very specialised patterns of habitat use. *Gobiodon* spA was only found in *A. tenuis* and *Gobiodon* spD was only found in *A. divaricata* and *A. solitaryensis* (Table 2.4). *Gobiodon axillaris* occupied only four species of coral (Fig 2.3). It used *Acropora digitifera* more frequently than expected and used two other species, *A. millepora* and *A. nasuta*, in proportion to their availability (Table 2.4). *Gobiodon histrio* was observed in 10 species of *Acropora* (Fig 2.3), however, *A. nasuta* was the was the only species of coral used more frequently than expected from availability (Table 2.4). *G. histrio* used five other species of coral in proportion to their availability (Table 2.4). The light and dark forms of *G. rivulatus* were both observed in 11 species of *Acropora* (Fig 2.3). The light form used *A. gemmifera* more frequently than expected and used *A. anthocercis*, *A. humilis*, *A. microclados*, *A. secale* and *A. tenuis* approximately in accordance with their availability (Table 2.4). In contrast, the dark form of *G. rivulatus* used *A. secale* and *A. microclados* more frequently than expected and used *A. gemmifera* in accordance with its availability (Table 2.4). The dark form of *G. rivulatus* also used *A. anthocercis*, *A. humilis* and *A. tenuis* in proportion to availability. *Gobiodon quinquestrigatus* exhibited the least specialised pattern of habitat use. It inhabited 12 of the 15 species of *Acropora* and used four of these species, *A. cerealis*, *A. selago*, *A. species* and *A. valida*, more frequently than expected from their availability. It also used another 2 species, *A. humilis* and *A. nasuta*, in proportion to their availability (Table 2.4).

Two distinct categories were apparent in the relationship between habitat specialisation (number of coral species used in accordance with availability or more frequently than expected) and total abundance (Fig 2.4). Species of *Gobiodon* that used only 1-3 species of coral were less abundant in Kimbe Bay than species of *Gobiodon* that used 6 or more species of coral. There is a greater probability of finding abundant species of fish in rarely used corals and, therefore, the positive relationship between habitat specialisation and total abundance could be a statistical artifact if all coral species were included in the comparison. This problem was avoided by defining habitat specialisation as the number of coral species used in accordance with availability or used more frequently than expected. Using this method the comparison of habitat specialisation and abundance is not confounded by the increased likelihood of finding abundant species in habitats that are rarely used.

Patterns of abundance

The abundance of each species of *Gobiodon* within and among zones and exposures was associated with the abundance of the corals they most frequently inhabited (Table 2.5). The only exception was the abundance of *Gobiodon* spA which was only weakly associated with the abundance of *A. tenuis* (Table 2.5), despite this being the only coral species inhabited. In contrast, the abundance of *Gobiodon* spD was strongly associated with the availability of *A. divaricata* and *A. solitaryensis*, the only two coral species inhabited. The abundance of *G. axillaris* was associated with the abundance of *A. digitifera*, the coral species most commonly inhabited. The abundance of *G. axillaris* was also positively associated with abundance of *A. millepora*, a coral species used in proportion to its availability, but negatively associated with *A. nasuta*, another coral species used in proportion to availability (Table 2.5). The abundance of *G. histrio* was closely associated with the abundance of *A. nasuta*, the coral species usually inhabited and also with *A. valida*, a coral species inhabited in proportion to availability (Table 2.5). The abundance of the light form of *G. rivulatus* was associated with *A. gemmifera*, the only coral species used more frequently than expected (Table 2.5). Similarly, the dark form of *G. rivulatus* was associated with the abundance of *A. secale* and *A. microclados* (Table 2.5), the coral species used most frequently. The abundance of *G. quinquestrigatus* was associated with the abundance of all coral species used more frequently than expected or used in proportion to availability, except for *A. selago*. Also, *G. quinquestrigatus* was associated with *A. secale*, despite this species of coral being inhabited less frequently than expected from its availability (Table 2.5).

The abundances of *G. histrio*, *G. quinquestrigatus* and *G. rivulatus* (dark form) were associated with particular exposure regimes and reef zones, independently of the availability of corals. *Gobiodon histrio* was on average more abundant at sheltered sites in comparison to exposed sites, independently of coral availability (Table 2.5). In addition, *G. histrio* was more abundant on the reef crest and reef flat compared to the reef slope (Table 2.5). *Gobiodon quinquestrigatus* was more abundant at sheltered and moderate sites compared to exposed sites, but less abundant on the reef crest and reef flat compared to the reef slope (Table 2.5). The dark form of *G. rivulatus* was less abundant at sheltered sites than exposed sites and more abundant on the reef crest than the reef slope (Table 2.5). The abundances of *G. axillaris*, *G. rivulatus* (light form), *Gobiodon* spA and *Gobiodon* spD were apparently not influenced by exposure regime or reef zones (Table 2.5).

TABLE 2.1. Log-linear models used to test patterns of habitat use. Models were tested sequentially until there was no further improvement in the fit of the model to the observed data. Either model 3 or model 4 was included at the third step in each analysis, depending on which model gave the best improvement in the goodness-of-fit statistic.

Model	Factors included	Hypothesis tested
1	exposure*zone	habitat use is proportional to availability
2	coral + exposure*zone	habitats used disproportionately to availability and the pattern uniform among exposures and zones
3	coral*exposure + exposure*zone	habitats used disproportionately to availability, but the pattern changes among exposures
4	coral*zone + exposure*zone	habitats used disproportionately to availability, but the pattern changes among zones
5	coral*exposure + coral*zone + exposure*zone	habitats used disproportionately to availability, but the pattern changes among exposures and zones
6	coral*exposure + coral*zone coral*exposure*zone	habitats used disproportionately to availability, but the pattern changes with an interaction between exposures and zones

TABLE 2.2. Analysis of habitat use by species of *Gobiodon* among reef zones and exposure regimes in Kimbe Bay, PNG. Log-linear models were tested sequentially until there was no significant improvement in the deviance between models. The best fitting model is underlined for each species. ** = 0.001<*P*<0.01, *** = *P*<0.001, ns = non significant.

Species	Model	Deviance	df	Difference	df
G. axillaris	habitat use proportional to availability	92.63 ns	126		
				76.06***	14
	habitat use disproportional to availability and uniform among exposures and zones	16.57 ns	112		
				11.73 ns	28
	habitat use disproportional to availability but pattern varies among exposures	4.84 ns	84		
				4.84 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	0.003 ns	56		
G. histrio	habitat use proportional to availability	259.39***	126		
				206.87***	14
	habitat use disproportional to availability and uniform among exposures and zones	52.52 ns	112		
				22.01 ns	28
	habitat use disproportional to availability but pattern varies among exposures	30.51 ns	84		
				14.96 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	15.55 ns	56		
G. quinquestrigatus	habitat use proportional to availability	202.69***	126		
				137.87***	14
	habitat use disproportional to availability and uniform among exposures and zones	64.82 ns	112		
				25.51 ns	28
	habitat use disproportional to availability but pattern varies among zones	39.31 ns	84		
				20.55 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	18.76 ns	56		

TABLE 2.2. continued.

G. rivulatus (light)	habitat use proportional to availability	217.88***	126		
				164.03***	14
	habitat use disproportional to availability and uniform among exposures and zones	53.85 ns	112		
				26.15 ns	28
	habitat use disproportional to availability but pattern varies among zones	27.7 ns	84		
				22.84 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	4.86 ns	56		
G. rivulatus (dark)	habitat use proportional to availability	224.56***	126		
				172.7***	14
	habitat use disproportional to availability and uniform among exposures and zones	51.86 ns	112		
				24.84 ns	28
	habitat use disproportional to availability but pattern varies among zones	27.02 ns	84		
				22.67 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	4.35 ns	56		
Gobiodon spA	habitat use proportional to availability	54.13 ns	126		
				47.69***	14
	habitat use disproportional to availability and uniform among exposures and zones	6.44 ns	112		
				2.21 ns	28
	habitat use disproportional to availability but pattern varies among zones	4.23 ns	84		
				3.95 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	0.28 ns	56		
Gobiodon spD	habitat use proportional to availability	191.35***	126		
				189.34***	14
	habitat use disproportional to availability and uniform among exposures and zones	2.013 ns	112		
				1.05 ns	28
	habitat use disproportional to availability but pattern varies among exposures	0.96 ns	84		
				0.01 ns	28
	habitat use disproportional to availability but pattern varies with exposures and zone	0.95 ns	56		

TABLE 2.3. ANOVA results for heterogeneity of coral assemblage structure among exposure regime and reef zone. Heterogeneity estimated using the Shannon-Weiner Index. Note the zone by site interaction term is pooled with the residual in a split-plot ANOVA without replication. NS = non significant.

Source of variation	df	MS	*F*	*p*
Exposure	2	0.0373	2.645	NS
Site	6	0.0141	1.564	NS
Zone	2	0.0878	9.739	0.003
Exposure * Zone	4	0.0059	0.654	NS
Error	126	0.009		

TABLE 2.4. Significance of habitat use by species of *Gobiodon* in Kimbe Bay using resource selection ratios and Bonferroni corrected 95% confidence intervals. NS: habitat used in proprtion to availability, +: habitat used significantly more than expected, -: habitat used significantly less than expected.

Species	*G. axillaris*	*G. histrio*	*G. quinq.*	*G. rivulatus* (light)	*G. rivulatus* (dark)	*G*. spA	*G*. spD
A. anthocercis	-	-	-	NS	NS	-	-
A. cerealis	-	NS	+	-	-	-	-
A. digitifera	+	NS	-	-	-	-	-
A. divaricata	-	-	-	-	-	-	+
A. gemmifera	-	-	-	+	NS	-	-
A. humilis	-	-	NS	NS	NS	-	-
A. microclados	-	-	-	NS	+	-	-
A. millepora	NS	NS	-	-	-	-	-
A. nasuta	NS	+	NS	-	-	-	-
A. secale	-	-	-	NS	+	-	-
A. selago	-	-	+	-	-	-	-
A. solitaryensis	-	-	-	-	-	-	+
A. sp.	-	-	+	-	-	-	-
A. tenuis	-	NS	-	NS	NS	+	-
A. valida	-	NS	+	-	-	-	-

TABLE 2.5. Results of stepwise regression analysis on abundance of fish and corals in transects at all reef zones and exposures. Only significant coefficients are shown. Exposed reefs and reef slope are the contrast groups for categorical variables.

Variable	*G. axillaris*	*G. histrio*	*G. quinq.*	*G. rivulatus* (light)	*G. rivulatus* (dark)	*G.* spA	*G.* spD
constant	0.04	-0.13	0.46	0.09	0.1	0.02	0.01
sheltered		0.08	0.24		-0.13		
moderate			0.12				
reef crest		0.32	-0.49		0.25		
reef flat		0.20	-0.51				
A. anthocercis							
A. cerealis			0.64				
A. digitifera	0.5						
A. divaricata							1.17
A. gemmifera				0.76			
A. humilis			0.27				
A. microclados					0.43		
A. millepora	0.21	0.29					
A. nasuta	-0.19	0.63	0.33				
A. secale			0.31		0.37		
A. selago						-0.09	1.62
A. solitaryensis							
A. sp.			0.44				
A. tenuis						0.25	
A. valida		0.24	0.32				
adj. r squared	0.44	0.63	0.82	0.36	0.34	0.16	0.82

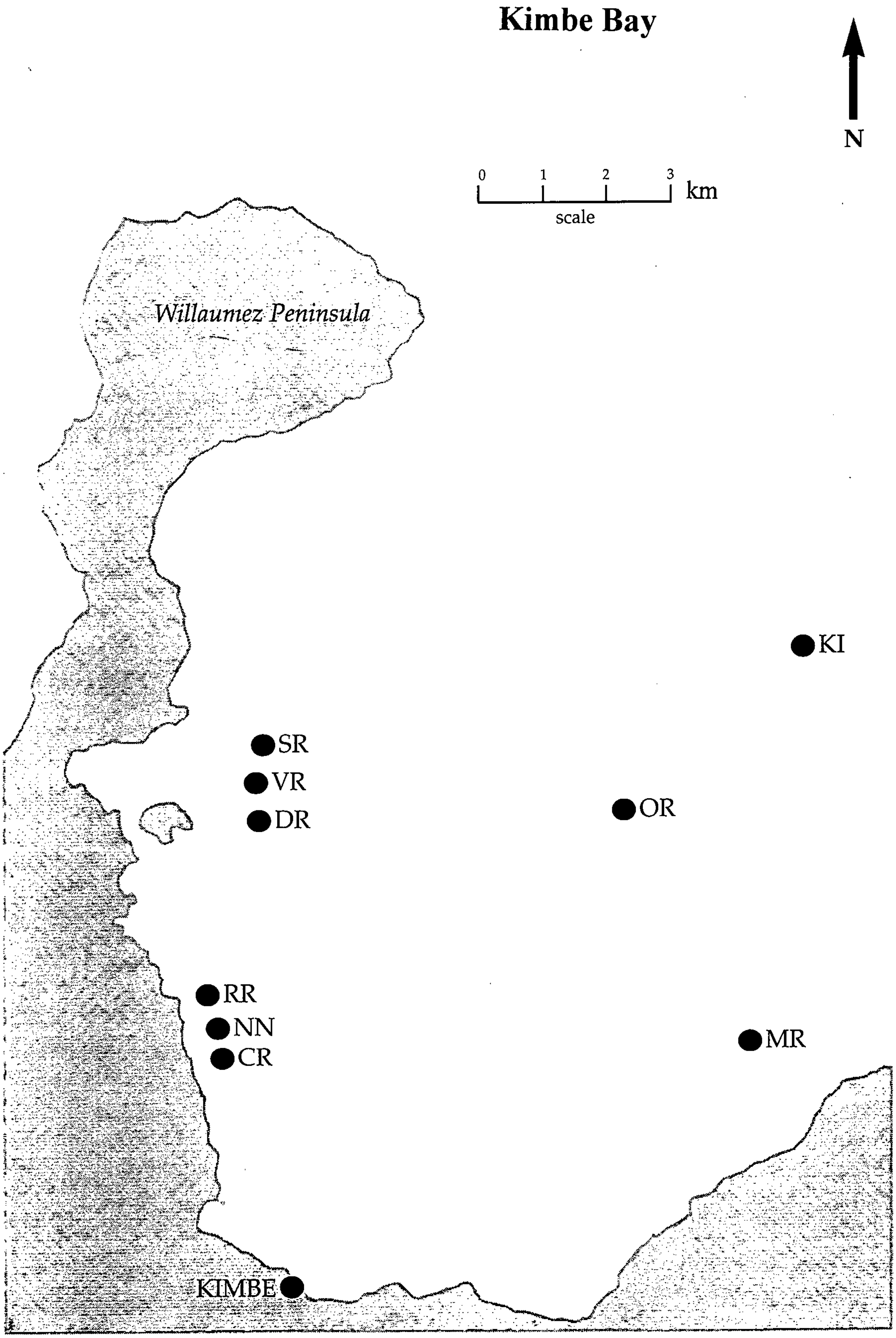


Fig 2.1. Map of Kimbe Bay, New Britain, Papua New Guinea showing sites sampled in this study. Exposed sites; KI = Kimbe Island, OR = Otto Reef, MR = Margets Reef. Moderate sites; SR = Susans Reef, VR = Vanessas Reef, DR = Donnas Reef. Sheltered sites; RR = Rosemaries Reef, NN = Noname Reef, CR = Crater Reef.

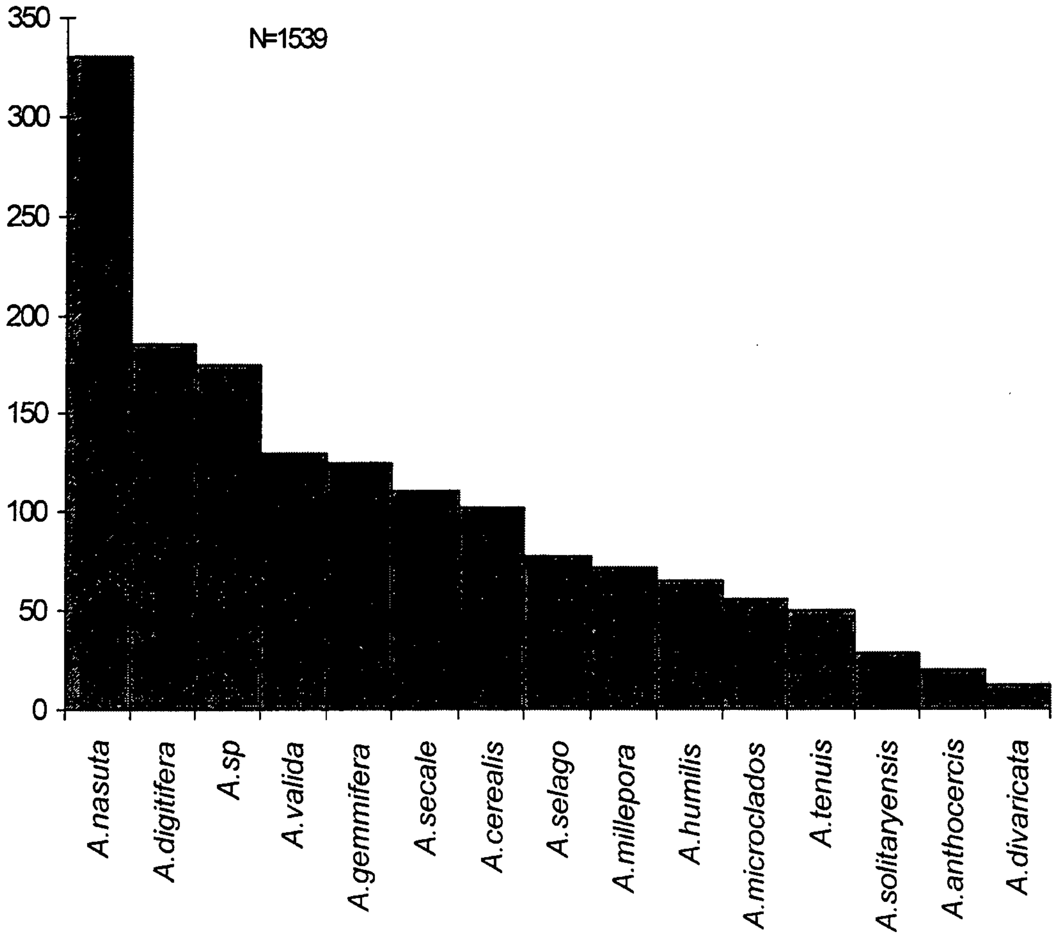


Fig 2.2. Total number of coral colonies from each species of *Acropora* examined for the presence of coral-dwelling gobies in Kimbe Bay.

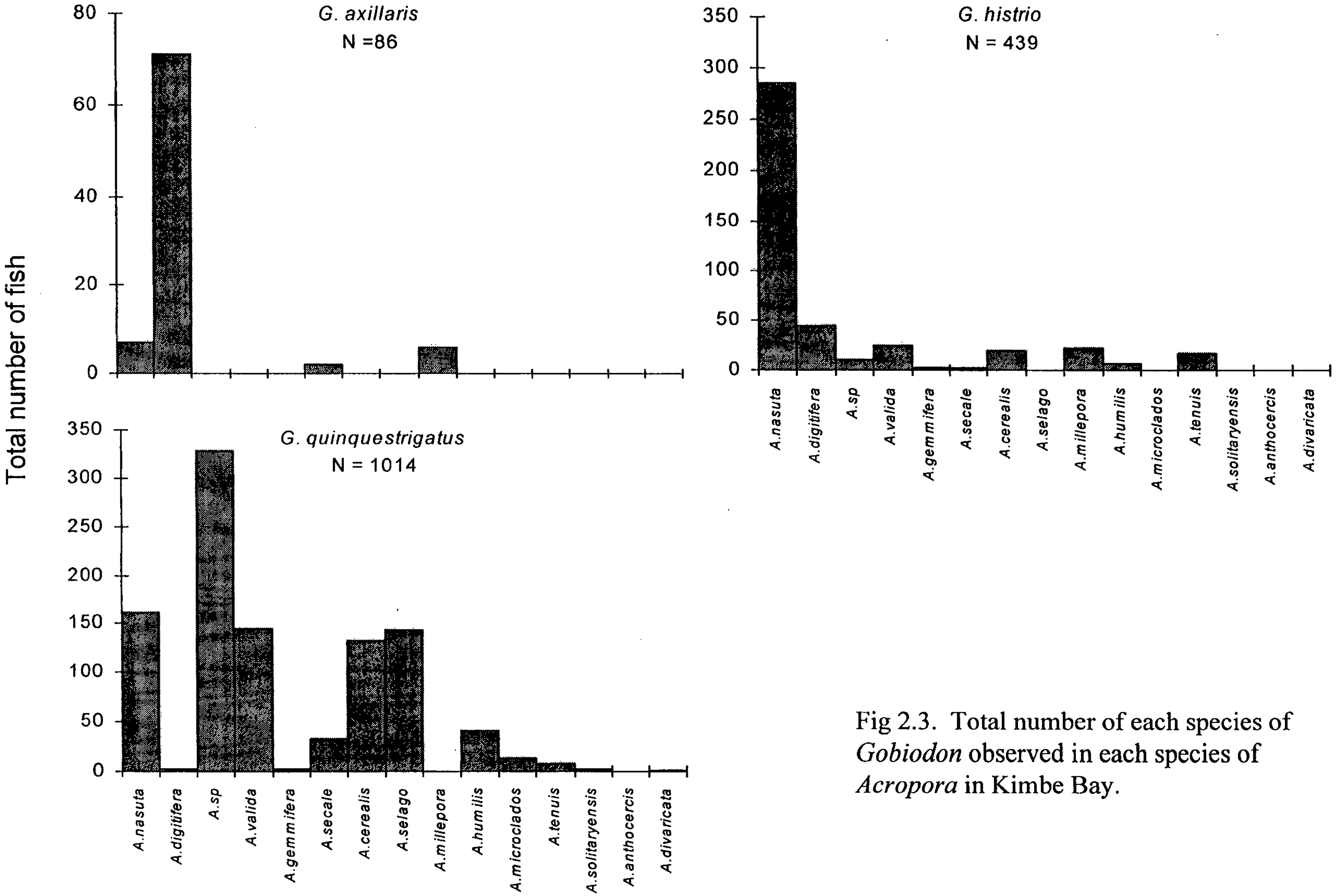


Fig 2.3. Total number of each species of *Gobiodon* observed in each species of *Acropora* in Kimbe Bay.

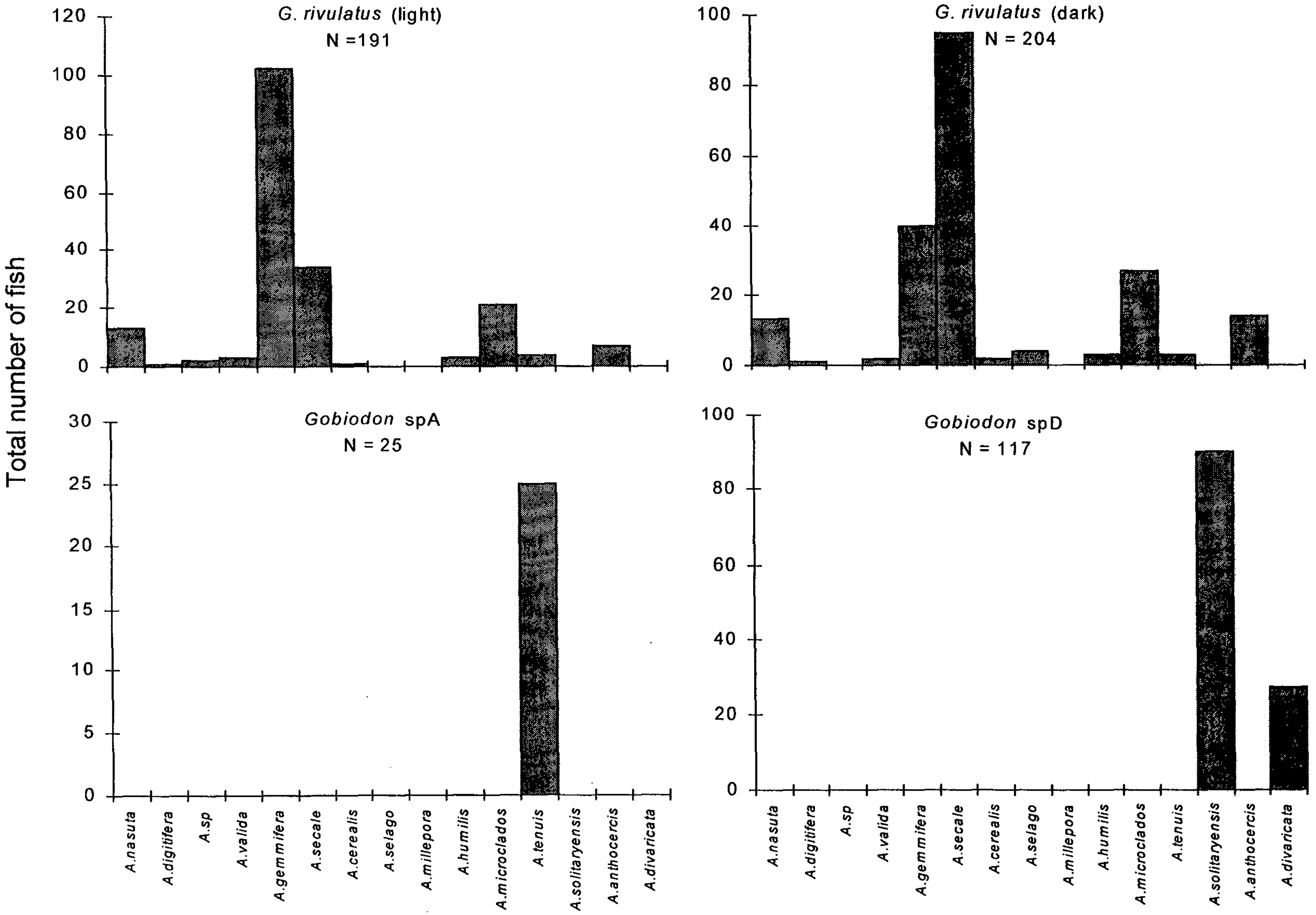

Total number of fish
G. rivulatus (light)
N =191
G. rivulatus (dark)
N = 204
Gobiodon spA
N = 25
Gobiodon spD
N = 117
120
100
80
60
40
20
0
30
25
20
15
10
5
A.nasuta
A.digitifera
A.sp
A.valida
A.gemmifera
A.secale
A.cerealis
A.selago
A.millepora
A.humilis
A.microclados
A.tenuis
A.solitaryensis
A.anthocercis
A.divaricata

Fig 2.3. Cont.

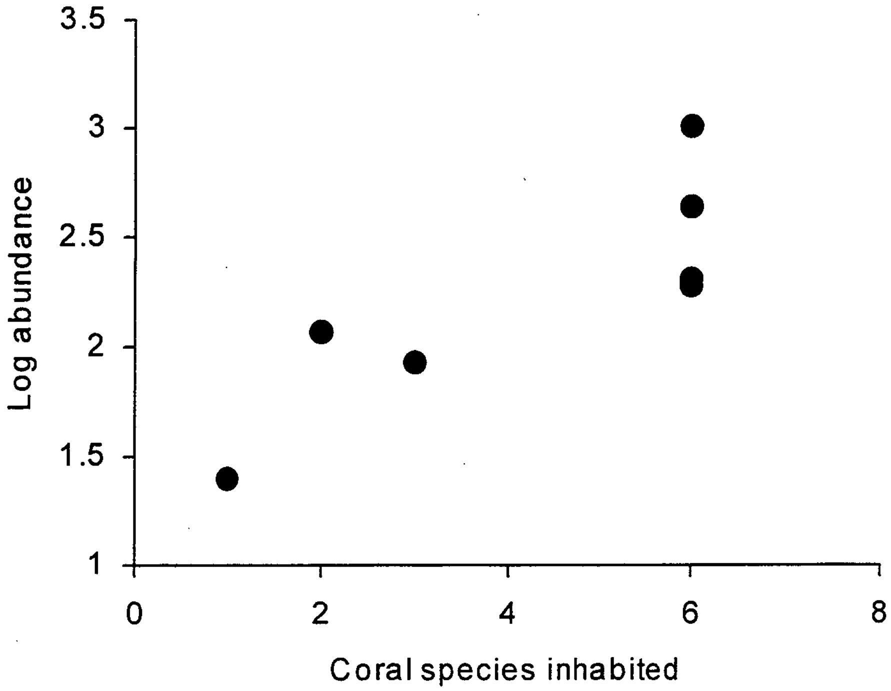


Fig 2.4. Relationship between habitat specialisation and the total number of each species of *Gobiodon* recorded in Kimbe Bay. Habitat specialisation is defined as the number of coral species used in accordance with availability or more frequently than expected by chance.

2.5. DISCUSSION

Each species of *Gobiodon* exhibited consistent patterns of habitat use among reef zones and exposure levels within Kimbe Bay. This consistency in habitat use occurred despite changes in the relative abundance of coral species among reef zones. Therefore, patterns of habitat use were very conservative at the spatial scales examined here. Such conservative patterns of habitat use might be expected if particular habitats offer considerable fitness advantages and individuals consistently select these habitats. Alternatively, consistent patterns of habitat use would be expected if patterns of habitat use are a consequence of interactions with other species, and these interactions occur with similar intensity among the sites examined. The coral species used most frequently by *G. histrio* in Kimbe Bay was also the coral species used most frequently on the Great Barrier Reef (Munday et al. 1997). In contrast, *G. axillaris* used different species of corals in Kimbe Bay to those most frequently used on the Great Barrier Reef. Therefore, the processes driving patterns of habitat use appear to differ among species. Manipulative experiments will be required to determine the relative importance of habitat preference, competitive interactions or other processes underlying patterns of habitat use among species of *Gobiodon*.

The abundance of most species of *Gobiodon* was associated with the abundance of the coral species they usually inhabited. A similar pattern was observed for species of *Gobiodon* on the Great Barrier Reef (Munday et al. 1997). These correlations are consistent with the notion that habitat availability is an important determinant of the local abundances of species of *Gobiodon*. The abundance of other habitat specialists such as *Paragobiodon echinocephalus* (Kuwamura et al. 1994), *Amphiprion* species (Ross 1978) and *Acanthemblemaria* species (Buchheim and Hixon 1992, Clarke 1996) and the abundances of obligate coral feeders from the family Chaetodontidae (Bell and Galzin 1984, Bouchon-Navaro 1986, Bouchon-Navaro and Bouchon 1989) have also been found to be closely associated with the availability of preferred habitats. Therefore, it appears that the availability of habitats can influence the abundance of specialised species of fishes, not just their presence or absence on coral-reefs. In contrast, it appears that habitat availability is relatively unimportant in determining species abundances of many other species of reef fishes (Sale and Douglas 1984, Sale et al. 1994). These different results indicate that the relative importance of microhabitat availability in determining the distribution and abundance of coral-reef fishes varies considerably among species.

In contrast to other species, the abundance of *Gobiodon* spA was not closely associated with the abundance of the only coral species it inhabited. Therefore, habitat availability might determine the presence of this species in Kimbe Bay, but does not significantly influence abundance within the bay. *Gobiodon* spA was the most habitat specialised species of *Gobiodon* examined here and, therefore, might be expected to exhibit the strongest relationship between abundance and habitat availability. However, *Gobiodon* spA was relatively uncommon in Kimbe Bay and there were numerous vacant colonies of *A. tenuis*, the only coral inhabited. Therefore it appears that the abundance of *Gobiodon* spA is insufficient for habitat availability to have a significant affect on patterns of abundance. The contrast between *Gobiodon* spA and the other species of *Gobiodon* considered here demonstrates that even among the most specialised species of reef fish, the relationship between abundances and habitat availability varies greatly.

In general, the most specialised species of *Gobiodon* were less abundant than more generalist species. This has implications for understanding patterns of commonness and rarity in fish assemblages. Relative abundances are predicted to be associated with the degree of habitat specialisation (Brown 1984), however, such relationships have rarely been described for reef fish. Because each species of *Gobiodon* exhibited conservative patterns of habitat use, the relationship between habitat specialisation and relative abundances is likely to be robust over the spatial scales studied here. Using data presented by Munday et al. (1997) a broadly similar relationship between habitat specialisation and relative abundances is found for species of *Gobiodon* at Lizard Island. However, the trend in the Lizard Island data is largely driven by one highly specialised species that is relatively rare and two more generalist species that are highly abundant. Further comparisons of habitat use and relative abundances of *Gobiodon* at other locations are required to assess the generality of the relationship between relative abundances and habitat specialisation.

The abundances of some species of *Gobiodon* were associated with particular reef zones or exposure regimes, independently to the availability of habitat availability. Therefore, habitat availability alone does not determine patterns of abundance in these species. For example, *Gobiodon histrio* and *G. quinquestrigatus* were more abundant at moderate and sheltered sites than at exposed sites. A similar pattern was reported for these species on the Great Barrier Reef (Munday et al. 1997). Although a number of pre- or post-settlement processes could generate this pattern, it seems likely that these species have a preference for sheltered sites. Broadscale habitat selection before settlement has been documented in other coral-reef fishes (Doherty et al. 1996) and could explain the greater abundance of *G. histrio* and *G. quinquestrigatus* at sheltered sites. Moreover, it appears that habitat selection is a multiscale process for these species because *G. histrio* and *G. quinquestrigatus* were also more abundant on particular reef zones, independently of habitat availability. In the process of settling to the reef, larvae might first select the general reef environment (Doherty et al. 1996), or select hydrodynamic conditions that transport them to these locations (Cowen and Castro 1994). At the reef they could select particular reef zones (Wellington 1992) and then settle to preferred corals within these zones. Although other processes could generate these multiscale distribution patterns, habitat selection at settlement has been shown to be an important contributor to the distribution and abundance of coral-reef fishes within zones (Sweatman 1983, Shulman 1984, Sale et al. 1984, Eckert 1985, Booth 1992, Öhman et al. 1998), among zones (Wellington 1992, Gutiérrez 1998) and among reefs (Tolimieri 1995) and could easily explain a large proportion of distribution and abundance patterns observed for *Gobiodon* in Kimbe Bay.

The importance of reef type to patterns of distribution and abundance is most apparent for *Gobiodon okinawae*. This species is present in Kimbe Bay, but is completely restricted to lagoonal reefs (which were not considered here), despite the corals it inhabits being present on reefs throughout the bay (PLM unpublished data). Similar observations have been made at Lizard Island on the Great Barrier Reef (Munday et al. 1997) and in Micronesia (Myers 1991). Therefore, it appears that the distribution of *G. okinawae* is primarily determined by the presence of lagoons rather than the distribution of corals.

Habitat use is frequently analysed using chi-squared and proportional tests (Nue et al. 1974, Thomas and Taylor 1990, Alldredge and Ratti 1992, Munday et al. 1997). Chi-squared tests are first used to determine if habitats use is disproportionate to availability. Proportional tests are then used to determine which particular habitats are favoured or avoided. These tests suffer several disadvantages. Firstly, it is not possible to simultaneously consider the influence of multiple independent variables, such as different locations or different spatial scales of sampling. Secondly, decisions made about the types of habitats to include in the analysis can substantially influence the results of chi-squared and proportional tests (Manly et al. 1993). For example, the results of proportional methods of habitat selection analysis can depend on whether or not common, but rarely used habitats are included (Thomas and Taylor 1990, Manly et al. 1993). The use of log-linear analysis and resource selection ratios largely overcomes these problems (Manly et al. 1993).

Log-linear analysis was used to analyse habitat use in relation to several independent variables (zones and exposures). Although no significant differences were detected in patterns of habitat use among zones or exposures, preliminary analyses indicated that log-linear modelling could detect such patterns if present. For example, patterns of habitat use varied among zones when the light and dark form of *G. rivulatus* were combined during preliminary analyses. In contrast, the two forms of *G. rivulatus* exhibited very different, but consistent patterns of habitat use when analysed separately.

Considerable interest has focused on the relationship between the microhabitat availability and the abundance of fish at increasing spatial scales (Caselle and Warner 1996, Sale 1998). This study demonstrated that the local scale abundance of coral-dwelling fishes can be closely associated with the abundance of the coral species most frequently inhabited. However, even for these habitat specialised fishes, factors other than habitat availability influence abundances in predictable ways. As the spatial scale of sampling increases, it is possible that different habitat types or environmental regimes will be encountered. These environmental regimes should be incorporated in the analysis because they may independently influence patterns of abundance. Failure to incorporate these variables may lead to misinterpretation of relationships between microhabitat availability and the abundance of fish at increasing spatial scales. Consideration of multiple variables in analyses of habitat use should lead to a more comprehensive understanding of relationships between habitat availability and the abundances of reef fishes.

CHAPTER 3: HABITAT USE OF CORAL-DWELLING FISHES AT MULTIPLE SPATIAL SCALES

3.1. ABSTRACT

Many species of coral-reef fishes associate with particular habitats, however, it is unclear how important these patterns of habitat use are in determining local and larger scale patterns of abundance. I examined patterns of habitat use and abundances of obligate coral-dwelling fishes (genus *Gobiodon*) within and among four geographic locations, from the southern Great Barrier Reef to northern Papua New Guinea. Two species, *G. histrio* and *G. brochus,* exhibited conservative patterns of habitat use within and among geographic locations. These species did not change the species of corals they usually inhabited despite changes in the diversity and relative abundances of corals within and among locations. For two other species, *G. axillaris* and *G. quinquestrigatus*, the species of corals usually inhabited changed among geographic locations. Plasticity in habitat use apparently enabled them to use abundant species of coral at any location and additional species at high diversity locations. Only one species, *G. rivulatus*, exhibited a pattern of habitat use that varied both within and among geographic location.

The abundances of each species of *Gobiodon* were apparently influenced by processes acting on a variety of spatial scales. The abundances of most species of *Gobiodon* were closely associated with the abundances of the corals they most frequently inhabited. Therefore, it appears that the availability of preferred habitats helps determine local abundances and patterns of abundance among geographic locations. In contrast, the abundance of *G. axillaris* was not closely associated with the abundance of the coral species it most frequently inhabited and factors other than habitat availability must determine local and larger-scale abundance of this species.

The abundances of *G. histrio, G. axillaris*, and *G. quinquestrigatus* were closely associated with particular reef zones and exposure regimes, independently of the abundance of corals. Therefore, these factors influence abundances within and among locations in addition to the availability of habitats. Multi-scale habitat

selection can most easily explain this hierarchical pattern of abundance. The abundances of these three species also varied among geographic locations, independently of coral abundances. This pattern indicates that regional-scale processes also influence abundances of these species among geographic locations. This study demonstrates that the abundances of habitat-specialised fishes may be closely associated with the availability of preferred microhabitats among widespread locations. However, even for these species, habitat selection may act at multiple spatial scales and variations in abundance among geographic locations are influenced by processes acting at larger spatial scales.

3.2. INTRODUCTION

Habitat selection is a prevalent ecological characteristic of animals (Orians and Wittenberger 1991, Rozenzweig 1991) that can dramatically influence the distribution and abundance of species at various spatial scales (Brown 1984, Morris 1992). If particular habitats consistently confer greater fitness than others, then use of these habitats could become a conservative feature of the animal's biology. Species exhibiting such conservative patterns of habitat use would be regarded as specialists (Futuyma and Moreno 1988). Alternatively, species may vary their patterns of habitats use, depending on the availability of habitats and the intensity of ecological interactions (Werner et al. 1983, Morris 1989). The degree of habitat specialisation exhibited by a species is predicted to have important implications for patterns of distribution and abundance (Fox and Morrow 1981, Brown 1984, Gaston and Lawton 1990, Rosenzweig and Lomolino 1997). Highly specialised species might exploit preferred habitats more effectively than generalist species but their distribution and abundance might be restricted by the availability of preferred habitats. In contrast, species that use a range of habitats may be less effective in exploiting the best habitats but their distribution and abundance are less likely to be restricted by the availability of particular habitats.

Although habitat preference helps determine the distribution and abundance of species, its influence is likely to vary with spatial scale (Morris 1992, MacNally

1995). As spatial scales increase, factors such as dispersal characteristics are likely to have increased importance in determining patterns of distribution and abundance (eg Butman 1987, Williams 1991, Cowen and Castro 1994, Palmer et al. 1996, Underwood and Chapman 1996). Recently, the importance of both local and regional processes has been emphasised in explaining similarities and differences among widely separated assemblages of animals (Ricklefs 1987, Menge and Olson 1990, Ricklefs and Schluter 1993, Caley 1995a, b, 1997, Caley and Schluter 1997, Cornell and Karlson 1996). In particular, attempts are being made to understand regional variation in the structure of animal assemblages by integrating ecological processes that operate on a local scale (eg habitat selection, competition, predation) with processes that can act on much larger scales (eg larval supply) (Hubbell 1997, Connolly and Roughgarden 1998). Multi-scale analyses and comparisons among geographic locations will be useful for distinguishing the spatial scales at which different processes operate (Ricklefs and Schluter 1993, Hughes et al.1999).

For species with a dispersive larval phase, such as coral-reef fishes and many other marine organisms, there is likely to be considerable variability among locations in the types of habitats available when settling to the benthic environment. Furthermore, due to the patchiness of the coral reef environment, there may be limited potential for movement to a more suitable location following settlement (Warner 1991). Therefore, these species might benefit from the ability to change their patterns of habitat use, depending on the types and abundances of habitats available where they settle. Such plasticity in habitat use might result in strong correlations between abundance and habitat availability at local scales but much weaker correlations as spatial scale increases. Alternatively, if particular habitats are strongly preferred and used in all locations, then both local and larger scale abundances may be closely associated with habitat availability.

Microhabitat associations have been widely reported among coral reef fishes (Jones 1991, Williams 1991, Munday and Jones 1998) and the potential influence of these associations on the distribution of reef fishes at local spatial scales (ie 10's -100's m) has been demonstrated by empirical observations (eg Williams 1980, Shulman 1984, Sale et al. 1984, Booth 1992, Munday et al. 1997) and experimental manipulations (eg Sweatman 1983, Wellington 1992, Tolimieri 1995, Gutiérez 1998, Öhman et al. 1998). For some species of coral reef fishes the local-scale distribution of the adult population is influenced by habitat selection during settlement or recruitment (Wellington 1992, Tolimieri 1995, Öhman et al. 1998, Gutiérrez 1998). For other species, patterns of habitat use change with ontogeny (McCormick and Makey 1997, Munday and Jones 1998).

Microhabitat associations also influence the abundance of some coral-reef fishes (Jones 1991). For example, local-scale abundances of coral-reef fishes have been correlated with coral cover (eg Bell and Galzin 1984, Bouchon-Navaro and Bouchon 1989, Jennings et al 1996, Munday et al. 1997), availability of shelter holes (Roberts and Ormond 1987, Hixon and Beets 1989, Buchheim and Hixon 1992), structural complexity (Luckhurst and Luckhurst 1978, Carpenter et al. 1981, 1996, Friedlander and Parish 1998) and microhabitat heterogeneity (Kaufman and Ebersole 1984). In contrast, other studies have found that the local-scale abundances of coral-reef fishes are not closely related to microhabitat characteristics (Robertson and Sheldon 1979, Wellington 1992, Sale et al. 1994, Green 1996). Therefore, it may only be among the more habitat specialised coral-reef fishes that microhabitat availability will substantially influence population densities.

Although patterns of habitat use among coral-reef fishes have been often examined at local scales (within and among reefs), rarely have comparisons been made among widespread locations. Consequently, it is not known whether patterns of habitat use are conservative features of a species biology or whether they change with habitat availability across larger spatial scales. Furthermore, the importance of habitat availability on the distribution and abundance of coral-reef fishes at larger spatial scales is poorly understood (Fowler et al. 1992). There is some indication that the importance of habitat associations in determining the distribution and abundance of coral-reef fishes may decline with increasing spatial scale (Tolimieri 1995, Caselle and Warner 1996). However, the importance of habitat availability in determining distributions and abundances of coral-reef fishes at regional or geographical scales (100's –1000's km) remains unknown.

Careful comparisons of population abundance and habitat correlates, sampled in the same manner at replicate sites within different locations, are useful for interpreting the importance of habitat availability on population dynamics at local and larger spatial scales (Caselle and Warner 1996, Tolimieri 1998). If habitat associations help determine abundances of reef fishes, we would expect a close relationship between the abundances of these species and the abundances of the habitats they use most frequently. Where habitat associations influence abundances in a similar manner at different locations, we would expect very similar relationships between habitat availability and fish abundances among locations (Fig 3.1a and 3.1b). If, however, abundances among locations are also influenced by processes operating on large spatial scales, we would expect similar, but separate, relationships between fish abundances and habitat availability (Fig 3.1c). A similar pattern might be observed if habitat associations influence abundances in a similar manner among locations but other local-scale processes (eg competition or predation) act with different intensities among locations. Alternatively, habitat availability might influence abundances at some locations but not others, resulting in a weak overall relationship between abundances and habitat availability among locations (Fig 3.1d).

If habitat availability does influence patterns of distribution and abundance among widespread locations, then this effect should be most apparent for species with strong habitat associations. Obligate coral-dwelling gobies from the genus *Gobiodon* are some of the most habitat specialised fishes on coral reefs and their distributions and abundances are influenced by habitat availability within and among reefs (Munday et al. 1997, Chapter 2). The abundances of some species of *Gobiodon*, however, appear to be more closely correlated to habitat availability across zones (10's m apart) than among sites (100's m apart) (Munday et al. 1997). The abundances of these species also appear to be influenced by physical characteristics of the reef location, such as exposure to prevailing winds (Munday et al. 1997, Chapter 2). Therefore, the distribution and abundance of coral-dwelling gobies among geographic locations might be influenced by a combination of factors including habitat availability, exposure regime, and processes influencing abundances on regional scales. In this study I examine patterns of habitat use among coral-dwelling gobies at four locations separated by 1000's km. Firstly, I determine whether patterns of habitat use are (1) conservative features of each species biology or (2) change with the availability of habitats within and among locations. I then examine the relationship between habitat availability, exposure regime, geographic location and the abundance of coral-dwelling gobies within and among geographic locations.

3.3. METHODS

Study species

Gobiodon species are small (< 60 mm total length) obligate coral-dwelling fishes (family Gobiidae) that live among the branches of corymbose and digitate corals mostly from the genus *Acropora* (Munday et al. 1997, 1999). Five species of *Gobiodon* that are abundant in Papua New Guinea and the Great Barrier Reef are considered in this study; *G axillaris*, *G. histrio*, *G. brochus*, *G. quinquestrigatus*, and *G. rivulatus* (Munday et al. 1999).

Study locations

Patterns of habitat use of coral-dwelling gobies were examined at four widely separated geographic locations, (1) One Tree Island (23^{0} 30' S; 152^{0} 06') on the southern Great Barrier Reef, (2) Lizard Island (14^{0} 40' S; 145^{0} 28' E) on the northern Great Barrier Reef, (3) Bootless Bay (09^{0} 31' S; 147^{0} 17' E) in southern Papua New Guinea and (4) Kimbe Bay (5^{0} 15' S; 150^{0} 15' E), in northern Papua New Guinea (Fig. 3.2). Detailed descriptions of the morphology and structure of reefs at each location are given in Heatwole (1981), Pichon and Morrissey (1981), Meekan et al. (1995), Weber (1973) and Holthus and Maragos (1996). The number of species of *Acropora*, which are the primary habitat of *Gobiodon* species, increases from 36 in the vicinity of One Tree Island, 49 at Lizard Island, 52 in the vicinity of Motupore Island, to 72 species in Kimbe Bay (Veron 1993, Wallace and Wolstenholme personal communications), providing a gradient of habitat diversity which might influence the patterns of habitat use of coral-dwelling gobies. Furthermore, there are changes in the relative abundances of species of corals across this geographic gradient which might influence the abundances of coral-dwelling gobies.

Exposure to prevailing winds appears to influence the abundances of *Gobiodon* among reefs within a location (Munday et al. 1997, Chapter 2). Therefore, the reefs at each geographic location were separated into exposed, moderate and sheltered exposures. Exposed reefs were classified as those reefs exposed to the prevailing winds and where waves break on the reef crest and flat for most of the year. Sheltered reefs were classified as reefs mostly protected from prevailing winds and where waves rarely break on the reef crest or flat. Moderate reefs were intermediate in exposure. Three representative sites were selected within each of these exposure regimes at each location (ie 36 sites total) (Fig. 3.2). Although there is undoubtedly considerable variation among locations in features such as the gross structure of reefs and the duration of prevailing winds, reefs within the three exposure regimes appeared to be broadly similar among locations.

Sampling design

To determine whether species of *Gobiodon* associate more frequently than expected with particular species of *Acropora*, and whether these associations change within and among geographic locations, I compared the observed distribution of *Gobiodon* among *Acropora* corals with that expected if each species of *Acropora* was used in proportion to its availability. The species of *Acropora* to be censused for *Gobiodon* were determined during a preliminary investigation of habitat use by *Gobiodon* at each location, where all species of *Acropora* were carefully searched for the presence of *Gobiodon*. I then censused *Gobiodon* in all colonies of *Acropora* species used by *Gobiodon*, within random transects on the reef flat at each site. In addition to determining habitat selection by species of *Gobiodon*, this sampling design allowed me to examine relationships between the abundances of *Gobiodon* and the abundances of coral species within and among exposure levels and geographic locations. To examine relationships between the abundances of *Gobiodon* and the abundances of coral species across reef zones, I extended the sampling design to the reef crest and slope at all moderately exposed sites, except for sites in Bootless Bay. Reefs in Bootless Bay did not have distinct crest and slope zonation, therefore, it was not possible to sample across reef zones in this location.

At each site, five replicate 10m x 1m belt transects were established on the outer reef flat, running roughly parallel to the reef crest. At each moderately exposed site, five transects were also laid along the contour of the reef crest and along the middle of the reef slope. The starting position of each transect was haphazardly selected. A 10m tape was placed along the centre of the transect and a 1m plastic bar was used to measure the transect width. Each coral colony of *Acropora* species used by *Gobiodon,* located at least half within the transect and with a diameter greater than 5 cm, was carefully searched for *Gobiodon* with the aid of a small underwater light. Gobies always remained within coral colonies during the census.

Analysis of habitat use

Log-linear modelling and resource selection ratios were used to compare patterns of habitat use within and among locations. Firstly, log-linear models were used to determine whether patterns of habitat use were consistent within and/or among locations. In this analyses the frequency distribution of fish among species of corals was compared to the proportional availability of the coral species at each combination of geographic location and exposure. Resource selection ratios were then used to determine the particular species of corals that were used more frequently than expected by each species of *Gobiodon.* In this analysis the proportional use of each coral species was compared to its proportional availability.

Log-linear modelling is a powerful method for analysing changes in habitat use that could be related to a variety of extrinsic factors (Heisey 1985, Manly et al. 1993). Here these extrinsic factors are geographic location (southern GBR, northern GBR, southern PNG, northern PNG) and exposure regime (sheltered, moderate, exposed). To examine the frequency distribution of each species of *Gobiodon* among the corals available at each geographic location and each exposure level, I used a series of models with increasing complexity. The models were (1) habitat use proportional to habitat availability within and among locations, (2) habitat use disproportionate to availability but the pattern of habitat use uniform within and among locations, (3) habitat use disproportionate to availability but the pattern varies among geographic locations, (4) habitat use disproportionate to availability but the pattern varies among exposures and, (5) habitat use disproportionate to availability but the pattern varies among geographic locations and exposures. The models were tested sequentially, until there was no significant improvement in the difference of the goodness-of-fit statistic (likelihood ratio chi-square) from one model to the next. Manly et al. (1993) provide a more detailed explanation of this method for testing habitat use.

The nine species of coral most commonly used by species of *Gobiodon*, and present at each location, were used in the log-linear analyses. These corals were *Acropora cerealis, A. digitifera, A. gemmifera, A. humilis, A. millepora, A. nasuta, A. secale, A. tenuis* and *A. valida*. *Gobiodon brochus* frequently uses *A. loripes* but neither species was found in Kimbe Bay. Therefore, the model for *G. brochus* included *A. loripes* but not Kimbe Bay. Application of log-linear modelling to analysis of habitat use requires that observations are independent (Manly et al. 1993). Aggregations of *Gobiodon* individuals of the same species within coral colonies would violate this assumption if total abundance data were used. Therefore, to ensure independence of habitat use observations, presence or absence of each *Gobiodon* species per colony was used, as recommended by Thomas and Taylor (1990). Rarely were more than two individuals of any species of *Gobiodon* found in a coral colony, therefore, the use of presence – absence data did not bias estimates of habitat use among coral species. Data were then pooled within exposure levels at each location to provide adequate cell counts for reliable analysis.

Among the species of *Gobiodon* tested, patterns of habitat use frequently changed among locations but rarely changed among exposures. To determine whether the greater frequency of changes in habitat use among locations, in comparison to exposures, was associated with larger changes in the structure of the coral community among locations, I examined the heterogeneity of coral community structure within and among locations. Heterogeneity at each site was estimated for the nine coral species used in previous analyses, using the Shannon-Weiner Index:

$$H = \sum (p_i)(\log p_i)$$

Where p_i is the proportion of the raw total number of corals sampled at each site belonging to species *i*. A two way, fixed factor ANOVA was then used to examine variation in heterogeneity (Shannon-Weiner Index) within and among locations.

Resource selection ratios were used to determine the particular corals that each species of *Gobiodon* used more frequently than expected. Resource selection ratios compare the proportion of resources used to the proportion of resources available. Resource selection ratios are preferred over more commonly used methods of determining habitat preferences because they are robust to decisions made about the types of habitats included in the analysis (Manly et al. 1993).

The nine species of coral used in the log-linear analyses were used in the calculation of selection ratios. In addition, three other coral species (*Acropora* sp., *A. loripes* and *A. selago*) commonly used by some species of *Gobiodon*, but present at only some locations, were included in the analyses. These corals could be included because separate selection ratios were calculated for each location for every species of *Gobiodon*. Selection ratios (w_i) were estimated using the formula:

$$w_i = o_i/a_i$$

where o_i is the proportion of the total coral colonies occupied by a species of *Gobiodon* for coral species *i*, and a_i is the proportion of total available coral colonies for coral species *i*.

To determine if corals were used in proportion to their availability, used more frequently that expected from their availability, or used less frequently than expected, a Bonferroni corrected 95% confidence interval was estimated for each selection ratio using the formula:

$$Z_{a/2k}\sqrt{\left\{o_i\left(1-o_i\right)/\left(u_+a_i^{\,2}\right)\right\}}$$

where $z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $\alpha/2k$, $\alpha = 0.05$, k = the number of coral species, o_i is the proportion of the total coral colonies occupied by a species of *Gobiodon* for coral species i, u_+ is the total number of coral colonies used, and a_i is the proportion of total available coral colonies for coral species i. The use of a coral species was considered to be proportional to its availability when the 95% confidence interval of its selection ratio encompassed 1 (Manly et al. 1993). A species of coral was otherwise considered to be used disproportionately to its availability.

Analysis of variation in abundance

Log-linear models and selection ratios only examine the frequency distribution of the habitats used in relation to the proportion available, they provide no information on the relationship between the absolute abundance of coral gobies and the absolute abundances of the corals at the different spatial scales sampled. Stepwise multiple regression (forward selection, $p = 0.05$ for retention and deletion of variables) was used to examine the relationship between the abundance of each species of *Gobiodon*, geographic location, exposure level and the abundance of each coral species. If the availability of preferred corals were the only variables influencing the abundances of gobies within and among locations, then those coral species should be the only significant variables retained in the regression model. However, if regional effects also contribute to the patterns of abundance among locations, then one or more locations will be a significant factor in the model. Similarly, if exposure levels help determine variation in abundances they will be a significant factor in the model. Stepwise multiple regression was also used to examine the relationship between the abundance of each species of *Gobiodon*, geographic location, reef zone, and the abundance of coral species. Exposure level was not included in this analysis because the reef crest and reef slope were only sampled at moderate exposure sites. Southern PNG was omitted from the analysis that included reef zones because reefs in this location did not exhibit distinct zonation.

The inclusion of categorical variables, such as location, exposure and zone, requires the use of contrast groups (Aiken and West 1991). Southern GBR, exposed reefs, and reef flat were arbitrarily selected as the contrast groups in the respective analyses.

Abundances among locations, exposures and zone were compared to these contrast groups when interpreting each analysis. For each comparison the magnitude of the regression coefficient is a direct indicator of the difference between the variable of interest and it's contrast group. Abundances of fish and corals per transect were transformed [log(x +1)] to improve the distribution of residuals.

3.4. RESULTS

Habitat use

The absolute and relative abundances of coral species inhabited by *Gobiodon* varied among geographic locations (Fig. 3.3). Each species of *Gobiodon* inhabited one or more of these species of coral more frequently than expected from their availability, occurred significantly less frequently than expected in a range of coral species and inhabited a number of other species approximately in proportion to their availability. However, species of *Gobiodon* differed in the consistency of these patterns of habitat use among geographic location and exposures (Table 3.1). *Gobiodon brochus* exhibited a very conservative pattern of habitat use (Table 3.1). It used *A. loripes* and *A. tenuis* more frequently than expected, rarely used any other species of coral, and this pattern of habitat use was constant among locations (Tables 3.2).

For *G. histrio* the difference in deviance between models 3 and 4 was only just significant (Table 3.1, $p = 0.44$), also the deviance value for model 3 is already non significant, indicating that model 3 is not significantly different from the saturated model. Therefore, *Gobiodon histrio*'s overall pattern of habitat use changed among locations, but not among exposures (Table 3.1). However, *G. histrio* used only one coral species, *A. nasuta*, more frequently than expected at all geographic locations (Table 3.2). Changes in the overall pattern of habitat use of *G. histrio* were due to changes in the relative frequency of use of non-preferred corals (Table 3.2). Therefore, *G. histrio* also exhibited a conservative pattern of habitat use.

Patterns of habitat use by *G. axillaris* and *G. quinquestrigatus* clearly differed among locations, but not among exposures (Table 3.1). *Gobiodon axillaris* inhabited *A.*

nasuta more frequently than expected at most locations but was largely confined to *A. digitifera* in northern PNG (Table 3.2). Changes in habitat use among locations for this species were largely due to an increasing use of *A. digitifera* and a decreasing use of *A. valida* from the southern GBR to northern PNG (Table 3.2). *Gobiodon quinquestrigatus* used between one and four species of corals more frequently than expected at each location and these species varied among locations (Table 3.2). In particular, *G. quinquestrigatus* exhibited a preference for *A. nasuta* at both locations on the GBR but more frequently used the closely related *A. cerealis* at both locations in PNG. In addition, *G. quinquestrigatus* was the only species to select *A. selago* and *Acropora* sp. which were abundant on reefs in northern PNG (Table 3.2). Although the pattern of habitat use by *G. quinquestrigatus* varied greatly among locations, habitat use did not vary significantly among exposures (Table 3.1).

Patterns of habitat use by only one species, *G. rivulatus*, varied with both location and exposure regime (Table 3.1). *Acropora gemmifera* and/or *A. secale* were the most frequently used corals at each location, however, a decline in the use of *A. gemmifera* on the southern GBR combined with an increased use of *A. humilis* appears to drive the significant differences in habitat use among locations (Table 3.2). Examination of selection ratios for each exposure at each location revealed no apparent structure in the way that selection for *A. gemmifera*, *A. secale* and *A. humilis* differed among exposures (Table 3.3). However, two forms of *G. rivulatus* (dark and light) were observed during this study and the dark form was usually found in *A. secale* while the light form was more often observed in *A. gemmifera* (Table 3.3).

Heterogeneity in coral assemblage structure varied jointly with geographic location and exposure (Table 3.4). Also, changes in coral assemblage structure were of equivalent magnitude among locations (Fig 3.4; heterogeneity range from 0.551 at south GBR to 0.817 at north PNG) and among exposures within locations (Fig 3.4; heterogeneity range from 0.523 to 0.817 at north PNG). Therefore, the greater frequency of change in patterns of habitat use among geographic locations, compared to exposures, was not associated with greater changes of coral assemblage structure among locations compared to exposures.

Variation in abundance: correlations with abundances of corals

The abundance of each species of *Gobiodon* varied among geographic locations and exposures (Fig. 3.5). For several species of *Gobiodon* these patterns of abundance were associated with the abundances of the corals they most frequently inhabited (Table 3.5). The abundance of *G. brochus* was correlated with the abundance of *A. loripes* and, to a lesser extent, *A. tenuis*. The abundance of *G. histrio* was correlated with the abundance of *A. nasuta* and less closely with *A. millepora* and *A. tenuis*. *Gobiodon rivulatus* was correlated with the abundance of *A. gemmifera* and less closely with *A. humilis* and *A. nasuta* (Table 3.5).

The abundance of *G. quinquestrigatus* was correlated with the abundance of *A. cerealis* and *A. nasuta*, two of the corals it most frequently inhabited at several locations (Table 3.5). However, the abundance of *G. quinquestrigatus* was not correlated with the abundance of *A. valida*, *A. selago* or *A.* sp., corals which were frequently inhabited at some locations. The abundance of *G. axillaris* was correlated with *A. digitifera* and *A. nasuta*, but the coefficients were not large (Table 3.5).

Variation in abundance: influence of exposure level

If the availability of preferred corals were the only variables influencing the abundances of *Gobiodon* within and among locations, then those corals should be the only variables retained in the regression model. However, exposure regime was a significant factor in the regression equations for all species of *Gobiodon* (Table 3.5). Independently of the availability of corals, *Gobiodon brochus* was slightly more abundant in sheltered sites, compared to exposed sites. The abundance of *G. histrio* was considerably higher at sheltered sites in comparison to exposed and moderate sites. In direct contrast, *G. axillaris* much less abundant at sheltered sites in comparison to exposed and moderate sites. *Gobiodon quinquestrigatus* was significantly more abundant at sheltered and moderate locations compared to exposed sites. *Gobiodon rivulatus* was more abundant at moderate sites than exposed sites, regardless of the corals usually inhabited (Table 3.5).

Variation in abundance: influence of geographic location

Geographic location had a significant effect on the abundance of three species; *G. histrio, G. axillaris* and *G. quinquestrigatus*, independently of coral availability (Table 3.5). The abundance of *G. histrio* was significantly higher on the northern GBR, southern PNG and northern PNG in comparison to the southern GBR. The magnitude of the coefficients indicate that *G. histrio* was approximately twice as abundant at the locations in Papua New Guinea compared to the Great Barrier Reef. *Gobiodon quinquestrigatus* was also more abundant in southern PNG and northern PNG than at either of the GBR locations (Table 3.5). In contrast *G. axillaris* was less abundant at the locations in Papua New Guinea than on the Great Barrier Reef. Geographic location did not appear to influence the abundance of *G. brochus* or *G. rivulatus* (Table 3.5).

Variation in abundance: influence of reef zone

The abundance of each species of *Gobiodon* varied among reef zone (Fig. 3.6). Multiple regression analysis indicated that abundances of *G. histrio*, *G. quinquestrigatus* and *G. axillaris* were associated with particular reef zones, independently of coral availability (Table 3.6). *Gobiodon histrio* was more abundant on the reef crest than the reef slope or flat. *Gobiodon quinquestrigatus* was more abundant on the reef crest and reef slope compared to the reef flat (Table 3.6). Reef zone did not appear to influence the abundance of *G. brochus* or *G. rivulatus* (Table 3.6).

Across reef zones the abundances of *G. histrio* and *G. quinquestrigatus* were correlated with the abundances of their preferred corals (Table 3.6). *G. histrio* was positively correlated with *A. nasuta*, while the abundance of *G. quinquestrigatus* was positively correlated with the abundance of *A. cerealis*, *A. nasuta* and *Acropora sp.* In contrast, *G. axillaris* was not closely correlated with the abundance of preferred corals across reef zones. *G. axillaris* was less abundant on the reef slope than the crest or reef flat and was only weakly correlated with the abundance of *A. digitifera* (Table 3.6). *Gobiodon brochus* was only weakly correlated with the abundance of *A. loripes*, the coral species it usually inhabited. *Gobiodon rivulatus* was positively correlated with the abundance of frequently used corals *A. digitifera, A. gemmifera, A, secale* and also with *A. loripes.*

TABLE 3.1. Analysis of habitat use among geographic locations and exposure regimes by species of *Gobiodon*. Models were tested sequentially. Geographic location rather than exposure is shown at the third level because it resulted in a better fitting model for all species tested. The best fitting model is underlined for each species. *= $0.01<P<0.05$, ** = $0.001<P<0.01$, ***= $P<0.001$, ns = not significant.

Species	Model	*deviance*	*df*	*difference*	*df*
G. brochus	habitat use proportionate to availability	226.1 ***	81		
				205.62 ***	9
	habitat use disproportionate to availability but pattern uniform within and among locations	20.48 ns	72		
				13.18 ns	18
	habitat use disproportionate to availability but pattern varies with location	7.3 ns	54		
				7.17 ns	18
	habitat use disproportionate to availability but pattern varies with location & exposure	0.128 ns	36		
G. histrio	habitat use proportionate to availability	695.4 ***	96		
				570.31 ***	8
	habitat use disproportionate to availability but pattern uniform within and among locations	125.09 **	88		
				65.36 ***	24
	habitat use disproportionate to availability but pattern varies with location	59.73 ns	64		
				26.81 (0.044)	16
	habitat use disproportionate to availability but pattern varies with location & exposure	32.92 ns	48		
G. axillaris	habitat use proportionate to availability	504.95 ***	96		
				272.04 ***	8
	habitat use disproportionate to availability but pattern uniform within and among locations	232.91 ***	88		
				192.05 ***	24
	habitat use disproportionate to availability but pattern varies with location	40.86 ns	64		
				21.29 ns	16
	habitat use disproportionate to availability but pattern varies with location & exposure	19.57 ns	48		
G. quinquest.	habitat use proportionate to availability	546.11 ***	96		
				372.08 ***	8
	habitat use disproportionate to availability but pattern uniform within and among locations	174.03 ***	88		
				118.99 ***	24
	habitat use disproportionate to availability but pattern varies with location	55.04 ns	64		
				25.45 ns	16
	habitat use disproportionate to availability but pattern varies with location & exposure	29.59 ns	48		
G. rivulatus	habitat use proportionate to availability	566.64 ***	96		
				332.43 ***	8
	habitat use disproportionate to availability but pattern uniform within and among locations	234.21 ***	88		
				129.35 ***	24
	habitat use disproportionate to availability but pattern varies with location	104.86 **	64		
				47.46 ***	16
	habitat use disproportionate to availability but pattern varies with location & exposure	57.4 ns	48		

TABLE 3.2. Significance of habitat use (coral spp.) by *Gobiodon* species at four geographic locations using selection ratios and Bonferroni corrected 95% confidence intervals. NS: habitat used in proprtion to availability, +: habitat used significantly more than expected, -: habitat used significantly less than expected.

Species	Location	*A. cerealis*	*A. digitifera*	*A. gemmifera*	*A. humilis*	*A. millepora*	*A. nasuta*	*A. secale*	*A. tenuis*	*A. valida*	*A. loripes*	*A. selago*	*A. sp.*
G. brochus	sth GBR	-	-	-	-	-	-	-	+	NS	+		
	nth GBR	-	-	-	-	-	-	-	+	-	+		
	sth PNG	-	-	-	-	-	-	-	+	NS	+	-	
G. histrio	sth GBR	-	-	-	-	NS	+	-	NS	-	-		
	nth GBR	-	NS	-	-	NS	+	-	NS	NS	-		
	sth PNG	-	NS	-	-	-	+	-	-	NS	-	-	
	nth PNG	-	NS	-	-	NS	+	-	NS	NS		-	-
G. axillaris	sth GBR	-	-	-	-	NS	+	-	-	NS	-		
	nth GBR	NS	NS	-	-	+	+	NS	-	NS	-		
	sth PNG	-	NS	-	-	-	+	-	-	-	-	-	
	nth PNG	-	+	-	-	NS	NS	-	-	-		-	-
G. quinqest.	sth GBR	NS	-	-	NS	-	+	-	-	+	NS		
	nth GBR	NS	-	-	NS	NS	+	NS	NS	NS	NS		
	sth PNG	+	-	-	NS	+	-	-	-	NS	NS	NS	
	nth PNG	+	-	-	NS	-	-	-	NS	+		+	+
G. rivulatus	sth GBR	-	NS	NS	+	-	-	+	NS	NS	-		
	nth GBR	NS	NS	+	NS	-	-	NS	-	-	NS		
	sth PNG	NS	NS	+	NS	-	-	+	-	NS	-	-	
	nth PNG	NS	-	+	NS	-	-	+	-	NS		-	-

TABLE 3.3. Significance of habitat use by *Gobiodon rivulatus* at exposed, moderate and sheltered exposures at each geographic location. NS: habitat used in proprtion to availability, +: habitat used significantly more than expected, -: habitat used significantly less than expected.

Location	Exposure	*A. cerealis*	*A. digitifera*	*A. gemmifera*	*A. humilis*	*A. millepora*	*A. nasuta*	*A. secale*	*A. tenuis*	*A. valida*	*A. loripes*	*A. selago*	*A. sp.*
southern GBR	exposed	-	NS	-	NS	-	-	NS	-	NS			
	moderate	-	NS	-	+	-	-	NS	NS	NS			
	sheltered	-	NS	NS	-	-	-	NS	NS	NS	-		
northern GBR	exposed	NS	NS	+	NS	-	NS	NS	-	-	NS		
	moderate	NS	NS	+	NS	NS	-	NS	-	-	NS		
	sheltered	-	-	+	NS	-	-	-	-	-	NS		
southern PNG	exposed	NS	-	+	NS	-	-	-	-	NS	-		
	moderate	NS	NS	NS	NS	NS	-	NS	NS	-	-		
	sheltered	NS	-	+	NS	-	-	+	-	-	-	-	
northern PNG	exposed	-	-	+	NS	-	-	+	-	NS		-	-
	moderate	-	-	+	NS	-	-	+	-	-		-	-
	sheltered	NS	-	+	-	-	-	NS	-	NS		-	-

TABLE 3.4. ANOVA results for heterogeneity of coral assemblage structure among geographic locations and exposures. Abundance of corals were pooled at the level of site and heterogeneity estimated using the Shannon-Weiner Index.

Source of variation	df	MS	*F*	*p*
Geographic location	3	0.028	5.73	0.004
Exposure	2	0.033	6.812	0.005
Geographic location*Exposure	6	0.026	5.284	0.001
Error	24	0.0048		

TABLE 3.5. Results of stepwise regression analysis on abundance of fish (dependent variable) and corals in transects on the reef flat at all exposures and locations. Only significant coefficients are shown. Southern GBR and exposed reefs are the contrast groups for categorical variables.

Variable	*G. brochus*	*G. histrio*	*G. axillaris*	*G. quinqestrigatus*	*G. rivulatus*
constant	-0.03	-0.37	0.34	-0.28	0.29
north GBR		0.22			
south PNG		0.44	-0.39	0.30	
north PNG		0.41	-0.21	0.25	
sheltered	0.07	0.28	-0.22	0.37	
moderate				0.11	0.13
A. cerealis			-0.26	0.39	
A. digitifera			0.25		
A. gemmifera					0.54
A. humilis					0.30
A. loripes	0.64				
A. millepora		0.16			
A. nasuta		0.66	0.31	0.41	
A. secale				0.21	0.19
A. selago					
A. sp.					
A. tenuis	0.33	0.28			
A. valida			0.16		
adj. r squared	0.56	0.72	0.58		0.50

TABLE 3.6. Results of stepwise regression analysis on abundance of fish (dependent variable) and corals in transects across reef zones at moderately protected sites on the southern GBR, northern GBR and northern PNG. Only significant coefficients are shown. Southern GBR and reef flat are the contrast groups for categorical variables.

Variable	*G. brochus*	*G. histrio*	*G. axillaris*	*G. quinqestrigatus*	*G. rivulatus*
constant	0.001	-0.2	0.54	0.15	0.27
north GBR		0.27		-0.20	
north PNG		0.28	-0.45		
reef crest		0.20		0.20	
reef slope			-0.14	0.38	
A. cerealis				0.65	
A. digitifera			0.26	-0.29	0.24
A. gemmifera					0.59
A. humilis					
A. loripes	0.26		-0.50	-0.53	0.77
A. millepora					
A. nasuta		0.59		0.49	
A. secale					0.35
A. selago		-0.48			
A. sp.				0.63	-0.44
A. tenuis					
A. valida					
adj. r squared	0.18	0.50	0.59	0.63	0.60

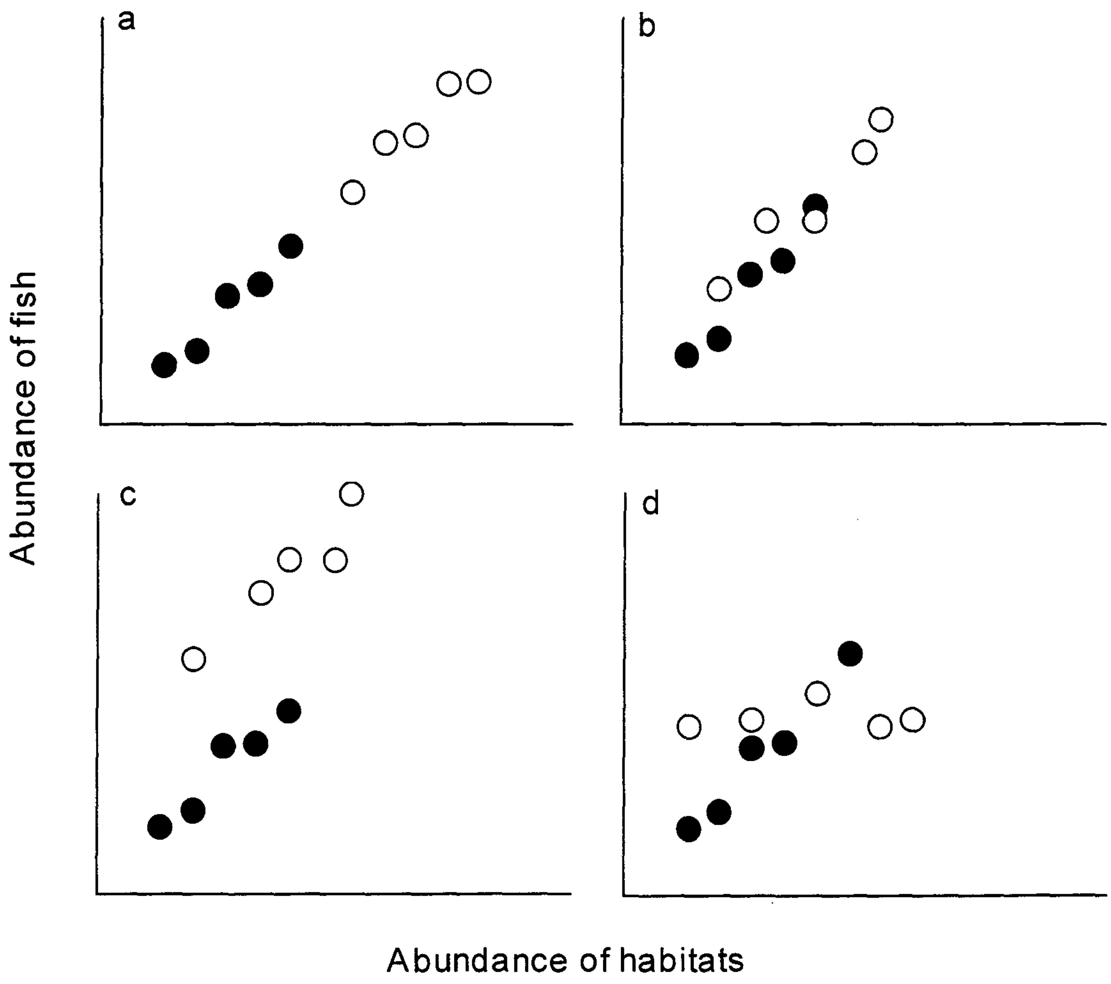
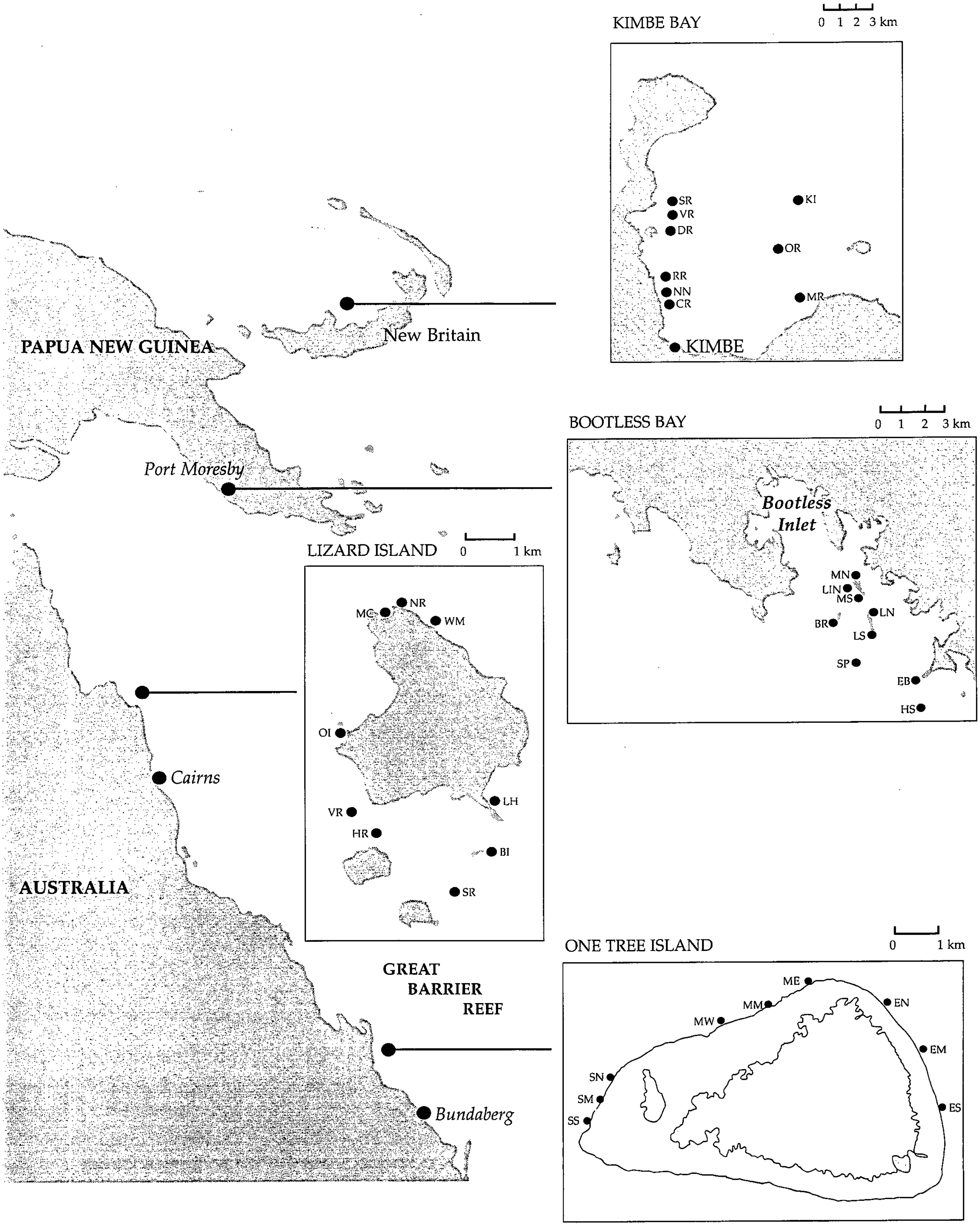


Fig. 3.1. Predicted relationship between habitat abundance and fish abundance at two locations (open vs closed circles) where (a, b) habitat associations influence abundances in a similar manner between locations, (c) abundances between locations are also influenced by processes on large spatial scales and (d) habitat availability influences abundance at only one location.

Fig. 3. 2. Study sites at (1) Kimbe Bay, PNG; exposed sites; KI = Kimbe Island, OR = Otto Reef, MR = Margets Reef; moderate sites, SR = Susans Reef, VR = Vanessas Reef, DR = Donnas Reef; sheltered sites, RR = Rosmaries Reef, NN = Noname Reef, CR = Crater Reef. (2) Bootless Bay, PNG; exposed sites, EB = End Bommie, HR = Horseshoe Reef, SP = South Patch; moderate sites, BR = Big Reef, LS = Loloata Island south, MS = Motupore Island south; sheltered sites, LN = Loloata Island north, MN = Motupore Island north, LIN = Lion Island north. (3) Lizard Island, Great Barrier Reef; exposed sites, LH = Lizard Head, BI = Bird Islet, SR = South Reef; moderate sites, WM = Washing Machine, NR = North Reef, MC = Mermaid Cove; sheltered sites, OI = Osprey Island, VR = Vickis Reef, HR = Horseshoe Reef. (4) One Tree Island, Great Barrier Reef; exposed sites, ES = East Wall south, EM = East Wall mid, EN = East Wall north; moderate sites, ME = moderate east, MM = moderate mid, MW = moderate west; sheltered sites, SN = sheltered north, SM = sheltered mid, SS = sheltered south.


KIMBE BAY
0 1 2 3 km
SR
VR
DR
KI
OR
RR
NN
CR
MR
KIMBE
New Britain
PAPUA NEW GUINEA
BOOTLESS BAY
0 1 2 3 km
Bootless Inlet
MN
LIN
MS
LN
BR
LS
SP
EB
HS
Port Moresby
LIZARD ISLAND
0 1 km
NR
MC
WM
OI
LH
VR
HR
BI
SR
Cairns
AUSTRALIA
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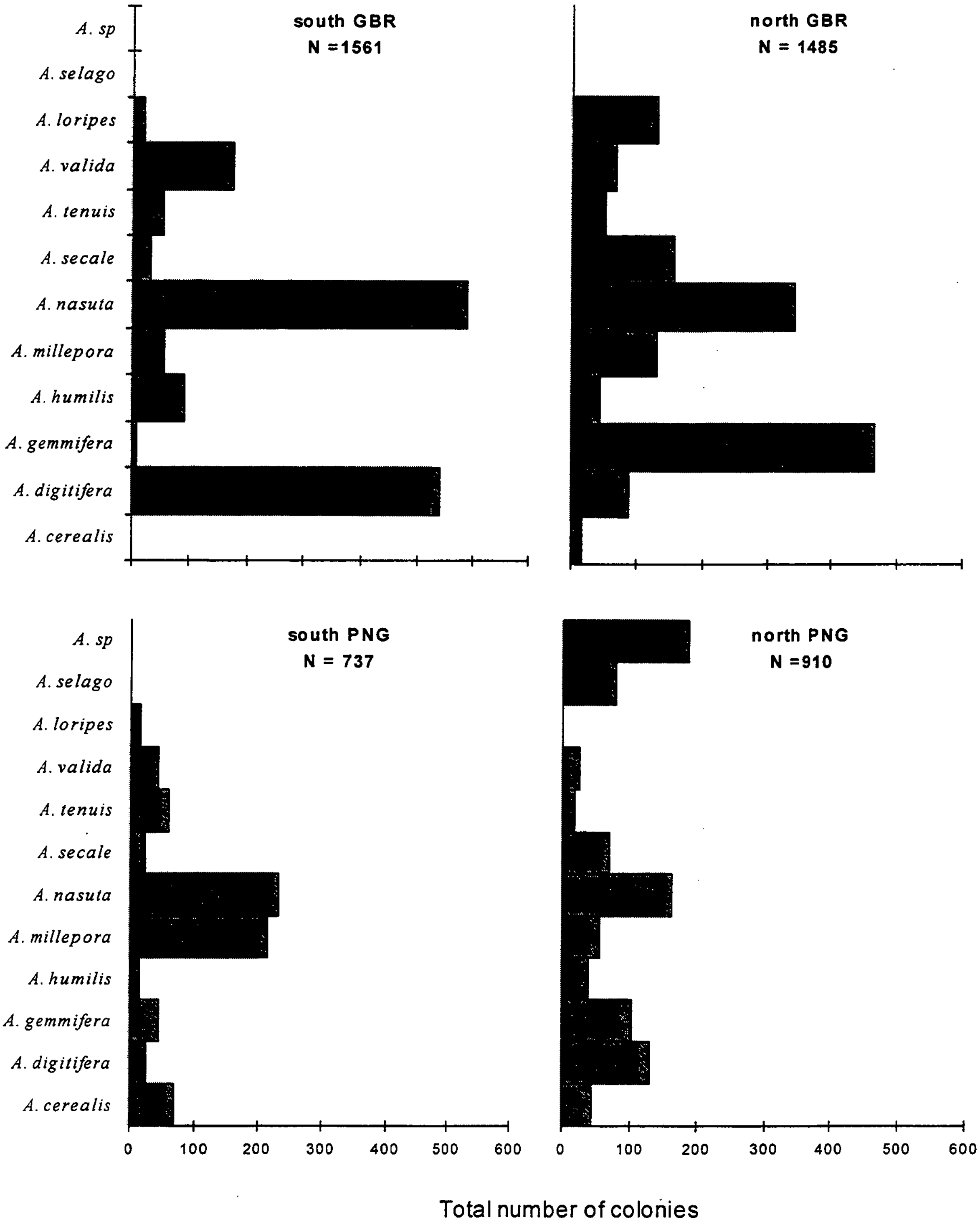

Fig. 3.3. Total number of coral colonies censused of species used by *Gobiodon* at each geographic location.

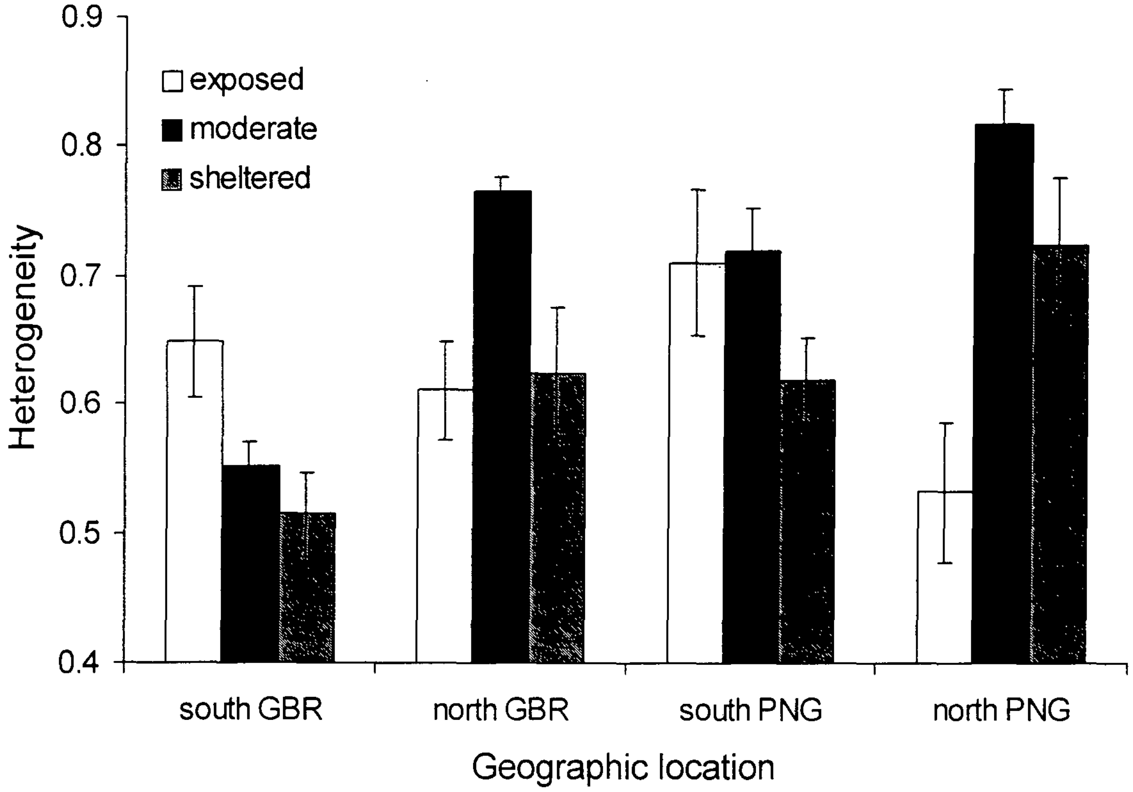

Fig. 3.4 Heterogeneity (mean ± SE) of coral assemblage at each exposure and geographic location. Shannon-Weiner Index used to estimate heterogeneity from the pooled abundance of the nine most commonly used corals at each site.

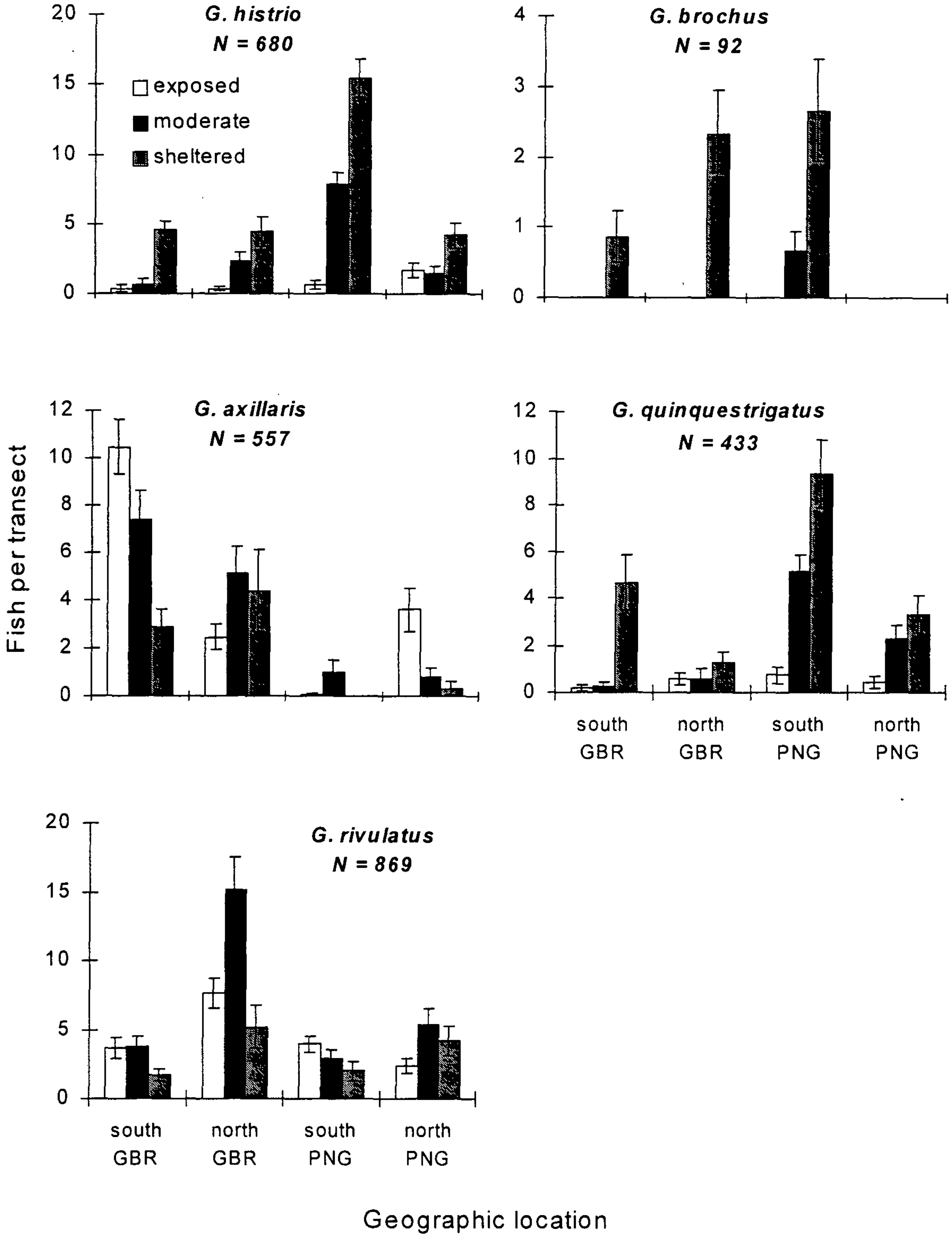

Fig 3.5. Number of fish per transect (mean ± SE), for each species of *Gobiodon*, at each geographic location and exposure level.

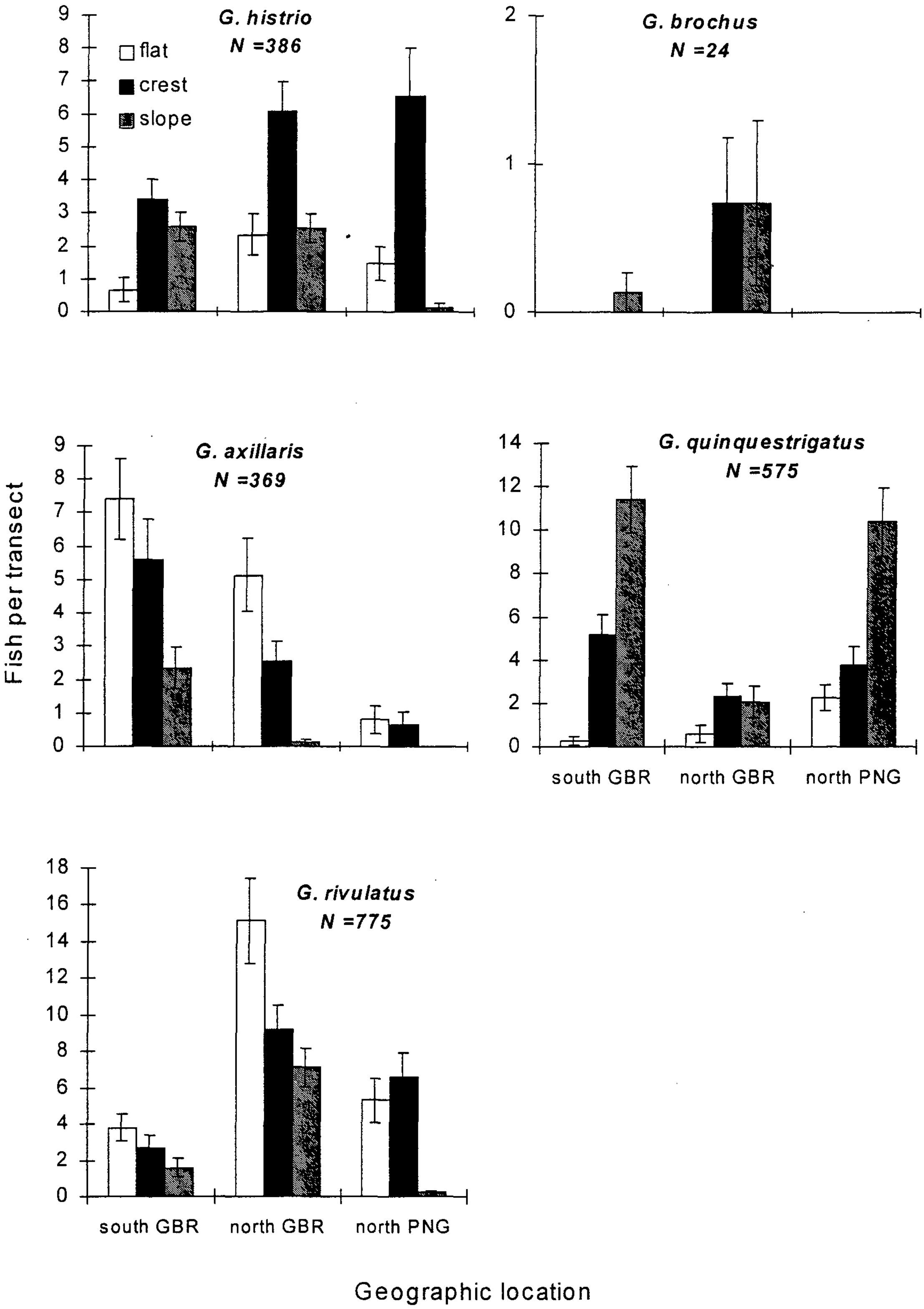

Fig. 3.6 Number of fish per transect (mean ± SE), for each species of *Gobiodon*, across reef zones at moderately exposed sites.

3.5. DISCUSSION

Habitat use

Although habitat specialisation is predicted to influence the distribution and abundance of species both (Brown 1984, Gaston and Lawton 1990), very little is known about how patterns of specialisation might vary within and among locations (MacNally 1995). Each species of *Gobiodon* considered here inhabited one or more species of *Acropora* more frequently than expected from the availability of these corals. Therefore, species of *Gobiodon* may be regarded as habitat specialists in a broad sense. However, the consistency of patterns of habitat use among geographic locations and exposure levels varied substantially among the species studied.

Two species, *G. histrio* and *G. brochus* exhibited very conservative patterns of habitat use within and among locations. Despite an increasing diversity of suitable acroporid species from the southern GBR to northern PNG, and changes in the relative abundances of corals among locations, these species of fish consistently inhabited the same species of coral. Such conservative patterns of habitat use among widespread locations might be expected if (1) the corals inhabited offer considerable fitness benefits and/or (2) interspecific interactions operate in a similar manner at each location, thereby producing similar patterns of habitat use. *Acropora nasuta*, the coral most frequently inhabited by *G. histrio*, has a complex but relatively open branching structure, that favours growth and survival (Chapters 5 and 6). Furthermore, in tank experiments, *G. histrio* was found to be a superior competitor to the other species considered here (Chapter 4). Therefore, the conservative pattern of habitat use by *G. histrio* appears to be the result of a superior competitor using the best habitat. The corals most frequently used by *G. brochus*, however, do not favour growth or survival of this species (Chapter 5 and 6). Similar patterns of habitat use among locations for *G. brochus* are more likely the result of similar interspecific interactions at different locations producing similar patterns of habitat use.

In contrast to the conservative pattern of habitat use exhibited by *G. histrio* and *G. brochus*, the coral species most frequently used by *G. axillaris* and *G. quinquestrigatus* changed among locations. The diversity and abundances of coral species changed among locations and flexibility in habitat use apparently enabled these species of *Gobiodon* to make use of new or abundant coral species at each location. The greatest plasticity in habitat use was observed in *G. quinquestrigatus*, which was positively associated with a total of six different coral species among the four geographic locations and was the only species to frequently use *A. selago* and *Acropora* species, which were abundant at the PNG locations but not at the GBR locations. Only one species, *G. rivulatus*, exhibited changes in habitat use with both geographic location and exposure level. For this species, however, two colour morphs were identified and changes in habitat use among exposures could be due to differences in habitat preferences of the colour morphs. For all species of *Gobiodon*, including *G. rivulatus*, the inclusion of geographic location rather than exposure in log-linear models resulted in a better-fitting model. Therefore, patterns of habitat use were more consistent among exposures than among locations. However, community structure of the nine most commonly inhabited coral species was similar among exposure regime and geographic location. Therefore, variation in coral community structure does not appear to explain the greater frequency of changes in habitat use at the level of geographic locations compared to exposures.

Variation in abundance

There has been considerable debate about the importance of habitat availability in determining abundances of coral-reef fishes. This study and others (Kuwamura et al. 1994, Clarke 1996, Munday et al. 1997) indicate that abundances of habitat specialist fishes often appear to be strongly influenced by the availability of specific microhabitats. Moreover, this study demonstrates that these correlations may hold among geographic locations. In particular, the abundance of two species, *G. brochus* and *G. rivulatus*, were closely associated with the availability of preferred corals but not with other variables such as reef zone, exposure or geographic location. Therefore, the among geographic location distribution and abundance of these species appears to be primarily influenced by the availability of suitable corals. This conforms to the first model of habitat-fish abundances (Fig. 1a and 1b).

The abundance of *G. axillaris*, *G. histrio* and *G. quinquestrigatus* were associated with particular reef zone, independently of the corals available across zones. These same species were also associated with particular exposure regimes independently of coral abundances. Although a variety of processes could produce these patterns, they are most easily explained by multi-scale habitat selection. Habitat selection at the scale of individual coral heads is common among coral reef fishes at the time of settlement (Sweatman 1983, Sale et al. 1984, Shulman 1984, Booth 1992, Öhman et al. 1998). Habitat selection is also known to occur at the scale of reef zones (Wellington 1992, Gutiérrez 1998) and some species appear to select habitats for settlement at whole-reef scales (Doherty et al. 1996). Indeed larvae of reef fishes competent to settle are capable of directed movement at scales that can influence their distributions over whole reefs (Leis et al. 1996, Stobutzki and Bellwood 1994, 1997). Alternatively, they might make use of hydrodynamic characteristics that could result in differential reef-scale distributions (Cowen and Castro 1994). *Gobiodon* settling to the reef might first select the broad environment preferred (ie reef crest on sheltered reefs for *G. histrio*), either by directed movement to that environment, or selection of hydrodynamic characteristics that favour transport to those sites. Within these sites they may then select habitat at the scale of individual coral colonies.

The abundances of *G. axillaris*, *G. histrio*, and *G. quinquestrigatus* also vary among geographic locations, independently of reef zone, exposure level and the corals available at these locations. In addition to processes acting at the local scale these species are apparently influenced by processes acting on regional or geographical scales. This is the second model of habitat-fish abundances (Fig. 1c). Processes influencing the abundance of coral-reef fishes on these spatial scales are not well understood (Thresher 1991). However, patterns of larval supply help determine geographical patterns of abundance in other marine animals (Butman 1987, Alexander and Roughgarden 1996, Connolly and Roughgarden 1998) and could account for the patterns observed here. Larvae may be preferentially advected to particular locations or conditions in the plankton might favour survival in some locations but not others. For example, food for larvae may be generally abundant in some locations but sparse in others. In addition, changes in physical conditions among widespread locations make it is likely that physiological tolerances will also help determine patterns of abundance at geographical scales. Water temperatures, salinity and a variety of other physical variables differ among the locations in this study and may influence the survival of larvae and post-settlement fishes.

Although regional-scale processes interact with local-scale processes to influence diversity and abundance among widespread locations (Schluter and Ricklefs 1993, Caley 1995a, b, 1997, Connolly and Roughgarden 1998), the patterns of abundance among widespread locations observed here could be entirely determined by different intensities of local-scale processes. However, this study demonstrates that habitat availability alone cannot account for the differences in abundances among geographic locations. It is not known whether the intensity of interspecific interactions among species of *Gobiodon*, or with other species, varies significantly among the locations considered here. However, the species composition of the *Gobiodon* assemblage changes very little over the geographic range of this study (Munday et al. 1999). There are no species replacements that might dramatically alter the nature of interactions among species of *Gobiodon*. Furthermore, few other species of fishes use *Acropora* corals in a similar manner to *Gobiodon*, so competitive interactions with other species of fish are not likely to be common. Overall, processes acting on larger scales, such as larval supply, most easily account for the observed differences in abundance not explained by habitat availability and local-scale habitat selection.

In contrast to most other species of *Gobiodon*, the abundance of *G. axillaris* was not closely associated with the abundance of preferred corals among zones, exposures or geographic locations. Therefore, the abundance of *G. axillaris* is determined by factors other than habitat availability. The distribution and abundance of *G. axillaris* across reef zones and among exposures was almost opposite of that observed for *G. histrio*. Both species of fish inhabit a similar range of corals and both use *A. nasuta* much more frequently than all other species of *Acropora*. Habitat partitioning of the type observed for these species would be expected if they compete strongly for access to *A. nasuta* but partition habitats at larger spatial scales in order to avoid competitive exclusion. Manipulative experiments are required to determine if these species actually compete for space.

Due to the distances and spatial scales involved, it is extremely difficult to sample or conduct properly replicated experiments, at appropriate spatial scales, to examine processes influencing abundances among geographic locations. Comparisons of data collected in the same way, at the same intensity, at replicate sites and locations can be useful for generating hypothesis on the processes that influence patterns of distribution and abundance among widespread locations, and can focus attention on the spatial scales where these processes operate (Ricklefs and Schluter 1993, Caselle and Warner 1996, Underwood and Chapman 1996, Hughes et al. 1999). The importance of habitat availability on the distribution and abundance of coral-reef fishes has remained a strongly debated question. Recently, the debate has centred on the spatial scales where habitat availability is important. This study indicates that, even for very habitat-specialised fishes, a hierarchy of processes acting on different spatial-scales appears to determine abundances within and among locations.

CHAPTER 4: INTERSPECIFIC COMPETITION IN A GUILD OF CORAL-DWELLING FISHES

4.1. ABSTRACT

I investigated the effects of interspecific competition on habitat use and the abundance of six species of obligate coral-dwelling gobies (genus *Gobiodon*) that inhabit a range of acroporid coral species at Lizard Island, Great Barrier Reef. First I estimated the pair-wise similarity in habitat use among species. I then used experiments in aquaria to determine the ability of each species to compete against an apparently dominant species, *G. histrio*, and to determine the effect that body size and prior residency have on competitive ability. A field-based recolonisation experiment was carried out to determine whether characteristics of individual coral colonies can influence the outcome of interactions between *G. histrio* and other species of *Gobiodon*. Finally, I used a manipulative experiment in the field, in which *G. histrio* was removed from replicate patches of reef, to determine if competition with this species limits the abundance of the other five species of *Gobiodon*.

G. axillaris exhibited high overlap in habitat use with *G. histrio* and experiments in aquaria demonstrated that they are equivalent competitors. Both body size and prior residency had significant effects on the outcome of competitive interactions in aquaria. The abundance of *G. axillaris* increased significantly on patches of reef where *G. histrio* was removed demonstrating that these species compete for habitats in the field. *G. quinquestrigatus* also exhibited high overlap in habitat use with *G. histrio* and experiments in aquaria demonstrated that it was an inferior competitor to *G. histrio*. However, the abundance of *G. quinquestrigatus* did not change where *G. histrio* was removed. The recolonisation experiment revealed that *G. quinquestrigatus* uses coral colonies that are subtly different to those usually inhabited by *G. histrio* which might limit competition between these two species. *G. unicolor* also exhibited high overlap in habitat use with *G. histrio* but these two species were able to co-habit the same coral colonies and therefore did not compete for habitats in aquaria or in the field.

The remaining species, *G. brochus* and *G. rivulatus*, exhibited low overlap in habitat use with *G. histrio*. Experiments in aquaria demonstrated that *G. brochus* is an inferior competitor to *G. histrio* and is excluded from prefered coral colonies unless individuals are larger than *G. histrio* or are an equal size and are prior residents of the coral colony. The abundance of *G. brochus* increased significantly on patches of reef where *G. histrio* was removed demonstrating that these species compete for habitats in the field. Experiments in aquaria demonstrated that *G. rivulatus* and *G. histrio* have different habitat preferences and these two species did not compete for habitats in aquaria or in the field.

The results of these experiments clearly indicate that interspecific competition affects the abundance of some coral-dwelling fishes. Moreover, the effects of competition are largely predictable from knowledge of habitat use and an understanding of species' competitive abilities. These results contribute to the growing evidence that interspecific competition can be important in structuring animal communities.

4.2. INTRODUCTION

Interspecific competition has played a central role in the development of ecological theory (Diamond 1978, Brown 1981, Roughgarden 1983). While a variety of field experiments have detected significant effects of interspecific competition on the distribution and abundance of some organisms (reviews by Connell 1983, Schoener 1983, Hairston 1985, Roughgarden 1986, 1989), many others have not (Conner and Simberloff 1979, Lawton and Strong 1981, Lawton 1982, 1984, Underwood et al. 1983, Weins 1984, 1986). Determining the conditions under which competition will significantly influence population and community structure remains a key pursuit of modern ecology.

Interspecific competition for space was adopted as the basis of early models of community structure and population dynamics of coral-reef fishes (Smith and Tyler 1972, Roughgarden 1974, Sale 1977). However, experiments have rarely demonstrated any significant effects of interspecific competition on the distribution and abundance of these species (reviewed by Jones 1991 but see Robertson 1996). Experiments have shown that interspecific competition influences the abundance and habitat use of some fishes on temperate reefs (Hixon 1980, Larson 1980, Schmitt and Holbrook 1990) and in one group of territorial damselfishes on Caribbean reefs (Robertson 1996). In contrast, experiments have not found significant effects of interspecific competition on the abundance of fishes on the Great Barrier Reef (Doherty 1982, 1983, Jones 1987a, 1988). The experiments used to investigate the effects of interspecific competition on the Great Barrier Reef have largely concentrated on pairs of potentially competing damselfishes (family Pomacentridae). Pairwise comparisons, while useful, do not consider effects of competition across a range of interacting species. Most assemblages of coral-reef fish include numerous groups of species with similar ecological requirements (ie guilds). Experiments that examine the effect of interspecific competition on interacting guilds and on groups other than damselfishes are largely lacking.

In the lottery model of competition, first proposed for coral reef fishes (Sale 1974, 1977, 1978), guild members are expected to have similar competitive abilities and the acquisition of vacant space is determined by which species first arrives at the vacant space. In this model, patterns of abundance are determined by the relative abundance of recruits available to occupy vacant space. Although competitive lotteries have been the focus of considerable theoretical work (Chesson and Warner 1981, Warner and Chesson 1985, Chesson 1991) little empirical support has emerged for these systems, particularly in fishes (Robertson 1995). Contrary to the assumption of equal competitive abilities required by the lottery model, most competitive interactions have asymmetrical effects (Connell 1983, Schoener 1983). The ability of individuals to acquire and defend space can depend on the species competitive ability, body size or prior residency of the habitat space (Maynard Smith and Parker 1976, Hammerstein 1981, Robertson 1984, Fautin 1986, Clarke 1992, Itzkowitz et al. 1998). Understanding the ways these factors influence interactions among species can help interpret the distribution patterns of competing species (Clarke 1994, 1996) and aid the design of experiments to test for effects of interspecific competition.

Effects of interspecific competition for space are most likely to be apparent in guilds of animals with specialised but overlapping habitat requirements. Coral dwelling gobies of the genus *Gobiodon* (family Gobiidae) are a guild of fishes with specialised but often overlapping patterns of habitat use and species distributions overlap at scales where interspecific interactions can occur (ie. 10's of metres). *Gobiodon* are small (< 60 mm total length (TL)) obligate coral-dwelling fishes that mostly inhabit coral colonies of the genus *Acropora* (Munday et al. 1999). At Lizard Island on the Great Barrier Reef each species of *Gobiodon* uses one or two species of *Acropora* much more frequently than expected by chance and a range of other corals roughly in proportion to their availability (Munday et al 1997, Chapter 3). For most species of *Gobiodon*, patterns of abundance are correlated with the abundance of the coral species they usually inhabit (Munday et al 1997, Chapter 3). This correlation is consistent with the notion that preferred corals can be a limited resource for *Gobiodon* species. Because *Gobiodon* have specialised but overlapping patterns of habitat use and abundance is associated with the availability of coral colonies inhabited these species might be expected to compete for space.

In this study I investigated the effects of interspecific competition for habitats on the abundance of six common species of *Gobiodon* at Lizard Island on the Great Barrier Reef. First, I examined the degree of overlap in habitat use among species of *Gobiodon* to determine which species are most likely to compete for space. I then used experiments in aquaria to estimate the competitive ability of each species of *Gobiodon* and the effects of body size and prior residency on the outcome of interspecific interactions. I also determined if there are characteristics of individual coral colonies that can influence competitive outcomes by removing gobies from coral colonies and comparing the species that recolonise these colonies to the species removed. Finally I used a field based competitor removal experiment to determine whether interspecific competition can influence the abundance of *Gobiodon* species and to test prediction about the effect of removing a competitor (Table 4.1) for each species of *Gobiodon* based on knowledge of their habitat use and competitive ability.

4.3. METHODS

Study species and location

This study was conducted between March 1996 and December 1998 at Lizard Island (14^0 40'S, 145^0 28'E) on the Great Barrier Reef. There are 13 recognised species and at least 2 undescribed species of coral-dwelling goby (genus *Gobiodon*) on the Great Barrier Reef (Munday et al. 1999). In this study I concentrate on the six most common species of *Gobiodon* on reefs around Lizard Island (Table, 4.2; Munday et al. 1997). One species, *G. histrio* has two colour morphs, a "histrio" form which is green with red stripes and an "erythrospilus" form which is green with red spots (Table 4.2). These two colours forms have identical patterns of habitat use in the field (pers. obs) and are considered here as *G. histrio*, unless otherwise indicated.

Habitat use

Overlap in habitat use was estimated for these six species of *Gobiodon* from visual census of coral colonies of 10 species of *Acropora* known to be used by *Gobiodon* species at Lizard Island. These species of coral were *A. cerealis, A. digitifera, A. gemmifera, A. humilis, A. loripes, A. nasuta, A. millepora, A. secale, A. tenuis,* and *A. valida.* All colonies of these coral species within a total of 75 randomly placed 10 x 1m transects at nine sites around Lizard Island were searched for the presence of *Gobiodon* (see Munday et al. 1997 for further details). Overlap in habitat use among species pairs of *Gobiodon* was estimated using the percent similarity index (Krebs 1989):

$$P = \sum \text{minimum } (p1i, \text{p}2i)$$

where P = percent similarity in habitat use between *Gobiodon* species 1 and *Gobiodon* species 2, $p1i$ = the percent of *Gobiodon* species 1 that inhabited coral species i and $p2$i = the percent of *Gobiodon* species 2 that inhabited coral species i.

Habitat preference and competitive ability

The ability of each species of *Gobiodon* to compete for preferred corals was tested in aquaria. Firstly, to determine habitat preference in the absence of competitors, individuals of each species of *Gobiodon* were given the choice of two coral colonies, one of a species that is commonly used in the field and one of a species that is rarely used in the field. At Lizard Island *Acropora nasuta* is commonly used by most species of *Gobiodon* whereas *A. gemmifera* is only occasionally used by most species of *Gobiodon* (Munday et al. 1997, Chapter 3), therefore, these two coral species were used in all the choice experiments. Small colonies (15-20 cm diameter) of these two coral species were carefully removed from the reef, transported alive to the laboratory and then cleared of all infauna (gobies, crabs and shrimps). An approximately equal sized colony of each coral species was placed at opposite end of six glass aquaria. Each aquarium measured approximately 800 x 300 x 300 mm (Fig. 4.1). 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. The bottom of each aquarium was covered with coarse beach sand and fresh seawater entered from both ends. An outlet, slightly above the level of the sand was positioned at the front and centre of each aquarium and an external standpipe controlled water depth in the tank.

Fish for these trials were collected from the corals usually inhabited in the field by anaesthetising with clove-oil (Munday and Wilson 1997). New individuals were collected every 1-2 days and individuals of different species was held in separate aquaria until used. Each holding aquarium had a continual flow of fresh seawater and contained only small plastic tubes for fish to shelter in. At the beginning of each habitat preference one fish was transferred to an acclimatisation tube in the middle of each test aquarium. This tube extended from the sand to above the water surface so that the fish could not escape. The tube also had small holes around its circumference to enable water to flow through the tube. These holes were provided to aid in the acclimatisation of fish to the experimental apparatus. After 45 minutes the tubes were carefully lifted from the aquaria and each fish was allowed to choose between the two corals. Fish were released from the acclimatisation tubes between 18:00 and 19:00 and their choice of coral recorded between 06:00 and 07 :00 the following morning. Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 hours.

Having determined the preference of each species of *Gobiodon* for either *A. nasuta* or *A. gemmifera*, I then examined the use of these coral species in the presence of a competitor. *G. histrio* was chosen as the competitor because it is numerically dominant on *Acropora nasuta* which appears to be the preferred coral species for at least three species of *Gobiodon* at Lizard Island (Munday et al. 1997, Chapter 3). Because the two forms of *G. histrio* (Table 4.2) have identical patterns of habitat use in the field, I did not distinguish between these forms during interspecific tests of competitive ability. I did, however, test the ability of the two forms of *G. histrio* to compete against each other. Experiments used to estimate competitive ability were conducted using a similar protocol to the habitat preference experiments described above, except that two acclimatisation tubes and two fish were used in each trial. The second tube was positioned directly in front of the first. One *G. histrio* was placed in one of the acclimatisation tubes and one approximately equal sized individual (within 5mm total length (TL)) of another species was placed in the other tube. The location of each species in either the front or back tube was alternated between trials. It was not possible to use similar sized individuals in the *G. rivulatus-G. histrio* trials because *G. rivulatus* has a much smaller maximum size than *G. histrio*. However, differences in size between these species did not appear to influence the results for these species.

The effects of body size and prior residency on competitive ability against *G. histrio* were tested for two species, *G. axillaris* and *G. brochus*. These species were selected because they represent the range of competitive abilities detected in competition trials using fish of approximately equal body size (above). *G. axillaris* was competitively equivalent to *G. histrio* and *G. brochus* competitively subordinate to *G. histrio*. Experiments were conducted in a similar manner to the competition trials using fish of approximately equal body sizes (above) except that the individual competing against *G. histrio* in each trial was (1) either the same size, larger or smaller than *G. histrio* and, (2) either a prior resident to the preferred coral species or had no prior residency status. All combinations of body size and residency status were used. Individuals of different body size were a minimum of 5 mm and a maximum of 10 mm difference in TL. This size difference was found to be sufficient to detect effects of body size on competitive interactions. Where an individual of *G.*

axillaris or *G. brochus* was a prior resident to the preferred coral it was released directly on the preferred coral (*A. nasuta*) 12 hours prior to the release of *G. histrio*.

Data analysis

The frequency with which each species of *Gobiodon* used *A. nasuta* or *A. gemmifera* in the absence of a competitor was compared to random expectation using chi-squared analysis. Where a species of coral was used more frequently than expected this coral species was deemed to be the preferred. Chi-square analysis was also used to test the competitive ability of each species of *Gobiodon*. The frequency that each species of *Gobiodon* used *A. nasuta* or *A. gemmifera* in the presence of *G. histrio* was compared to the frequency these corals were used in the absence of *G. histrio* (preference trials). Where the frequency of coral use changed for both species of fish they were considered to be equal competitors. Where the frequency of coral use changed for only one species of fish it was considered to be a subordinate competitor. Where the frequency of coral use did not change for either species of fish they were considered to be not competing.

Log-linear modeling using a combination of explanatory and response variables was used to analyse the influence of body size and prior residency on competitive ability. A succession of increasingly complex models (Table 3) were fitted to the observed data until there was no significant improvement in the goodness-of-fit statistic (likelihood ratio chi-square) from one model to the next (following Wrigley 1985). Body size and prior residency status were used as explanatory variables and the final distribution of fish between coral colonies in each set of trials was the response variable. Three responses were recognised (1) win –*G. histrio* was excluded from its preferred coral by the second species, (2) draw - both species occupied the preferred coral and, (3) lose – the second species was excluded from its preferred coral by *G. histrio*. Separate analyses were conducted to test the outcomes between *G. histrio* and *G. axillaris* and *G. histrio* and *G. brochus*. Analyses were performed using SPSS for windows version 7.0.

Recolonisation experiment

In addition to species competitive ability, body size and prior residency, various characteristics of coral colonies might influence the outcome of competitive interactions. For example, *G. histrio*, *G. axillaris* and *G. quinquestrigatus* most frequently inhabit *A. nasuta* (Table 4.2), however, the colonies of *A. nasuta* used by *G. quinquestrigatus* are often subtly different from those used by *G. histrio* and *G. axillaris*. Coral colonies used by *G. quinquestrigatus* are often more finely branched and a browner colour than those used by *G. histrio* and *G. axillaris* (pers. obs). To determine if these subtle differences in colony morphology influence competitive interactions I removed gobies from approximately equal size coral colonies of *A. nasuta* that were inhabited by either *G. histrio*, *G. axillaris* and *G. quinquestrigatus*. I then observed the natural recolonisation of gobies to these coral colonies. If there were no significant differences in the coral colonies used by each species of *Gobiodon* I would expect to find similar patterns of recolonisation among coral colonies previously occupied by each species of fish. Alternatively, if there are characteristics of the corals that might influence habitat preferences and competitive interactions then recolonisation should be biased towards the species that had previously inhabited each coral colony. Fish were removed from coral colonies by anaesthetisation with clove oil on reefs near the lagoon entrance on the leeward side of Lizard Island. These colonies were visually censused three months after and the recolonising species recorded.

Competitor removal experiment

To determine if competition with *G. histrio* influences the abundance of other species of *Gobiodon* in the wild, I reduced the abundance of *G. histrio* in replicate plots of reef and compared the change in abundance of each species of *Gobiodon* to the change in abundance in control plots. A total of 24 plots, each approximately 25m^2 in area, were established on the reef flat at Horseshoe Reef and surrounding reefs on the leeward side of Lizard Island in January 1997. These reefs had patches of acroporid corals separated by areas of dense soft coral cover. I exploited this natural patchiness of coral distribution to help segregate plots and to reduce the potential for fish to move among experimental plots and from surrounding areas. All *G. histrio* (both forms) were removed from 8 randomly selected plots by anaesthetising the fish with clove oil and carefully removing them from the corals. Eight other plots were assigned as controls where *G. histrio* was not removed. In 8 additional plots only the *G. histrio* (*histrio* form) was removed from 4 plots and only the *G. histrio* (*erythrospilus* form) was removed from the remaining 4 plots. Any *G. histrio* that recolonised the removal plots were removed in January and May 1998. I monitored the abundance of all species of *Gobiodon* in these plots until December 1998. Mann-Whitney U tests were used to compare the change in abundance of each species in removal plots to the change in abundance in control plots. Because I was primarily interested in the effects of competition on the adult population I did not include new recruits in these analyses. Coral-dwelling gobies have rapid juvenile growth and can mature within a few months of settling to the reef (Kuwamura et al.1996). Therefore, the effects of competition on adult abundance should be detected earlier than in larger, slower growing species of coral-reef fish.

4.4. RESULTS

Habitat overlap

Gobies inhabiting 1368 colonies of 10 species of acroporid corals were censused. *G. axillaris* and *G. quinquestrigatus* exhibited a high percent similarity in habitat use with *G. histrio* (69% and 72% respectively, Table 4.4). This similarity was largely due to the frequent use of *A. nasuta* by all three of these species. In contrast, *G. brochus* and *G. rivulatus* exhibited low percent similarity in habitat use with *G. histrio* (18% and 29% respectively, Table 4.4). *G. brochus* most frequently inhabits *A. loripes* which is rarely used by *G. histrio*. However, the largest individuals of *G. brochus* are usually found in *A. nasuta* (pers. obs), the coral species usually inhabited by *G. histrio*. *G. rivulatus* mostly inhabits *A. gemmifera* which is rarely used by *G. histrio*. *G. unicolor* exhibited moderate percent similarity in habitat use with *G. histrio* (60%, Table 4.4) and was the only species of *Gobiodon* observed to co-habit with *G. histrio*.

Habitat preference and competitive ability

G. axillaris, *G. brochus*, *G. histrio* (*histrio* form), *G. histrio* (*erythrospilus* form), *G. quinquestrigatus* and *G. unicolor* all showed very strong preference for *A. nasuta* in the habitat choice experiments (Table 4.5). In contrast *G. rivulatus* used both species of coral but tended to prefer *A. gemmifera* (Table 4.5).

The presence of *G. histrio* influenced patterns of habitat use in some species of *Gobiodon* but not others (Fig 4.2). For both *G. axillaris* and *G. histrio* the use of their preferred coral (*A. nasuta*) was significantly reduced in the presence of the other species (Fig 4.2a) indicating that these two species are competitively equivalent. The presence of *G. histrio* significantly reduced the use of preferred habitat by *G. brochus* but not visa-versa (Fig 4.2b) indicating that *G. brochus* is an inferior competitor to *G. histrio*. The presence of *G. histrio* also significantly reduced the use of preferred habitat by *G. quinquestrigatus* but not visa-versa (Fig 4.2c) indicating that *G. quinquestrigatus* is also an inferior competitor to *G. histrio*. In contrast, the presence of *G. histrio* did not significantly influence the habitat use of *G. rivulatus* (Fig 4.2d) although a trend towards an increase in the use of *A. gemmifera* by this species was evident. Therefore these species do not appear to be compete directly for habitat space. Similarly, habitat use of *G. unicolor* did not change significantly in the presence of *G. histrio* (Fig 4.2e) and these two species do not appear to compete for habitat space. Each form of *G. histrio* used *A. nasuta* exclusively in habitat choice experiments but this pattern of habitat use changed in the presence of an individual of the other form (Fig 4.2f). *G. histrio* (*erythrospilus* form) used *A. nasuta* significantly less often in the presence of *G. histrio* (*histrio* form). *G. histrio* (*histrio* form) also used *A. nasuta* less frequently than in the preference experiments although this change was only significant at $P < 0.01$. Therefore, there appears to be a slight asymmetry in the competitive ability of the two forms of *G. histrio*.

Both body size and prior residency significantly effected the outcome of competition trials between *G. axillaris* and *G. histrio* (Table 4.6). The inclusion of body size in the model resulted in a much greater improvement in the fit of the model compared to the inclusion of residency status (Table 4.6). Body size, therefore, had a greater effect than prior residency on competitive ability of *G. axillaris*. *G. axillaris* is an equivalent competitor to *G. histrio* and where *G. axillaris* and *G. histrio* were of equal size and neither species was a prior resident of the preferred coral colony (*A. nasuta*), the results of competition trials were approximately equally spread among the possible outcome (Table 4.7). Larger individuals of *G. axillaris* almost always won and smaller individuals of *G. axillaris* almost always lost competition trials where neither species was a prior resident of the preferred coral colony (Table 4.7). When *G. axillaris* was a prior resident to the preferred coral colony, individuals of an equal or greater size to *G. histrio* nearly always won the preferred coral (Table 4.7).

Both body size and prior residency also significantly effected the outcome of competition trials between *G. brochus* and *G. histrio* (Table 4.8). As was the case with *G. axillaris*, the inclusion of body size in the model resulted in the greatest improvement in the fit of the log linear model (Table 4.8). Body size, therefore, had a greater influence than prior residency on competitive ability of *G. brochus*. In contrast to *G. axillaris*, *G. brochus* is an inferior competitor to *G. histrio* and equal sized or smaller individuals of *G. brochus* were nearly always excluded from the preferred coral by *G. histrio* (Table 4.9). However, in trials where *G. brochus* individuals were larger than *G. histrio* they were nearly always able to exclude *G. histrio* from the preferred coral (Table 4.9). Also, when *G. brochus* had prior residency to the preferred coral colony, individuals equal in size to *G. histrio* were able to retain the preferred coral in approximately half the trials (Table 4.9).

Recolonisation experiment

Vacant corals were reoccupied either new recruits or larger fish that had apparently moved from other coral colonies. Patterns of recolonisation varied among corals that were previously occupied by *G. histrio*, *G. axillaris* or *G. quinquestrigatus* (Fig. 4.3). Colonies of *A. nasuta* previously inhabited by *G. histrio* were mostly recolonised by *G. histrio* but also by *G. axillaris* and *G. brochus* and infrequently by *G. quinquestrigatus* and *G. unicolor* (Fig 4.3). Colonies of *A. nasuta* previously inhabited *by G. axillaris* were mostly recolonised by *G. histrio* and *G. axillaris* but also by *G. quinquestrigatus* and *G. unicolor*. In contrast, colonies of *A. nasuta* previously occupied by *G. quinquestrigatus* were almost exclusively recolonised by *G. quinquestrigatus* and only infrequently by *G. histrio* and *G. unicolor*. This indicates that colonies of *A. nasuta* inhabited by *G. quinquestrigatus* might have characteristics that influence which species recolonise them when they become vacant.

Competitor removal experiment

The repeated removal of *G. histrio* (both forms) from treatment plots resulted in a significant decline in the abundance of this species in treatment plots compared to controls (Table 4.10, Fig 4.4, Mann-Whitney U = 60.5, n_1, n_2 = 8 plots, $P < 0.001$). The removal of *G. histrio* also resulted in an increase in the abundance of *G. axillaris* (Fig 4.4, Mann-Whitney U = 49.5, n_1, n_2 = 8 plots, $P < 0.05$) and *G. brochus* (Fig 4.4, Mann-Whitney U = 52, n_1, n_2 = 8 plots, $P < 0.025$) in treatment plots compared to control plots. In addition the combined change in abundance of *G. axillaris* and *G. brochus* in all removal and control plots was closely correlated with the change in abundance of *G. histrio* in these plots (Fig 4.5). These results conform to predictions derived from percent similarity of habitat use and competitive abilities and demonstrate that *G. axillaris* and *G. brochus* compete for habitat space with *G. histrio*. The abundance of *G. quinquestrigatus* (Fig 4.4, Mann-Whitney U = 43, n_1, n_2 = 8 plots, $P > 0.1$) did not change in treatment plots compared to control plots despite this species exhibiting high overlap in habitat use and being an inferior competitor to *G. histrio*. As predicted the abundances of *G. rivulatus* (Fig 4.4, Mann-Whitney U = 44, n_1, n_2 = 8 plots, $P > 0.1$) and *G. unicolor* (Fig 4.4, Mann-Whitney U = 37, n_1, n_2 = 8 plots, $P > 0.1$) did not change in removal plots compared with control plots. The abundances of *G. rivulatus* and *G. unicolor* were not expected to change because the laboratory experiments revealed that they do not compete directly with *G. histrio*. In the four plots where only *G. histrio* (*histrio* form) was removed there was a corresponding and significant increase in the abundance of *G. histrio* (*erythrospilus* form) compared to controls (Fig 4.4, Mann-Whitney U = 29.5, n_1=8, n_2 = 4, $P < 0.025$). In the reciprocal plots, where only *G. histrio* (*erythrospilus* form) was removed, there was an observable increase in the abundance of the *G. histrio* (*histrio* form) (Fig 4.4) but which was just non-significant at the 5% level (Mann-Whitney U = 26.5, n_1=8, n_2 = 4, U critical = 27, $0.05<P<0.1$). This result conforms to predictions from the competitive ability trials where a slight asymmetry in competitive ability was detected between the two forms.

TABLE 4.1. Predicted effects on abundance of guild members where a competitor is reduced in abundance.

Species	Overlap in habitat use between species	
	high	low
Non-competitors	no change	no change
Equivalent competitors	increase	no change
Inferior competitors	increase	(i) increase if low overlap is due to exclusion from preferred habitats (ii) no change if low overlap due to different habitat preferences

TABLE 4.2. Species of *Gobiodon* considered in this study, maximum recorded lengths and the coral species usually inhabited at Lizard Island, Great Barrier Reef*.

Species	Maximum length (mm)	Coral species most frequently inhabited
Gobiodon axillaris	50.2	*A. nasuta*
Gobiodon brochus	40.0	*A. loripes*
Gobiodon histrio (*histrio* form)	51.3	*A. nasuta*
Gobiodon histrio (*erythrospilus* form)	50.8	*A. nasuta*
Gobiodon quinquestrigatus	45.0	*A. nasuta*
Gobiodon rivulatus	29.0	*A. gemmifera*
Gobiodon unicolor	45.0	*A. millepora*

* Source: Munday et al. 1997, 1999.

TABLE 4.3. Log-linear models used to test the effects of body size and prior residency on the outcome of competitive ability trials. Models were tested sequentially until there was no further improvement in the fit of the model to the observed data.

Model	Factors included	Hypothesis tested
1	outcome + size*residency	outcome is independent of body size or residency status
2	outcome*residency + size*residency	residency status influences competitive ability
3	outcome*size + size*residency	body size influences competitive ability
4	outcome*residency + outcome*size + size*residency	residency status and body size influence competitive ability
5	outcome*residency*size	an interaction between residency status and body size influences competitive ability

TABLE 4.4. Percent similarity in habitat use between species of *Gobiodon* at Lizard Island.

	G. histrio	*G. axillaris*	*G. brochus*	*G. rivulatus*	*G. unicolor*
G. axillaris	69				
G. brochus	18	25			
G. rivulatus	29	48	30		
G. unicolor	60	68	35	46	
G. quinquestrigatus	72	86	32	45	70

TABLE 4.5. Number of binary-choice trials in which species of *Gobiodon* chose either *A. nasuta* or *A.gemmifera*. Chi-squared comparison against the null expectation of equal habitat use. ** = P<0.01, *** = P<0.001, ns = not significant.

Species	*A. nasuta*	*A. gemmifera*	*P*
G. axillaris	16	1	***
G. brochus	15	0	***
G. histrio (*histrio* form)	17	0	***
G. histrio (*erythrospilus* form)	9	0	**
G. quinquestrigatus	15	2	**
G. rivulatus	6	11	ns
G. unicolor	16	0	***

TABLE 4.6. Log-linear analysis of relationships between competitive ability, body size and prior residency for *G. histrio* and *G. axillaris*. R = residency status, B = body size, C = competitive outcome. Model numbers and factors included follow Table 4.3. Factors R and B are explanatory variables, factor C is the response variable. *** $p<0.001$, ** $0.001<p<0.01$, * $0.01<p<0.05$, ns = not significant. The best fitting model is underlined.

Model	Deviance	d.f.	Difference between models	d.f.
1. RB, C	86.37 ***	10	(1&2) 10.34 **	2
2. RB, RC	76.03 ***	8	(1&3) 62.63 ***	2
3. RB, BC	13.37 *	6	(3&4) 12.38**	2
<u>4. RB, RC BC</u>	0.99 ns	4	(4&5) 0.99 ns	4
5. RBC	0.0	0		

TABLE 4.7. Results of competition experiments between *G. histrio* (H) and *G. axillaris* (A) for preferred (*A. nasuta*) and non-preferred (*A. gemmifera*) habitats. In prior residency trials, *G. axillaris* was placed on the preferred coral 12 hours prior to releasing *G. histrio*. Outcomes are displayed for *G. axillaris*. Win = *G. axillaris* defended preferred coral from *G. histrio*; lose = *G. axillaris* displaced from preferred coral by *G. histrio*; draw = both species using preferred coral.

Residency	Size	Outcome		
		Win	Lose	Draw
No prior residency	A < H	1	21	1
	A = H	4	6	7
	A > H	13	1	1
G. axillaris prior resident	A < H	2	10	1
	A = H	16	2	5
	A > H	13	0	0

TABLE 4.8. Log-linear analysis of relationships between competitive ability, body size and prior residency for *G. histrio* and *G. brochus*. R = residency status, B = body size, C = competitive outcome. Model numbers and factors included follow Table 4.3. Factors R and B are explanatory variables, factor C is the response variable. *** $p<0.001$, ** $0.001<p<0.01$, ns = not significant. The best fitting model is underlined.

Model	Deviance	d.f.	Difference between models	d.f.
1. RB, C	68.41 ***	10	(1&2) 9.38 **	2
2. RB, RC	59.03 ***	8	(1&3) 48.58 ***	2
3. RB, BC	19.83 **	6	(3&4) 12.69 **	2
<u>4. RB, RC BC</u>	7.14 ns	4	(4&5) 7.14 ns	4
5. RBC	0.0	0		

TABLE 4.9. Results of competition experiments between *G. histrio* (H) and *G. brochus* (B) for preferred (*A. nasuta*) and non-preferred (*A. gemmifera*) habitats. In prior residency trials, *G. brochus* was placed on the preferred coral 12 hours prior to releasing *G. histrio*. Outcome is displayed for *G. brochus*. Win = *G. brochus* defended preferred coral from *G. histrio*; lose = *G. brochus* displaced from preferred coral by *G. histrio*; draw = both species using preferred coral.

Residency	Size	Outcome		
		Win	Lose	Draw
No prior residency	B < H	0	14	2
	B = H	1	16	5
	B > H	12	1	2
G. brochus prior resident	B < H	1	13	5
	B = H	11	11	3
	B > H	13	1	1

TABLE 4.10. Abundance and of each species of *Gobiodon* in removal and control plots at the commencement and end of the competitor removal experiment.

Species	Removal plots				Control plots			
	start		end		start		end	
	mean	(range)	mean	(range)	mean	(range)	mean	(range)
G. histrio (both forms)	11.4	(8-15)	6.1	(3-11)	9.4	(8-12)	10.1	(8-15)
G. axillaris	2.1	(0-5)	3.8	(1-9)	1.8	(0-6)	1.5	(0-4)
G. brochus	2.6	(1-6)	3.5	(2-6)	3.6	(1-7)	2.8	(0-6)
G. quinquestrigatus	1.5	(0-4)	2.5	(0-4)	1.8	(0-4)	1.8	(0-4)
G. rivulatus	1	(0-4)	0.5	(0-2)	1.4	(0-5)	1.4	(0-6)
G. unicolor	5.4	(1-13)	3.9	(0-7)	3.4	(1-7)	1.9	(0-4)
G. histrio (*histrio*)	7.3	(5-9)	10	(7-12)	4.5	(2-7)	4.9	(2-8)
G. histrio (*erythrospilus*)	4.3	(3-5)	9.3	(6-12)	4.9	(1-7)	5.3	(1-10)

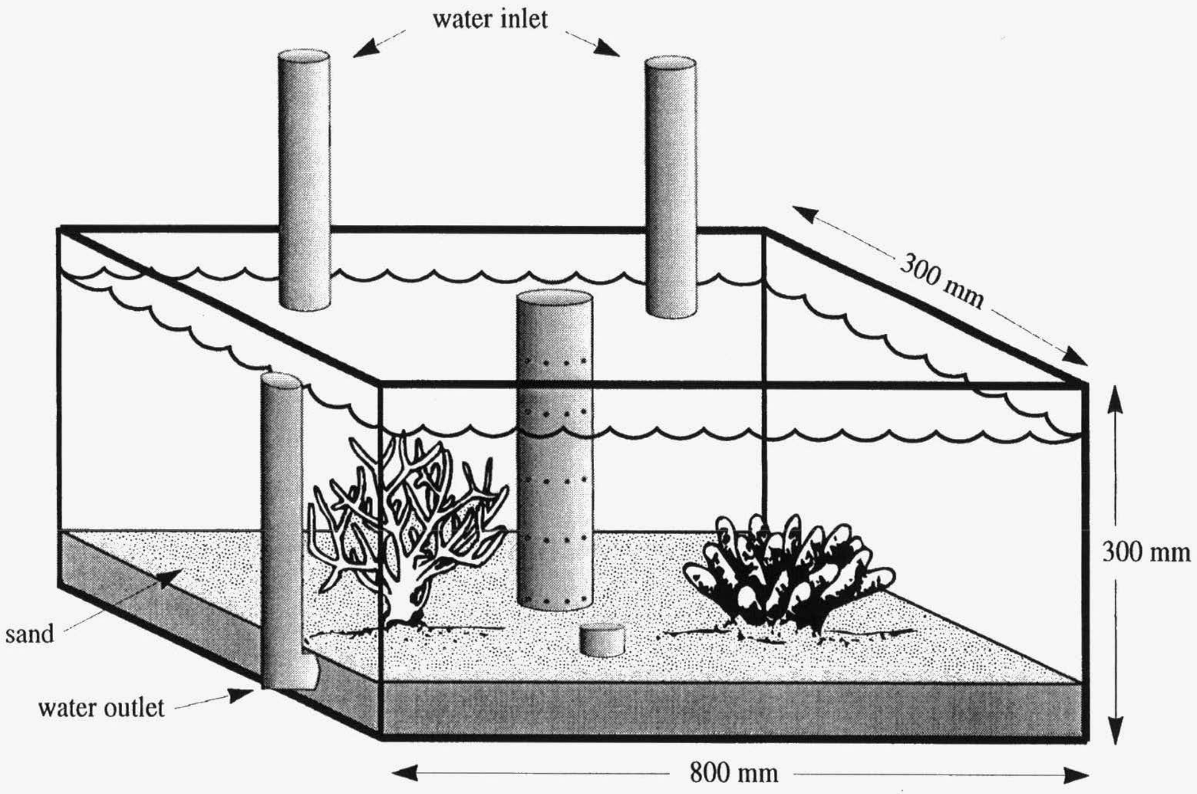

Fig 4.1. Design of aquaria used to test habitat preference and competitive ability of *Gobiodon*.

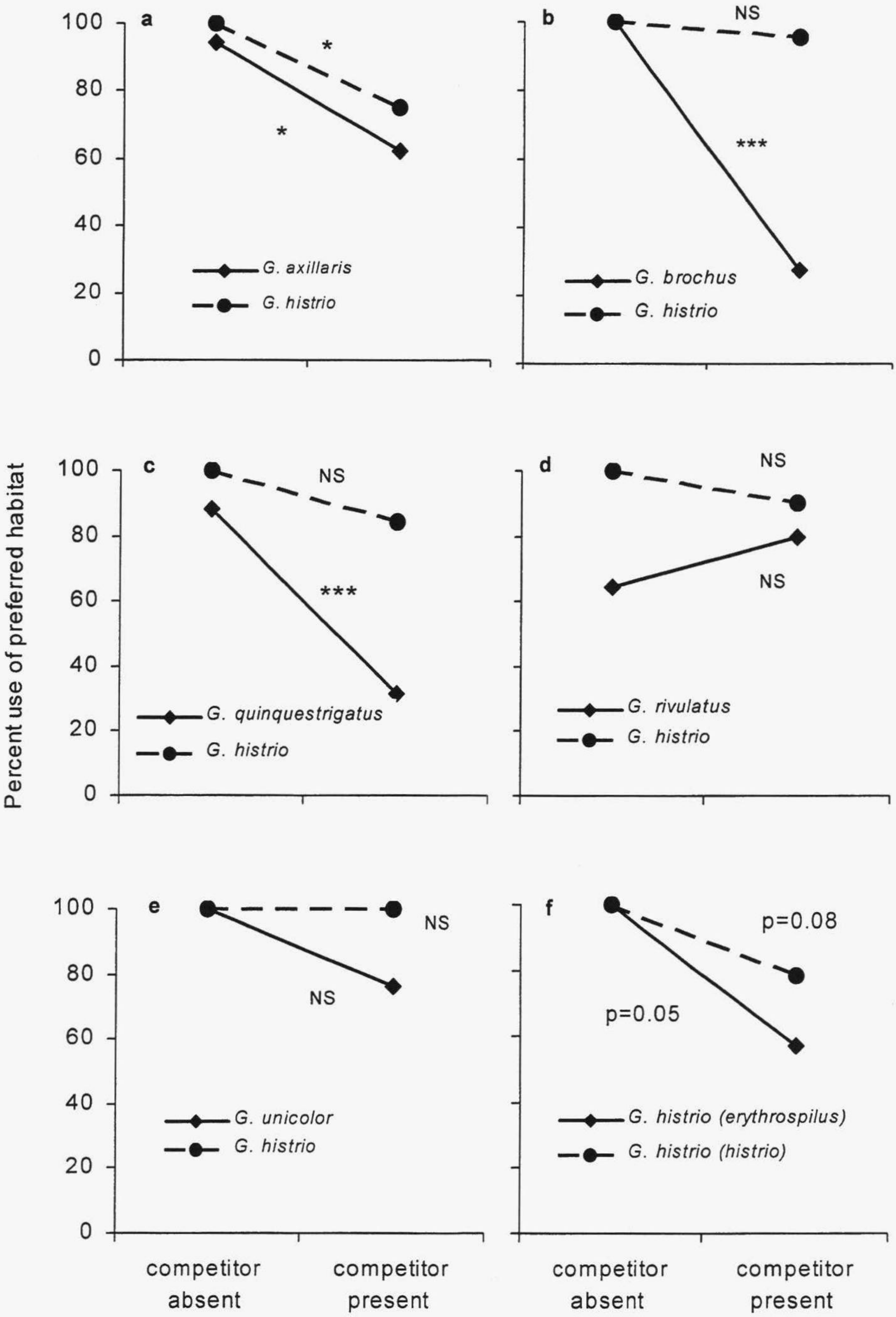

Fig 4.2. Percent of trials in which preferred habitat was used by each species of *Gobiodon* in the absence and presence of *G. histrio*. Significance of change in habitat use ** 0.001<p<0.01, * 0.01<p<0.05, ns = not significant.

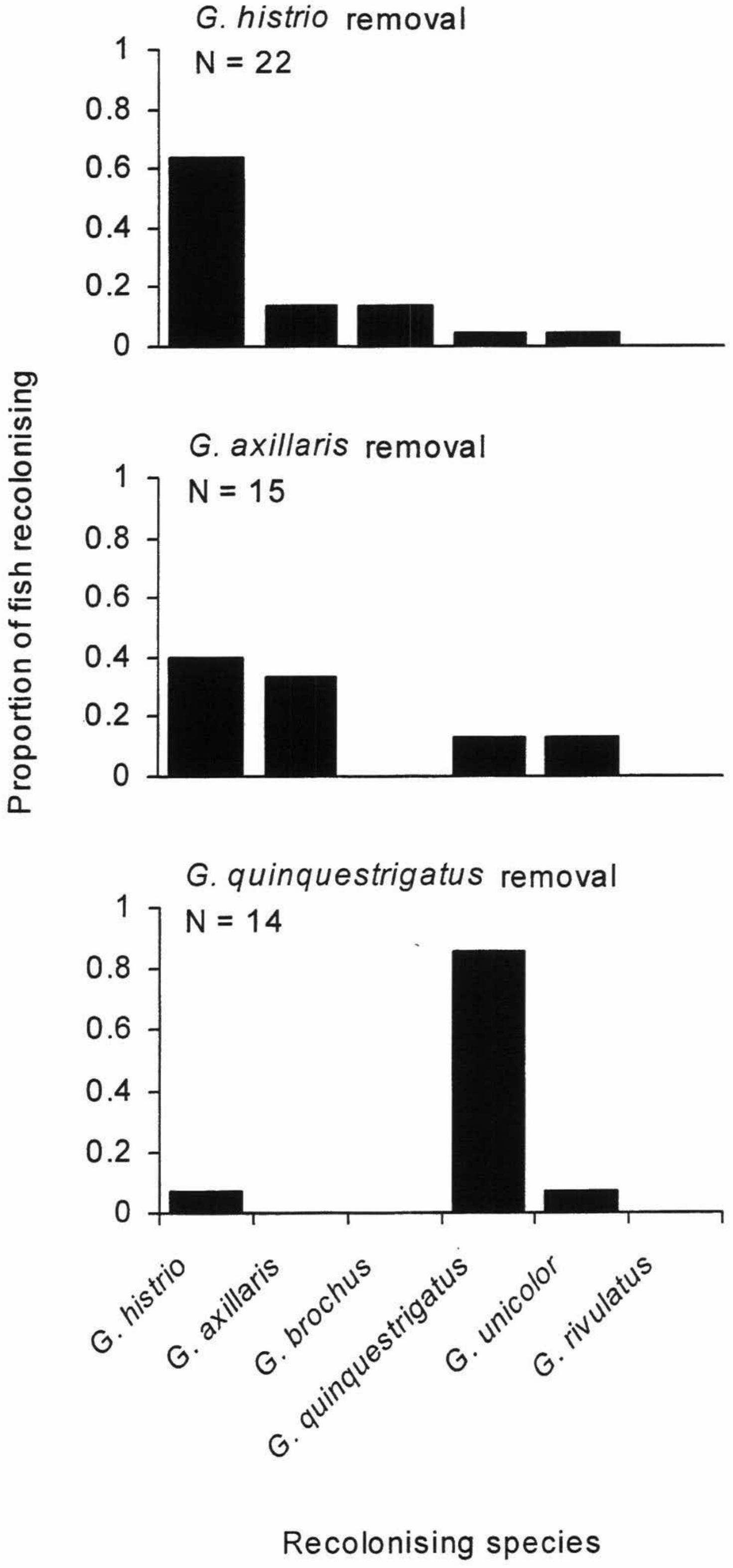

Fig 4.3. Proportion of colonies of *Acropora nasuta* recolonied by each species of *Gobiodon*. N = number of coral colonies previously occupied by *G. histrio*, *G. axillaris* and *G. quinquestrigatus*.

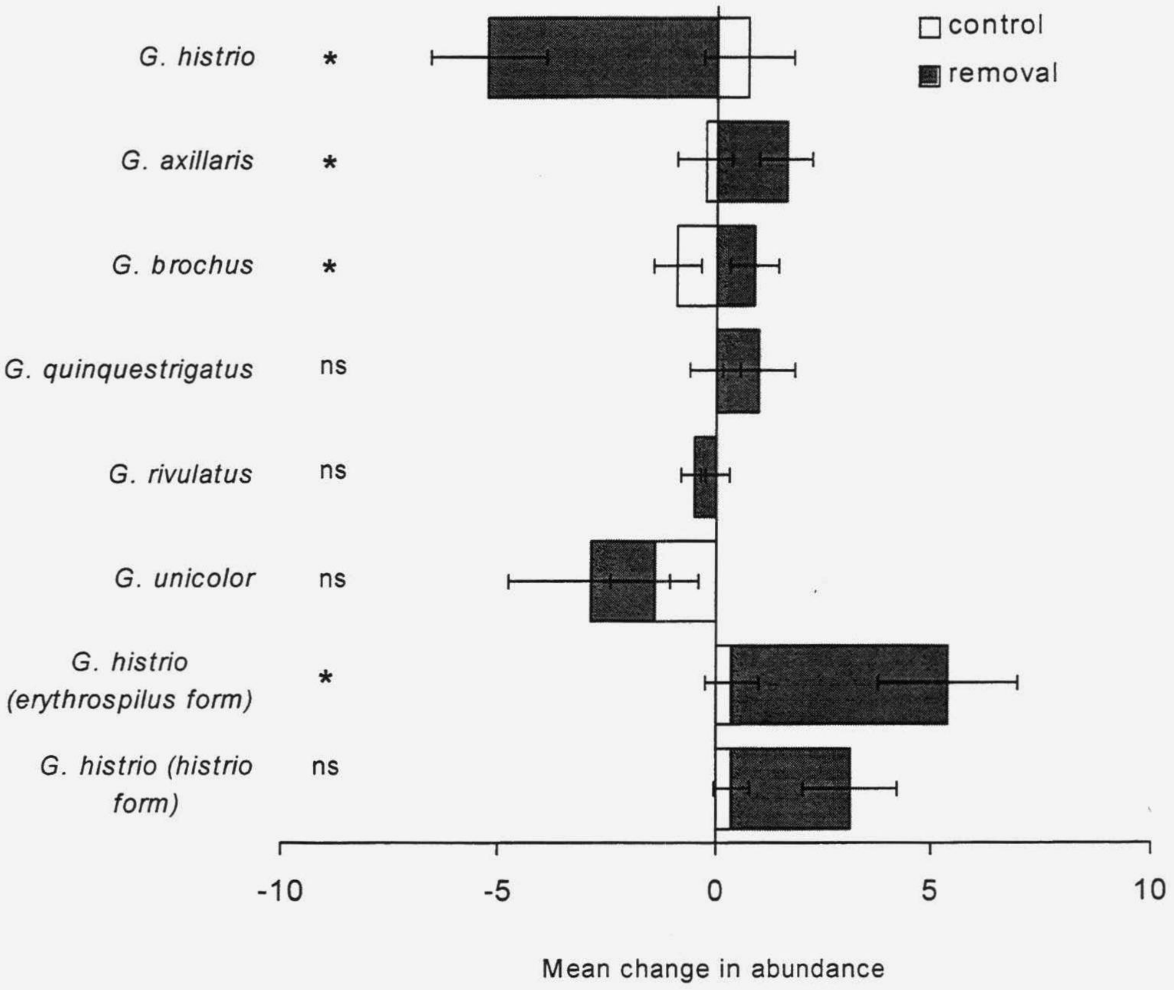

Fig 4.4. Mean change in abundance (± SE) of each species of *Gobiodon* in removal and control plots following the removal of *G. histrio*. Mann-Whitney U tests: * 0.01<p<0.05, ns = not significant.

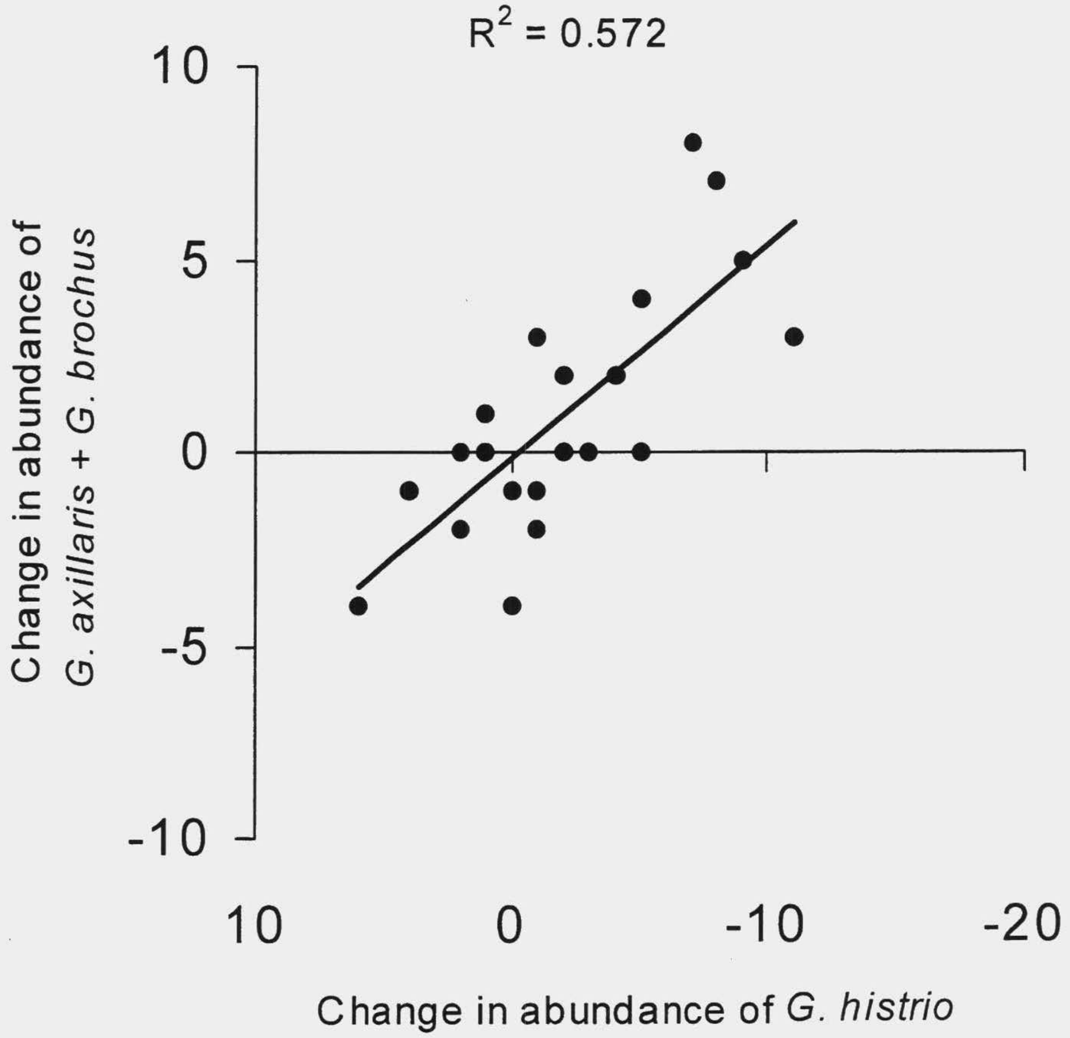

Fig 4.5. Relationship between change in abundance of *G. histrio* and combined change in abundance of *G. axillaris* and *G. brochus* in all plots (removals and controls) between the start and end of the competitor removal experiment.

4.5. DISCUSSION

This study demonstrates that interspecific competition can limit the abundance of some species in a guild of coral-dwelling gobies on the Great Barrier Reef. Reducing the abundance of a competitive dominant, *G. histrio*, resulted in a corresponding increase in the abundances of two species, *G. axillaris* and *G. brochus*. The abundances of both forms of *G. histrio* were also influenced by competition for preferred corals. The abundances of three other species, *G. quinquestrigatus, G. rivulatus* and *G. unicolor* were not affected by the removal of *G. histrio*. The plots in this study were surrounded by soft coral which is not habitat for coral dwelling gobies and, therfore, limited the opportunity of movement of gobies into the treatment plots. Consequently, the increases in abundance of *G. axillaris* and *G. brochus* are the result of a release from competition and not reshuffling of individuals from outside the treatment plots. This study, in conjunction with others (Robertson 1996, Schmitt and Holbrook 1999), provides increasing evidence from manipulative experiments that interspecific competition for space can influence the abundance of some small, sedentary fishes on coral reefs.

Comparisons among multiple species are particularly valuable because they provide insight to the species characteristics and conditions where competition or other processes might act. In the group of fish studied here the response of each species to removal of a dominant species was largely predictable from knowledge of habitat use and the competitive ability of each species. *G. axillaris* and *G. histrio* have a high percent similarity in habitat use and both species preferentially inhabit *A. nasuta* at Lizard Island. In addition, *G. axillaris* has equivalent competitive ability to *G. histrio* and the result of competitive interactions are largely determined by the relative body size of competing individuals. These characteristics indicate that *G. axillaris* and *G. histrio* should compete for preferred habitats if these habitats are a limited resource. The increase in abundance of *G. axillaris* following the removal of *G. histrio* supports this prediction. The two colour morphs of *G. histrio* also compete for access to colonies of *A. nasuta* in the field. Following the removal of one colour form the abundance of the other colour form increased in a manner consistent with predictions from the laboratory experiments. Clearly, *A. nasuta* is a limited resource for which *G. axillaris* and both forms of *G. histrio* are competing.

Despite a low percent similarity in habitat use with *G. histrio*, the abundance of *G. brochus* also increased where *G. histrio* was removed. The competitive ability experiments demonstrated that *G. brochus* is an inferior competitor and individuals are only able to gain access to *A. nasuta* if they are larger than *G. histrio* or they are an equal size and have gained access to the coral colony before *G. histrio*. In the field *G. brochus* usually inhabits *A. loripes* and only the largest individuals of *G. brochus* are found in colonies of *A. nasuta* (pers obs). This could occur if *G. brochus* is usually excluded from *A. nasuta* by *G. histrio*. The removal of *G. histrio* in the competitive removal experiment gave *G. brochus* access to colonies of *A. nasuta* from which it was previously excluded. Interspecific effects on habitat use have been demonstrated for other coral-reef fish (Ebersole 1985, Robertson and Gaines 1986, Clarke 1992) but only Robertson (1996) has previously demonstrated a link between changes in microhabitat use and an increase in abundance following the removal of a competitively dominant species.

G. rivulatus and *G. unicolor* do not compete for habitats with *G. histrio*. In the field *G. rivulatus* usually inhabits *A. gemmifera* rather than *A. nasuta* (Munday et al. 1997) and laboratory experiments demonstrated that this was due to preference rather than exclusion by *G. histrio*. As predicted, the abundance of *G. rivulatus* did not change when *G. histrio* was removed in the field. *G. unicolor* has a high percent similarity in habitat use with *G. histrio*, however, these species did not compete for space in the laboratory. *G. unicolor* is frequently observed to co-habit coral colonies with *G. histrio* and other species of *Gobiodon* in the field (Patton 1994, Munday et al. 1999). Therefore, this species does not appear to compete for space with *G. histrio* and as predicted the abundance of *G. unicolor* did not change when *G. histrio* was removed in the field.

G. quinquestrigatus and *G. histrio* have high percent similarity in habitat use and the competitive ability experiments demonstrated that *G. quinquestrigatus* is an inferior competitor. However, *G. quinquestrigatus* does not appear to be competing with *G. histrio* in the field because its abundance was not influenced by the removal of *G.*

histrio. The recolonisation experiment revealed that the colonies of *A. nasuta* inhabited by *G. quinquestrigatus* were nearly always recolonised by *G. quinquestrigatus*. In contrast, colonies of *A. nasuta* inhabited by *G. histrio* and *G. axillaris* are recolonised by a range of species, but mostly by *G. histrio*. The colonies of *A. nasuta* occupied by *G. quinquestrigatus* usually have subtle differences in branch structure and colour compared to those occupied by *G. histrio* and *G. axillaris* (pers obs). These results suggest that *G. quinquestrigatus* is using a different component of the *A. nasuta* population than that used by *G. histrio* and *G. axillaris*. Therefore, these species might not be competing for the same coral colonies in the field. Also, in comparison to other species, *G. quinquestrigatus* has a more generalist pattern of habitat use within and among geographic locations (Munday et al. 1997, Chapter 3). In particular, across geographic locations *G. quinquestrigatus* inhabits more species of *Acropora* than any other species of *Gobiodon* and patterns of habitat use within locations varied considerably from one location to another (Chapter 3). This generalist pattern of habitat use might mediate competitive effects by providing access to a variety of corals for which competition is not as intense.

Effects on abundance of post-settlement processes such as competition are expected to vary spatially and temporally due to variable supply of new recruits and interactions with other processes (Forrester 1990, Jones 1991, Caley et al. 1996). Detecting effects of competition may be difficult because of these interactions or because competition is sometimes relatively unimportant compared to other processes (Steele 1998). In this study, however, significant differences between treatments and controls were detectable with only small changes in absolute abundance of the interacting species. This indicates that the effects of competition on these species are strong and consistent at the scale studied here.

The exact mechanism of competition among coral-dwelling gobies is likely to be a combination of space exploitation and aggressive interference behaviour to prevent establishment of new recruits or to displace resident fish from superior coral colonies. The recolonisation experiment demonstrated that vacant coral colonies are quickly reoccupied by new recruits or larger fish that have apparently moved from nearby corals. Given that most coral colonies are only occupied by a pair of adult gobies but vacant corals are quickly colonised by new recruits, it seems likely that settlers are generally excluded from occupied corals as a result of agonistic behaviour from resident fish. In cases where adults and new recruits have been found on the same coral colonies I have observed agonistic behaviour by the resident adults towards the recruits.

The movement of adults into vacant corals in the recolonisation experiment indicates that adults are probably aware of the occupancy status of neighbouring coral colonies and are prepared to move into vacant corals of superior quality to those currently occupied. During the laboratory experiments individuals were observed to chase and in some cases fight each other, in order to gain sole access to prefered species of corals. Therefore it seems likely that coral gobies will defend their own coral colony from intruders in the field and might also attempt to displace resident fish from neighbouring corals where these corals are of superior quality. Because body size and prior residency were found to be important in determining the outcome of competitive interactions in the laboratory, it is likely that these factors will determine the outcome of competitive interactions in the field. Indeed there is a good correlation between the coral colony size and the size of resident fish for both *Gobiodon histrio* (Munday unpublished data) and *Paragobiodon* (Kuwamura et al. 1994). Such a pattern might be expected where habitat quality increases with size and where fish compete for the best habitat but the outcome of competitive interactions is dependent on the relative size of the competing individuals.

Although there has been considerable theoretical work on competitive lotteries in guilds of reef fishes (e.g., Sale 1977, Chesson and Warner 1981, Warner and Chesson 1985), little empirical support has emerged for such systems (Robertson 1995). A major tenet of lottery models is that species have equivalent competitive ability (Chesson 1991). Competitive ability and the outcome of competitive interactions are mostly asymmetrical in the coral-dwelling gobies studied here. In particular, the outcome of competitive interactions are largely dependent on the species involved in the competitive interaction, body size and to a lesser degree, prior residency. These characteristics are also important in determining the outcome of competition among Caribbean damselfishes (Ebersole 1985, Robertson 1995, 1996).

Body size appears to be the major factor determining the outcome of competitive interactions in the damselfishes studied by Robertson, although species effects may limit size effects where the smaller species is very aggressive (Robertson 1995). Schmitt and Holbrook (1999) also report asymmetric effects of competition between two species of damselfishes in Moorea. Therefore, in cases where interspecific competition has been shown to influence distributions and abundances of reef fishes it is unlikely that lottery systems are operating.

Demonstrated effects of interspecific competition on the abundances of coral-reef fishes are so far confined to small patches of reef (10's- 100's m^2 - Robertson 1996, this study) or individual coral heads (Sweatman 1985, Schmitt and Holbrook 1999). Whether competition can influence the distribution and abundance of species at larger spatial scales remains to be determined. For example, the distributions of *G. axillaris* and *G. histrio* overlap on individual reefs but there is clear partitioning of these two species between reef zones (Munday et al 1997, Chapter 3). *G. axillaris* is most abundant on the reef flat whereas *G. histrio* is most abundant on the reef crest. This distribution pattern is consistent with the concept of habitat partitioning due to competition. Alternatively, this patterns might simply be determined by preferences at settlement for particular reef zones and reef types as observed in other coral-reef fishes (Wellington 1992, Doherty et al. 1996, Gutierrez 1998). Competitor removal experiments, similar to those conducted here, could be used to determine if this distribution pattern is a result of current competition or other ecological processes. *G. axillaris* and *G. histrio* also have opposite patterns of abundance at larger spatial scales. For example, *G. histrio* is most abundant on reefs sheltered from prevailing winds, whereas *G. axillaris* is most abundant on reefs exposed to prevailing winds. Also, these two species exhibit opposite gradients in abundance from the south to the north of the Great Barrier Reef (Munday et al. 1999, Chapter 3). Competition for space is unlikely to explain partitioning at these spatial scales. A valid multi-scale model of the distribution and abundance of *Gobiodon* species might incorporate (1) physiological tolerances and broad patterns of larval distributions at large spatial scales, (2) macrohabitat selection and patchy larval supply among reefs and reef zones, (3) microhabitat selection and competition within reefs.

Interspecific competition has mostly been shown to influence the abundance of relatively small, sedentary or territorial fishes (Hixon 1980, Schmitt and Holbrook 1990, 1999, Robertson 1996, this study). The species studied here are very small, site attached species with specialised habitat requirements. Experimental manipulations of habitat availability (Buchheim and Hixon 1992) and predictable changes in abundances following natural changes to habitat availability (Kuwamura et al. 1994, Clarke 1996) indicate that other small, habitat-specialised species are limited by the availability of habitats. There are many small, habitat-specialised species of fish on coral reefs (Munday and Jones 1998) and it may be among these species that the effects of interspecific competition for space will become most apparent.

CHAPTER 5: FITNESS CONSEQUENCES OF HABITAT SELECTION AND COMPETITION AMONG CORAL-DWELLING FISHES

5.1. ABSTRACT

Differences in individual fitness among habitats may explain patterns of habitat selection and the role of competition for habitats. I used a transplant experiment in the field to examine growth and survival of two competing species of coral-dwelling fish (*Gobiodon histrio* and *G. brochus*) that inhabit two species of coral (*Acropora nasuta* and *A. loripes*) at Lizard Island on the Great Barrier Reef. For *G. histrio* growth was 3 times higher and survival was 5 times higher on *A. nasuta* compared to *A. loripes*. These fitness advantages may explain the consistent selection of *A. nasuta* observed for *G. histrio* in previous studies. The fitness advantages of inhabiting *A. nasuta* may also explain the strong competition for colonies of *A. nasuta* exhibited by *G. histrio*. In the field *G. brochus* mostly inhabits *A. loripes*, however, growth rates were 2.5 times higher on *A. nasuta* compared to *A. loripes*. This demonstrates a fitness cost to inhabiting *A. loripes* as a result of exclusion from *A. nasuta* colonies by *G. histrio*. Survivorship of *G. brochus* was higher on *A. loripes* in the first four months of the experiment and then higher on *A. nasuta* in the second six months of the experiment. Low survival of *G. brochus* on *A. nasuta* in the first four months was partly attributed to competition with *G. histrio*.

The results of this experiment were then used in a predictive model of lifetime reproductive success for individuals inhabiting each species of coral. For *G. histrio* the model predicted an order of magnitude greater reproductive success individuals inhabiting *A. nasuta* compared to those inhabiting *A. loripes*. For *G. brochus* the model predicted approximately equal reproductive success for individuals inhabiting *A. nasuta* or *A. loripes*. The predicted lifetime reproductive success was lower in *A. nasuta* because of the low early survivorship in this coral. Estimated lifetime reproductive success for *G. brochus* was 40% higher when calculated for individuals that first inhabited *A. loripes* and then moved to *A. nasuta*

when they reached a larger size. Size distributions of *G. brochus* in the field support an ontogenetic habitat-shift strategy. Small *G. brochus* are usually found on *A. loripes* and only the largest *G. brochus* inhabit *A. nasuta.*

5.2. INTRODUCTION

Animals are expected to select habitats where their survival and reproductive success is high (Orians and Wittenberger 1991). However, density dependent habitat selection or interspecific competition can reduce the proportion of preferred habitats used by a species (Pimm and Rosenzweig 1981, Werner and Gilliam 1984, Rosenzweig 1991). Where competition results in the use of inferior habitats there are likely to be effects on growth, survival and reproductive output (Huey 1991, Conradt et al. 1999). Furthermore, species interactions usually have asymmetrical effects which favour superior competitors (Connell 1983, Schoener 1983, Persson 1985). Therefore, where interspecific competition influences the use of preferred habitats, superior competitors are expected to have disproportionate effects on the growth, survival and reproductive output of inferior competitors.

Many coral-reef fish associate with particular microhabitats (Sale 1991a), perhaps because reproductive fitness is greatest in these habitats. Reef fish have a dispersive, pelagic larval phase followed by more sedentary juvenile and adult reef associated phases (Leis 1991, Victor 1991). Microhabitat associations are frequently the result of habitat selection during the transition from the pelagic to the reef environment (Williams and Sale 1981, Sale et al. 1984, Eckert 1985, Booth 1992, Elliott et al. 1995, Tolimieri 1995, Danilowicz 1996, Gutiérrez 1998, Ohman et al. 1998). Therefore, it appears that many coral-reef fish actively select habitats at settlement that might favour their individual fitness. For some other species, patterns of habitat use change with ontogeny (Helfman 1978, Waldner and Robertson 1980, Shulman and Ogden 1987, Lirman 1994) possibly due to size-related changes in individual fitness or physiological requirements (Munday and Jones 1998). While the relationship between microhabitat association and the abundance of coral-reef fish has been widely studied (see reviews by Jones 1991, Williams 1991) at a variety of scales (Tolimieri 1995, Caselle and Warner 1996, Munday et al. 1997, Chapter 3), less attention has been given to fitness consequences of habitat use by coral-reef fish. Microhabitat use is known to influence mortality of coral-reef fish (Shulman 1984, Jones 1988, Hixon and Beets, 1989, 1993, Caley and St John 1996, Tolimeri 1995, Nemeth 1998) but the effects of microhabitat use on growth and reproduction are poorly understood (Jones 1991).

Interspecific competition also influences habitat use of some coral-reef fishes (Ebersole 1985, Robertson and Gaines 1986, Robertson 1996, Chapter 4). The effects of competition for microhabitats (Ebersole 1985, Chapter 4) or larger areas of reef (Robertson and Gaines 1986, Robertson 1996) are usually asymmetrical. In general, larger species or superior competitors exclude smaller species or inferior competitors from particular microhabitats or sections of reef (Ebersole 1985, Robertson and Gaines 1986, Robertson 1996, Chapter 4). If habitats influence growth rates, mortality or reproduction then competition that reduces the use of preferred habitats will have consequences for the fitness of competing individuals.

Some of the most habitat specialised fishes on coral reefs are obligate coral-dwelling gobies of the genus *Gobiodon*. These small fish (< 60 mm total length) live among the branches of corals mostly from the genus *Acropora* (Munday et al. 1997, 1999). At Lizard Island on the Great Barrier Reef, each species of *Gobiodon* uses one or two species of *Acropora* much more frequently than expected by chance (Munday et al. 1997). For most species of *Gobiodon*, these patterns of habitat use appears be the result of habitat selection (Chapters 3 and 4). Also, some species of *Gobiodon* compete for coral colonies on reefs at Lizard Island (Chapter 4) and this might be expected if preferred corals offer considerable fitness advantages.

G. histrio and *G. brochus* are two of the species that compete for habitat space at Lizard Island (Chapter 4). Field observations and experiments have shown that *G. histrio* is a dominant competitor among the species of *Gobiodon* at Lizard Island (Chapter 4). *G. histrio* mostly inhabits *Acropora nasuta* (Munday et al. 1997) and laboratory experiments indicate that this pattern of habitat use is the result of habitat selection (Chapter 4). In contrast, *G. brochus* usually inhabits *A. loripes* (Munday et al. 1997, Chapter 3) and only the largest individuals of this species are found in colonies of *A. nasuta* (Table 5.1). In laboratory experiments *G. histrio* excludes *G. brochus* from colonies of *A. nasuta* unless *G. brochus* individuals are larger than competing individuals of *G. histrio* or are an equal size and have established prior residency of a vacant coral colony (Chapter 4). Therefore, it appears that *A. nasuta* is a preferred coral for both species of *Gobiodon* but interspecific competition limits the occurrence of *G. brochus* in *A. nasuta*. If inhabiting *A. nasuta* confers advantages to growth rates or survival for *G. histrio* this would demonstrate the fitness advantage of strong habitat selection and competition for colonies of *A. nasuta*. If inhabiting *A. nasuta* also confers advantages to growth rates or survival for *G. brochus* this would demonstrate the fitness consequences of exclusion from *A. nasuta* by competitive interactions with *G. histrio*. Here I use transplant experiments in the field to determine growth rates and survival of *G. histrio* and *G. brochus* in colonies of both *A. nasuta* and *A. loripes*. I then use these results in a predictive model the lifetime reproductive output for each species of *Gobiodon* in each species of coral. In this way I am able to investigate the costs and advantages of inhabiting each species of coral for both species of fish.

5.3. METHODS

Transplant experiments

To compare growth and survival of *G. histrio* and *G. brochus*, I transplanted juvenile fish of each species to approximately equal sized coral colonies of both *A. nasuta* and *A. loripes* during January 1997. Growth and survival of coral-reef fish can depend on the location inhabited, independently of microhabitat characteristics (Thresher 1983a, b, Jones 1986, 1997, Forrester 1990, Wellington 1992). Therefore, all coral colonies used in this experiment were located on one large patch reef between Palfrey Island and South Island in the Lizard Island lagoon ($14^0 40' $ S, $145^0 28'$ E). Colonies of *A. nasuta* and *A. loripes* on this reef were cleared of resident fish and other infauna (crabs and shrimps) that could influence the successful introduction of transplanted fish (Lassig 1977). Each coral was individual tagged with a coded metal-washer secured to a branch of the coral colony with a plastic cable-tie and the location of all tagged corals was mapped.

Juvenile *G. histrio* and *G. brochus* were collected from colonies of the corals they usually inhabit at Lizard Island (*A. nasuta* and *A. loripes* respectively) and transplanted to both *A. nasuta* and *A. loripes*. Fish were collected by anaesthetising the fish with clove-oil (Munday and Wilson 1997). *G. histrio* has two colour forms (spotted and striped forms) which occur in approximately equal frequency at Lizard Island (Munday et al. 1999). Because these two forms have identical patterns of habitat use I did not distinguish between them in this study. Fish were collected from reefs other than the one used in this experiment to prevent the possibility that transplanted fish would move back to their original coral colonies following release. Fish were transported to the laboratory, re-anaesthetised, measured (standard length (SL) to 0.1mm) and individually marked with a small fluorescent-elastomer tag injected into the dorsal musculature (North-West Technologies). The use of two tagging colours and three locations on two sides of the body allowed a sufficient number of tagging combinations for individual identification. Micro-tagging techniques have little effect on the mortality rates of coral-reef fish (Beukers et al. 1995) and tag loss is infrequent when fluorescent-elastomer tagging is used on coral-dwelling gobies (Munday unpublished data). Moreover, any potential mortality or tag loss are expected to be spread equally among the treatment fish and, therefore, should not affect the comparisons in this study. Tagged fish were held for 24 hours in aquaria with a continuous flow of fresh sea water to ensure recovery following the tagging procedure. Fish were then transported to the reef and one fish was released on each of the marked coral colonies. A total of 91 fish were transplanted and each fish was observed for several minutes following release to ensure it had successfully colonised the new coral colony.

The growth and survival of transplanted fish was estimated after four months and again after ten months. Fish were collected from each marked coral colony by anaesthetisation with clove oil and the SL of each tagged fish was measured to the nearest 0.1mm. Tagged fish were returned to their coral colonies after measuring at the four month census. To distinguish movement from mortality where a marked fish was not present at either census, all suitable coral colonies in the vicinity of the marked coral were searched for the presence of marked fish. Obligate coral-dwelling gobies are highly sedentary and monitoring of coral gobies on the reef used in this study revealed that movement was infrequent and, where it did occur, was limited to movement among coral colonies separated by only a few metres reef (Munday unpublished data). Also, the reef used in this study was separated from neighbouring reefs by a sandy substratum of at least 20 metres and movement beyond the reef perimeter can be assumed to be negligible. Therefore, by searching nearly all the suitable coral colonies on the patch reef I was able to reliably distinguish movement from mortality for tagged fish not found in either census. I used a fixed factor, repeated measures ANOVA to examine variation in growth per month of each species of fish inhabiting each species of coral and variation in growth between the first and second time intervals. Data were square root transformed to improve normality and only cases where growth was estimated for both time intervals were included in this analysis.

Modelling lifetime reproductive success

To predict lifetime reproductive success for each species of *Gobiodon* in each species of coral I combined the growth rate and survivorship data collected in the transplant experiments with data on the reproductive success of coral-dwelling gobies published by Kuwamura et al. (1993). Coral-dwelling gobies from the genera *Gobiodon* (Nakashima et al. 1996, Munday et al. 1998) and *Paragobiodon* (Lassig 1976, 1977, Kuwamura et al. 1993, 1994, 1996) form monogamous breeding pairs where the male and female are closely matched in size and only a single breeding-pair inhabits a coral colony. At each spawning the pair lays a single clutch of eggs on a branch of their host coral and the male defends the eggs (Lassig 1976, 1977, Kuwamura et al. 1993, Nakashima et al. 1996, personal observations). Kuwamura et al. (1993) have shown that reproductive success per spawning (number of newly hatched larvae) for *Paragobiodon echinocephalus* is determined by the size of each individual in the pair and can be estimated by the simple linear regressions; $y = 3.190 + 0.734x$ for females and $y = 1.921 + 0.784x$ for males, where x = mm total length (TL) and y = square root transformed reproductive success. The slopes and intercepts of these equations do not differ significantly between sexes (Kuwamura et al. 1993). Given the very similar mating system and reproductive biology of *Gobiodon* and *Paragobiodon* species (Kuwamura et al. 1993, 1994, Nakashima et al. 1995, 1996, Munday et al. 1998) the relationships between body size and reproductive success are likely to be similar for species from these two genera. I used the average of the equations reported by Kuwamura et al. (1993; $y = 2.56 + 0.76x$) to estimate reproductive success per spawning for coral gobies in this study.

The results of the transplant experiment were used to estimate the size of each species of goby on each species of coral at monthly intervals. Growth rates after 10 months were assumed to be the same as those between 6 - 10 months in the transplant experiment and then zero when the maximum recorded body size (Chapter 4) of each species was attained. Estimates of body size in SL were transformed to TL because Kuwamura's equation for reproductive success uses TL. The relationship between SL and TL ($TL = 1.22SL - 0.24$, $R^2 = 0.998$) was estimated from 60 *G. histrio* randomly collected at Lizard Island with body sizes covering the range from new recruits to maximum adult size. I then used the estimated TL at monthly intervals and Kuwamura's equation to calculate reproductive success per month for each species of goby in each species of coral. Coral dwelling gobies spawn at approximately weekly intervals (Lassig 1976, 1977, Kuwamura et al. 1993), although spawnings appear to be far fewer during winter (personal observations). Therefore, I multiplied reproductive success per spawning by 2 to estimate the average reproductive success per month (m_x).

Survival rates from the transplant experiment were used to calculate the proportion of individuals surviving (l_x) at monthly intervals for each species of fish on each species of coral. Survival rates after 10 months were assumed to be the same as those between 6 - 10 months in the experiment. I used a standardised cohort of 10 individuals to commence each calculation and the proportion of individuals surviving was considered to be 0 when the estimated number of individuals remaining was <1. Following Kuwamura et al. (1996) and standard life-table analysis (Stearns 1992), lifetime reproductive success (R_0) was calculated using the formula;

$$R_0 = \sum l_x m_x$$

5.4. RESULTS

Growth and survival

The average size of fish at the beginning of the experiment was 22.1 mm SL and there was no significant difference in the size of individuals transplanted to each species of coral either within species (Fig 5.1; t-test *G. histrio*, $t = 0.55$, df = 21, $p = 0.59$; *G. brochus*, $t = 1.65$, df = 17, $p = 0.12$) or between the two species of *Gobiodon* (Fig 5.1; t-test $t = 0.84$, df = 40, $p = 0.41$). Both *G. histrio* and *G. brochus* grew faster on *A. nasuta* compared to *A. loripes* (Fig 5.1, Table 5.2) and there was a significant difference in growth between the two species of fish (Table 5.2). Growth also differed with time (Table 5.2). In the first four months individuals of *G. histrio* grew over 3 times faster on *A. nasuta* compared to individuals on *A. loripes* (Table 5.3). Similarly, individuals of *G. brochus* grew over 2.5 faster on *A. nasuta* compared to individuals on *A. loripes* (Table 5.3). In the following six months growth rates of both species slowed, however, both *G. histrio* and *G. brochus* still grew over 3 times faster on *A. nasuta* compared to *A. loripes* (Table 5.3). Over the course of the experiment the ratio of mean monthly growth rate in *A. nasuta* versus mean monthly growth rate in *A. loripes* was larger for *G. histrio* (3.2) than *G. brochus* (2.7) indicating that the consequences on growth of using *A. loripes* rather than *A. nasuta* were more severe for *G. histrio* than *G. brochus*.

Survivorship of *G. histrio* was over 5 times higher on *A. nasuta* than on *A. loripes* (Fig 5.2). Only 5 of 39 (12.8%) *G. histrio* transplanted to *A. loripes* survived for ten months and most of this mortality occurred in the first four months (Table 5.4). In contrast 9 of 14 (64.3%) *G. histrio* transplanted to *A. nasuta* survived for ten months (Table 5.4). Overall survivorship of *G. brochus* was approximately equal on *A. nasuta* (21.7%) and *A. loripes* (26.7%) (Fig 5.2). However, survival of *G. brochus* in the first four months was much higher on *A. loripes* compared to *A. nasuta* (Fig 5.2, Table 5.4). In nearly all the cases where an individual of *G. brochus* was missing from a colony of *A. nasuta* after the first four months it had been replaced by *G. histrio*. In the final six months, when individuals of *G. brochus* were larger, the survivorship of *G. brochus* was higher on *A. nasuta* compared to *A. loripes* (Table 5.4).

Modelling Reproductive success

The predicted lifetime reproductive success of individuals using either *A. nasuta* or *A. loripes* differed greatly between the two species of fish (Fig 5.3). The predicted lifetime reproductive success of *G. histrio* was over an order of magnitude greater on *A. nasuta* compared to *A. loripes* (Fig 5.3). This was largely due to the very high survivorship of individuals on *A. nasuta* compared to *A. loripes*. Individuals of *G. histrio* were estimated to survive for up to 48 months after the start of the experiment. This is consistent with a known longevity of at least 4 years for tagged individuals of *G. histrio* inhabiting colonies of *A. nasuta* at Lizard Island (Munday unpublished data). The predicted lifetime reproductive success of *G. brochus* inhabiting *A. nasuta* and *A. loripes* was approximately equal (Fig 5.3). This similarity in predicted lifetime reproductive success, despite higher growth rates and reproductive potential in *A. nasuta*, was largely due to the much lower survival rate of *G. brochus* in *A. nasuta* during the first four months of the experiment. During this time *G. brochus* individuals were frequently replaced by *G. histrio*.

To model the effect on lifetime reproductive success of movement by *G. brochus* from *A. loripes* to *A. nasuta* once a larger body size had been attained, I estimated lifetime reproductive success for individuals that first inhabited *A. loripes* and then moved to *A. nasuta* after 4 months. The estimated lifetime reproductive success was approximately 40% higher for individuals that moved to *A. nasuta* once they attained a larger body size compared to individuals that inhabited only *A. nasuta* or *A. loripes* (Fig 5.4).

TABLE 5.1. Average and maximum standard length (SL) of *Gobiodon brochus* collected from randomly selected colonies of *Acropora nasuta* and *A. loripes* at Lizard Island. t-test on mean size; $t = 7.58$, $p < 0.001$.

Coral species	Number	Mean SL	Maximum SL
A. nasuta	9	28.0	29.7
A. loripes	9	22.4	24.8

TABLE 5.2. Results of repeated measures ANOVA for monthly growth rates of *G. histrio* and *G. brochus* (species) inhabiting *A. nasuta* and *A. loripes* (coral) over two consecutive time intervals (time).

Source of variation	MS	df	*F*	*P*
Between subjects				
Coral	2.077	1	70.01	<0.001
Species	0.171	1	5.764	0.027
Coral*Species	0.0008	1	0.028	NS
Error	0.0297	19		
Within subjects				
Time	3.152	1	45.77	<0.001
Time*Coral	0.174	1	2.521	NS
Time*Species	0.174	1	2.521	NS
Time*Coral*Species	0.001	1	0.019	NS
Error	0.069	19		

TABLE 5.3. Mean monthly growth rates (mm SL) of *G. histrio* and *G. brochus* transplanted to colonies of *A. nasuta* and *A. loripes*.

Species	0-4 months		4-10 months	
	A. nasuta	*A. loripes*	*A. nasuta*	*A. loripes*
G. histrio	1.63 (n=12)	0.52 (n=11)	0.46 (n=9)	0.15 (n=5)
G. brochus	1.34 (n=9)	0.50 (n=10)	0.18 (n=5)	0.06 (n=4)

TABLE 5.4. Number of individuals surviving and (monthly survival rate) of *Gobiodon histrio* and *G. brochus* transplanted to *Acropora nasuta* and *A. loripes*.

Species	0-4 months		4-10 months	
	A. nasuta	*A. loripes*	*A. nasuta*	*A. loripes*
G. histrio	12 /14 (0.9622)	11/39 (0.7288)	9/12 (0.9532)	5/11 (0.8769)
G. brochus	9/23 (0.7909)	10/15 (0.9036)	5/9 (0.9067)	4/10 (0.8584)

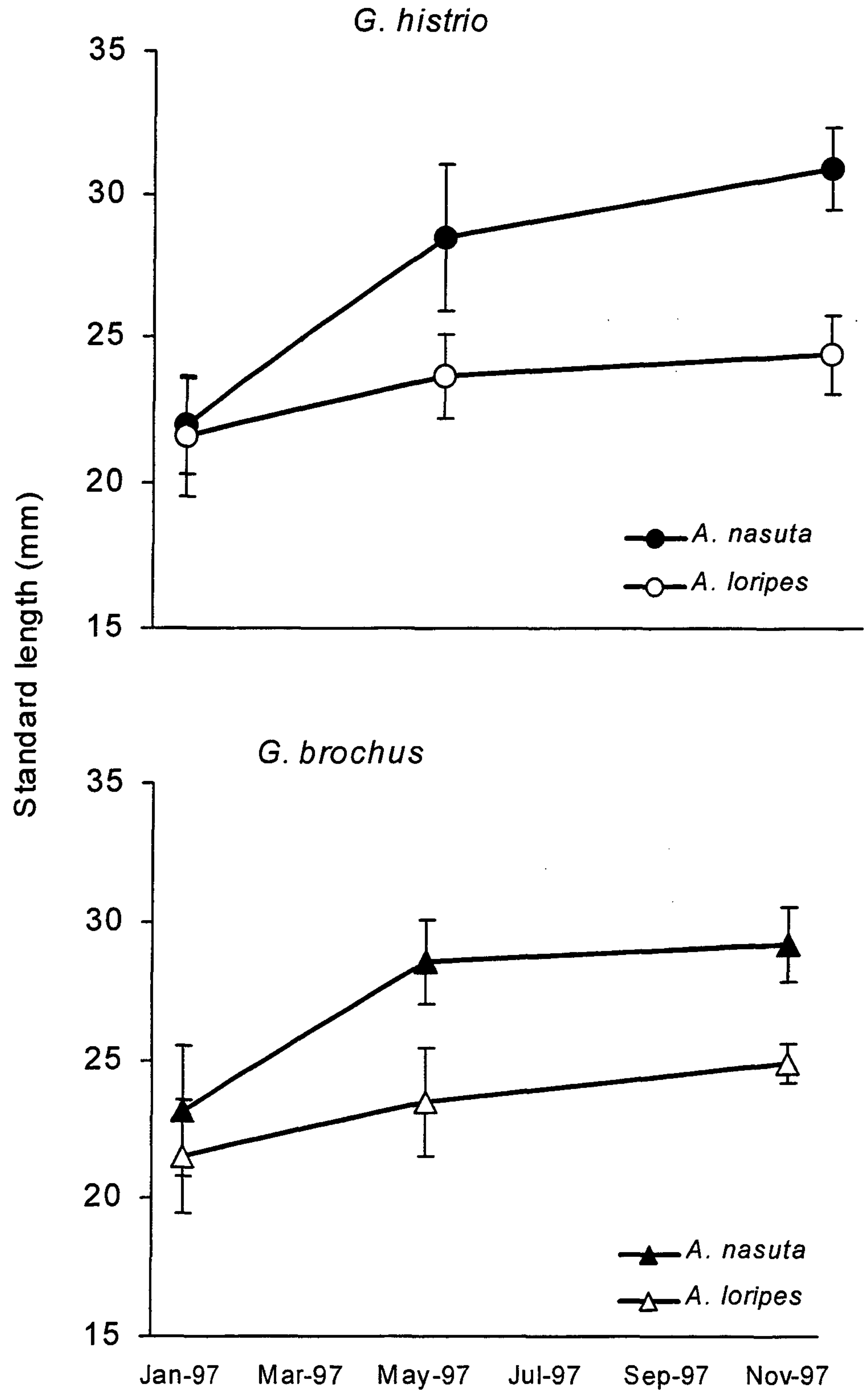

Fig. 5.1. Mean standard length ± SD of *G. histrio* and *G. brochus* after 0, 4 and 10 months inhabiting *A. nasuta* and *A. loripes*.

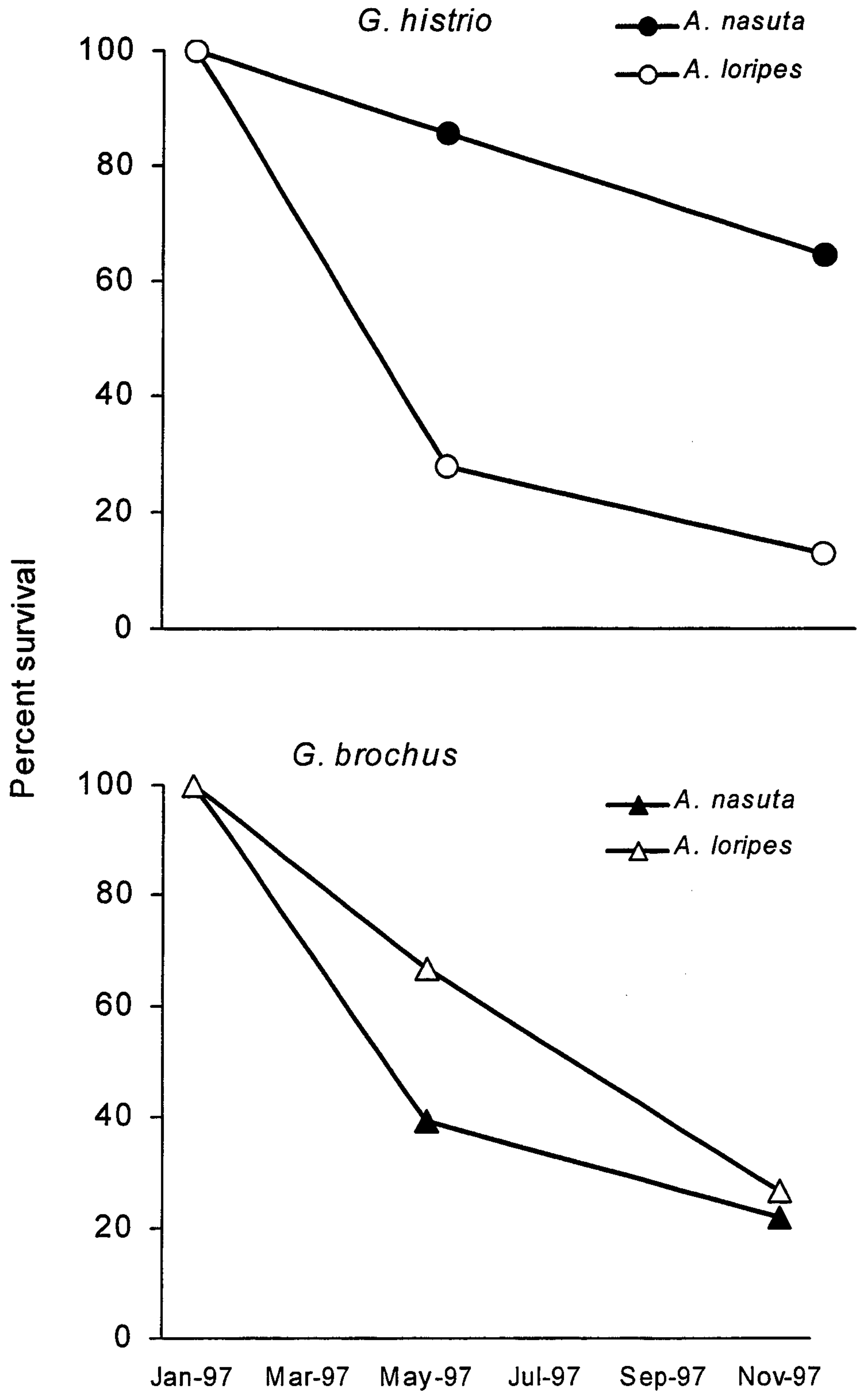

Fig. 5.2. Percent survival of *G. histrio* and *G. brochus* after 4 and 10 months inhabiting *A. nasuta* and *A. loripes*.

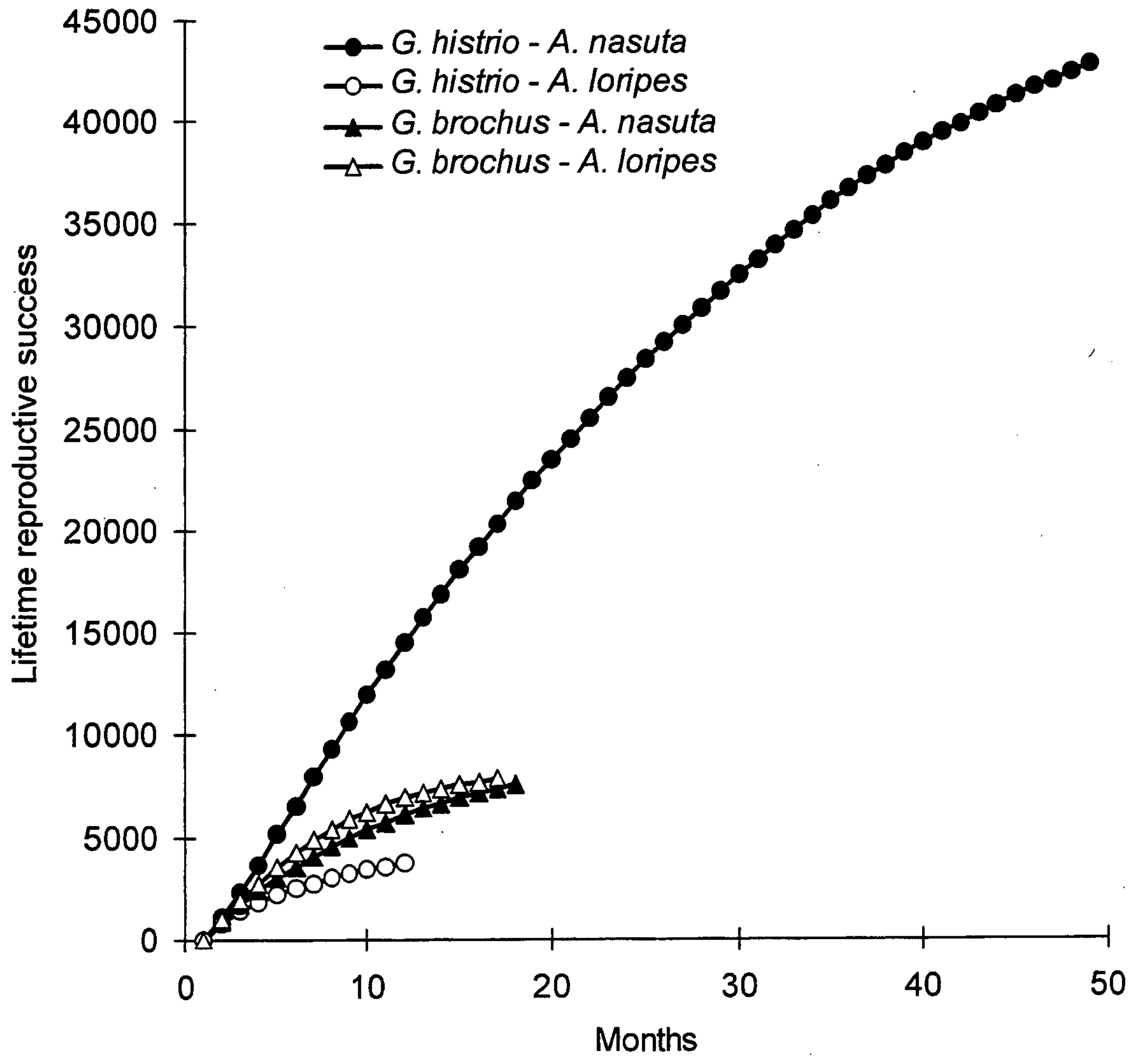

Fig. 5.3. Lifetime reproductive success estimated for individuals of *G. histrio* and *G. brochus* inhabiting *A. nasuta* and *A. loripes*.

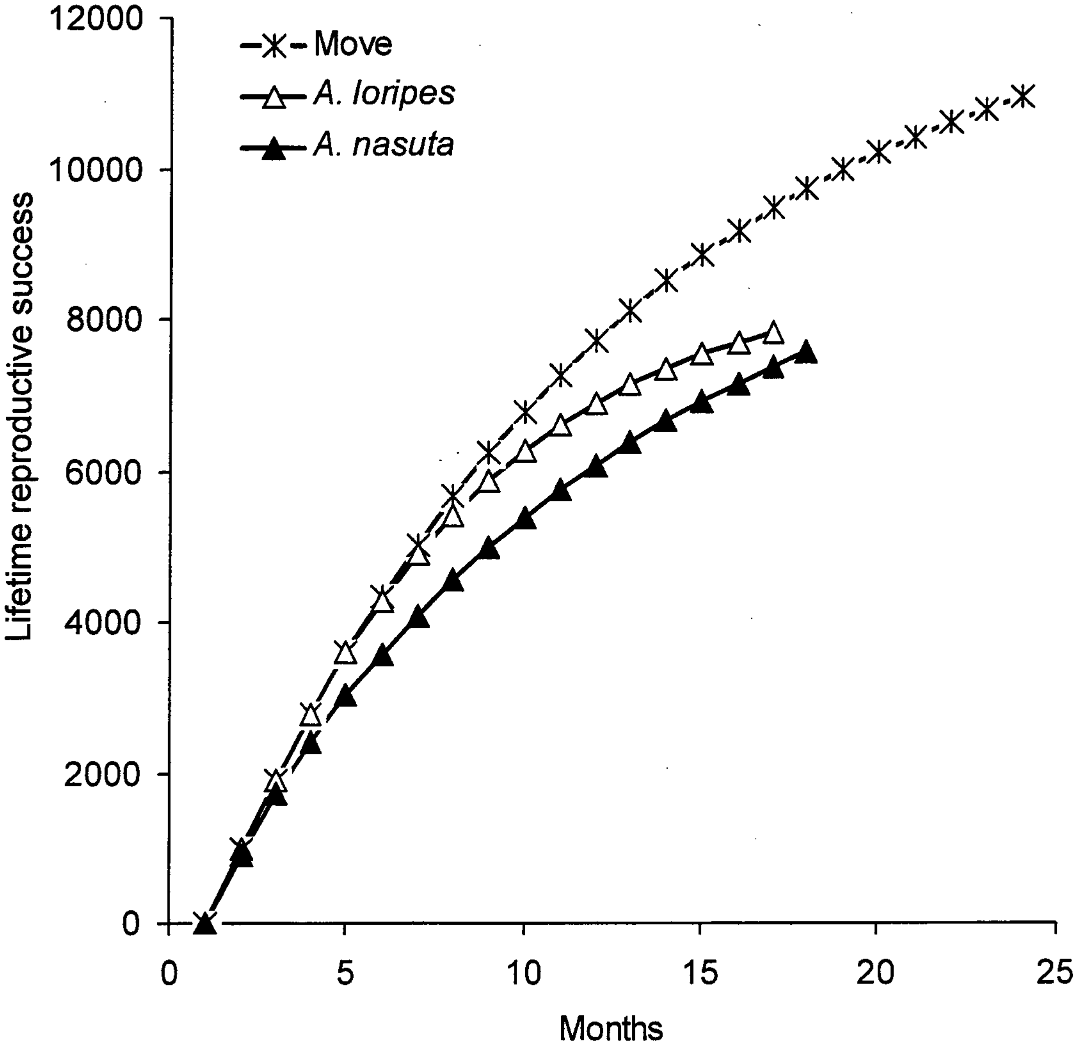

Fig. 5.4. Lifetime reproductive success estimated for individuals of *G. brochus* inhabiting only *A. loripes,* only *A. nasuta,* or moving from *A. loripes* to *A. nasuta* after 4 months.

5.5. DISCUSSION

Determining the fitness consequences of using different habitats is essential for understanding the roles of habitat selection and competition for habitats (Rosenzweig 1991, Conradt 1999). Although many coral-reef fish associate with particular habitats, often as a result of habitat selection at settlement, the reasons for these associations are rarely known (Sale 1991a). The benefits of high growth and survival for *G. histrio* individuals inhabiting *A. nasuta* could easily explain the strong habitat selection for *A. nasuta* exhibited by *G. histrio* (Chapter 4) and the consistent use of this coral species across geographical spatial scales (Chapter 3). *G. brochus* also grew faster in *A. nasuta* compared to *A. loripes* and had approximately equal survival in both species of coral across the duration of the experiment. Consequently, *G. brochus* might also be expected to inhabit *A. nasuta*, however, it is most commonly found in *A. loripes* (Munday et al. 1997). Experiments in the laboratory have shown that *G. brochus* is usually excluded from *A. nasuta* by the presence of *G. histrio* and only large *G. brochus* are able to defend colonies of *A. nasuta* from *G. histrio* (Chapter 4). Reduced growth in *A. loripes* demonstrates a potential fitness cost of exclusion from *A. nasuta* due to competition with *G. histrio*. Interspecific effects on habitat use have been demonstrated for many animals (Connell 1983, Schoener 1983, Roughgarden 1989) including some coral-reef fishes (Robertson and Gaines, 1986, Robertson 1996, Chapter 4), however, rarely have the fitness costs of competition been demonstrated.

The intensity of competition for habitats should be related to the consequences of using alternative habitats. The consequences of using *A. loripes* rather than *A. nasuta* were greater for *G. histrio* than *G. brochus*. Firstly, the effect of coral species on growth rates was strongest for *G. histrio*. Secondly, the effect of coral species on survivorship was much greater for *G. histrio*. Therefore, *G. histrio* is expected to compete most strongly for colonies of *A. nasuta*. This conforms with laboratory and field experiments which have found *G. histrio* to be a dominant competitor among the species of coral-dwelling gobies present at Lizard Island (Chapter 4).

When increased growth rates in a preferred habitat are combined with higher survivorship, as demonstrated for *G. histrio*, the fitness benefits of using that habitat are substantial. For *G. histrio* the model of lifetime reproductive success predicts the combined benefits of increased growth and survival may result in an order of magnitude difference in lifetime reproductive output between individuals inhabiting *A. nasuta* compared to those inhabiting *A. loripes*. For *G. brochus* growth was higher in *A. nasuta* but survival was lower in *A. nasuta* in the first four months, apparently because many *G. brochus* individuals were evicted by *G. histrio*. This represents a trade-off between growth and survival for individuals inhabiting either species of coral in the first few months. The model of lifetime reproductive success predicts that individuals are equally successful whether inhabiting *A. nasuta* or *A. loripes* and this result is largely driven by this trade-off between growth and survival.

Lifetime reproductive success of *G. brochus* is predicted to increase substantially if individuals first inhabit *A. loripes* and then move to *A. nasuta* when they reach a larger size. Indeed, this is what appears to happen in the field. Small to moderate sized *G. brochus* are common in colonies of *A. loripes* while the largest *G. brochus* are found in colonies of *A. nasuta*. This distribution among corals is consistent with size-specific movement from *A. loripes* to *A. nasuta*. Individuals recruiting to *A. loripes* would avoid competition with *G. histrio* while small and then benefit from increased growth if they move to a vacant colony of *A. nasuta* when they reach a large enough size to prevent exclusion by *G. histrio*. Ontogenetic habitat-shifts are observed in many animals and these shifts are expected to favour individual fitness in the manner predicted for *G. brochus* (Werner and Gilliam 1984).

The estimates of lifetime reproductive success calculated here for *Gobiodon* are based on models of size-related spawning success developed for *Paragobiodon* by Kuwamura et al. (1993). Although the exact relationships between body size and reproductive success are likely to differ between species of *Gobiodon* and *Paragobiodon* it is reasonable to assume the general form of the relationships will be similar between these genera because of the similarity in mating systems and reproductive biology (Kuwamura et al. 1993, 1994, Nakashima et al. 1995, 1996, Munday et al. 1998). In other words, the relative differences in reproductive success estimated here are likely to be a reasonable approximations even if the real absolute values are quite different. Moreover, although it is likely that the exact relationship between body size and reproductive success will differ between the two species of *Gobiodon* considered here, there would need to be very large difference in spawning success between *G. histrio* and *G. brochus* to change the order of estimated lifetime reproductive success between the two species of fish. For example, *G. brochus* would need a six fold greater spawning success than *G. histrio* in order to have the highest reproductive success in *A. nasuta*. Similarly, *G. histrio* would need twice the spawning success of *G. brochus* to have equivalent reproductive success in *A. loripes*. Clearly, differences in growth rates and survivorship have a far greater effect on the estimates of lifetime reproductive success than the differences in spawning success likely to occur between the two species of fish.

Estimates of growth and mortality are associated with error, which when combined could produce considerable variation in the predictions of lifetime reproductive success. The model used here also assumes that growth and survival rates after 10 months are the same as those observed in the 4-10 month period of this experiment. If growth rates do not remain the same after 10 months then the predictions of lifetime reproductive success will be either under or over estimates. More importantly, if any changes in growth are not consistent between the two species of fish or between the corals inhabited then the relative relationships of the predicted estimates will change. Consequently the predictions of lifetime reproductive success must be treated with caution. They do, however, provide testable predictions about the general consequences of patterns of habitat use and competition for habitats.

Estimates of habitat related fitness components can provide insights to a wide range of ecological distributions and behaviours, however, such estimates are rare for reef fish. This study has shown that growth and survival can vary dramatically for fish inhabiting different species of corals. Models of lifetime reproductive success for fish inhabiting these corals provide testable predictions about the potential advantages of habitat selection and the fitness consequences of competition for habitats.

CHAPTER 6: EXPERIMENTAL EVALUATION OF GEOGRAPHIC VARIABILITY IN RECRUITMENT AND GROWTH OF CORAL-DWELLING FISHES

6.1. ABSTRACT

I conducted identical experiments at One Tree Island (southern Great Barrier Reef), Lizard Island (northern Great Barrier Reef), and Kimbe Bay (Papua New Guinea) to investigate the importance of habitat type and availability on patterns of recruitment and growth of obligate coral-dwelling fishes (genus *Gobiodon*). In the first experiment, I monitored recruitment of one competitively dominant species (*G. histrio*) and one competitively subordinate species (*G. quinquestrigatus*) to colonies of a commonly preferred species of coral (*Acropora nasuta*) that had been cleared of resident fish. At Lizard Island and Kimbe Bay, the species of *Gobiodon* that recolonised these coral colonies was highly dependent on the species of *Gobiodon* that previously occupied each coral colony. Small differences in coral colony structure or position of colonies on the reef might be associated with fine-scale habitat partitioning among species of *Gobiodon*, leading to the coexistence of competing species on small spatial scales. At One Tree Island, the species of *Gobiodon* that recruited to vacant colonies of *A. nasuta* was less dependent on the species of *Gobiodon* that previously occupied each coral colony. Consequently, there is less evidence of fine-scale habitat partitioning among species of *Gobiodon* at this location. Competition for vacant colonies of *A. nasuta* may be less intense at One Tree Island because this location has a higher abundance of *A. nasuta* than the other locations.

In the second experiment, I transplanted juveniles of *G. histrio* and *G. brochus* to colonies of *A. nasuta* and *A. loripes* to determine if the consequences of inhabiting different species of coral were consistent among geographic locations. These species were chosen because *G. histrio* is competitively superior to *G. brochus* and these species compete for space at Lizard Island. *G. brochus* usually inhabits *A. loripes* and is excluded from colonies of *A. nasuta* due to competition with *G. histrio*. Growth of *G. histrio* inhabiting *A. nasuta* was similar among all locations. At both

Lizard Island and One Tree Island the growth of both *G. histrio* and *G. brochus* was over two times higher in *A. nasuta* compared to *A. loripes*. Growth of both species of fish was closely correlated with the interbranch space of the coral species inhabited. Therefore, habitat structure appears to be the mechanism underlying habitat related differences in growth.

6.2. INTRODUCTION

Establishing the generality of processes that determine the population ecology of animals is a fundamental goal of ecology. The abundance, behaviour and life histories of animals commonly vary among geographic locations (Ricklefs and Schluter 1993, Foster and Endler 1998). These differences may result from similar processes acting along a biotic or abiotic gradient. Alternatively, these differences may indicate that very different processes influence the population ecology of animals at different locations. Although experiments used to investigate the population ecology of animals are usually conducted on small spatial scales, the use of similar experiments in multiple locations provides the opportunity to test the generality of patterns and processes detected at single locations (Maurer 1999). Despite this, experiments designed to examine the factors influencing important demographic and life history parameters have seldom been repeated across geographical spatial scales.

Coral-reef fish have characteristic habitats in which they are found but the processes determining these patterns of habitat use and how these processes differ among species and locations is still poorly understood (Jones 1991, Williams 1991). Reef fish have a complex life-cycle comprising a pelagic larval phase followed by relatively site-attached juvenile and adult phases. Patterns of habitat use expressed by these species may be a result of one or more processes acting during one or more of these ontogenetic phases (Jones 1991, Forrester 1990, Hixon 1991, Tolimieri 1998). Habitat selection during settlement has been widely reported for coral-reef fish (Sale 1991a) and appears to be a major determinant of distribution patterns among microhabitat types for many reef fishes (Williams and Sale 1981, Sale et al. 1984, Booth 1992, Booth and Beretta 1994, Elliott et al. 1995, Tolimieri 1995, Danilowicz 1996, Gutierrez 1998, Ohman et al. 1998). Patterns of habitat use established at settlement may be modified by predation (Caley 1993, Connell 1997, Eggleston et al. 1997) and the intensity of these modifications may be a function of habitat structure (Hixon and Beets 1993, Caley and St. John 1996). Interspecific competition influences habitat use of some coral-reef fish (Sale et al. 1980, Robertson and Gaines 1984, Ebersole 1985, Hunte and Cote 1989, Clarke 1992, Robertson 1995, Chapter 4) with superior competitors expected to secure the best habitats or territories. Post-settlement movement (Helfman 1978, Shulman and Ogden 1987, Lewis 1997) and ontogenetic habitat shifts (Lirman 1994, Munday and Jones 1997, Chapter 5) may also contribute to observed patterns of habitat use. Determining the effects of these processes on patterns of habitat use at different locations will help establish their general importance to different groups of coral reef fishes.

Individuals may select and compete for particular habitats if they derive benefits in terms of growth, survival or reproductive success in these habitats (Orians and Wittenberger 1991, Conradt 1999). Experimental studies have demonstrated that the survivorship of reef fishes can vary dramatically among habitat types (Jones 1988, Tolimieri 1995, Nemeth 1998, Chapter 5) and often as a direct consequence of habitat structure (Shulman 1984, Hixon and Beets 1993, Caley and St John 1996, Beukers and Jones 1998). Although habitat dependent growth has been widely reported among marine and freshwater fishes (Sebens 1987), the effect of habitat type and habitat structure on the growth of coral-reef fishes is less clear. Growth differs among microhabitat types for some coral reef fishes (Jones 1988, Chapter 5) but does not appear to in others (Wellington 1992, Nemeth 1998). However, the statistical power to detect significant effects has not always been high (Nemeth 1998). Because fecundity is closely linked to body size in fish (Roff 1983) any habitat related differences in growth could have significant effects on individual reproductive success. Detecting habitat related differences in growth and survival will be important for understanding patterns of habitat selection and competition among coral-reef fishes.

Coral dwelling gobies (genus *Gobiodon*) are specialised fishes that live among the branches of live corals, mostly from the genus *Acropora* (Munday et al. 1999).

Because of their close association with branching corals it might be expected that the abundances and demographics of these fish will be closely associated with the availability and structure of the coral colonies they inhabit. Here I use two different experiments, each conducted at three widespread locations, to compare the importance of habitat type on the demographics of coral-dwelling gobies. The three locations are Kimbe Bay (5^0 15' S; 150^0 15' E) in northern Papua New Guinea, Lizard Island (14^0 40' S; 145^0 28' E) on the northern Great Barrier Reef and One Tree Island (23^0 30' S; 152^0 06') on the southern Great Barrier Reef. The populations of fish at these three locations are unlikely to be exchange individuals because they are separated from each other by approximately 1000 km. If similar processes determine patterns of habitat use in these different populations then I would expect similar results from identical experiments conducted at each location. If the processes determining patterns of habitat use differ among locations, or if there is an interaction between local and larger scale processes (eg., Caley 1995b), then the results of experiments should differ among locations.

Species of *Gobiodon* inhabit a range of acroporid corals but certain species of *Acropora* seem to be commonly preferred. For example, *A. nasuta* is preferentially inhabited by one or more species of *Gobiodon* species at all the geographic locations considered here (Chapter 3). If *A. nasuta* is a limited resource then most colonies should be occupied. Also, if a competitive hierarchy among species of *Gobiodon* determines access to preferred corals, then vacant colonies of *A. nasuta* should mostly become reoccupied by competitively dominant species. Subordinate species might recruit to *A. nasuta* but they would be excluded through time by superior competitors. Alternatively, to avoid competition with superior competitors, subordinate species might recruit directly to other corals in locations where access to colonies of *A. nasuta* is limited. This appears to be the case at Lizard Island where a competitive dominant, *G. histrio*, occupies most colonies of *A. nasuta* while a subordinate competitor, *G. quinquestrigatus* recruits to a distinct subset of the *A. nasuta* population (Chapter 4).

In the first experiment in this study, I used a recolonisation experiment conducted at all three locations to determine whether colonies of *A. nasuta* are (1) colonised by both *G. histrio* and *G. quinquestrigatus*, with the subordinate species (*G.*

quinquestrigatus) being excluded through time or, (2) *G. quinquestrigatus* always recruits to a specific subsets of the *A. nasuta* population. I also compare the abundances of *A. nasuta* colonies among locations to determine if changes in the availability of preferred habitats among locations might influence the patterns of recolonisation exhibited by *G. histrio* and *G. quinquestrigatus*.

For competition for habitats to be important, there should be benefits (eg., increased growth rates) for species inhabiting preferred species of coral. In chapter 5, I demonstrated that growth of two species, *G. histrio* and *G. brochus* was greater in *A. nasuta* compared to *A. loripes*. This might explain why *G. histrio* and *G. brochus* compete for colonies of *A. nasuta* (Chapter 4). To determine if the benefits in growth of inhabiting *A. nasuta* rather than *A. loripes* is a general phenomenon for *G. histrio* and *G. brochus*, I conducted a second experiment in which I transplanted juveniles of both *G. histrio* and *G. brochus* to colonies of both *A. nasuta* and *A. loripes* at all the locations where these coral species were present.

Differences in growth between coral-dwelling gobies inhabiting *A. nasuta* and *A. loripes* might be associated with the different branching structures of these corals. *A. nasuta* has a complex, but relatively open branching structure which would offer protection from predation yet sufficient room for movement and growth. *A. loripes* has a finer branching structure that might constrain the growth of fish inhabiting this species of coral. To determine whether habitat structure might be the factor determining habitat related difference in growth I also examined the relationship between habitat structure and growth of *G. histrio* and *G. brochus* inhabiting *A. nasuta* and *A. loripes* at different geographic locations.

6.3. METHODS

Habitat availability

If *A. nasuta* is a preferred coral species and habitat space is a limited resource for species of *Gobiodon*, then most colonies of *A. nasuta* should be occupied. To determine if colonies of *A. nasuta* might be limiting at One Tree Island, Lizard Island and Kimbe Bay I examined the abundance and occupancy rates of *A. nasuta* at all three locations. At each geographic location, five replicate 10m x 1m belt transects were established on the outer reef flat of each of three sheltered reefs. Each colony of *A. nasuta* located at least half within a transect and with a diameter greater than 5 cm, was carefully searched for *Gobiodon* with the aid of a small underwater light. Details of the sampling regime and protocols are given in Chapter 4. ANOVA followed by a Tukey's multiple comparison test was used to determine if the abundance of *A. nasuta* varied significantly among locations. A replicated chi-squared test was used to determine if the frequency distribution of the various species of *Gobiodon* varied among locations. In this analysis all pairwise comparisons between sites were performed and the critical chi-square value was corrected to maintain a 5% experimental error rate.

Recruitment and competition for vacant coral colonies

If the relative frequency with which *G. histrio* and *G. quinquestrigatus* recruit to vacant colonies of *A. nasuta* is primarily determined by the availability of recruits then the relative frequency of recruitment by *G. histrio*, *G. quinquestrigatus* and other species of *Gobiodon* should be similar among colonies of *A. nasuta* previously occupied by either *G. histrio* or *G. quinquestrigatus*. Any differences in the relative frequency of recruitment by *G. histrio* and *G. quinquestrigatus* among coral colonies previously occupied by each species would indicate that coral colonies have particular characteristics that influence which species is most likely to recruit. This pattern might be expected if fine-scale habitat partitioning occurs either as a result of differential habitat selection or competitive interactions among species of *Gobiodon*. Furthermore, if competitive asymmetries modify the distribution of these two species established at settlement then the relative abundance of the superior competitor (*G. histrio*) should increase following recruitment while the relative abundance of the subordinate competitor (*G. quinquestrigatus*) should decline following recruitment.

To compare recruitment and persistence in coral colonies previously occupied by *G. histrio* and *G. quinquestrigatus*, I cleared resident fish from 15 - 25 coral colonies occupied by *G. histrio* and 15 - 25 coral colonies occupied *G. quinquestrigatus* at each location. The spatial distribution of corals cleared of *G. histrio* was similar to the spatial distribution of corals cleared of *G. quinquestrigatus*. Coral colonies used in this experiment were located on the reef flat or shallow reef slope at (1) Horseshoe

Reef and adjacent reefs near the lagoon at Lizard Island, (2) outside the lagoon entrance at One Tree Island and, (3) Crater Reef and adjacent inshore reefs in Kimbe Bay (Fig 3.1). The experiment was established sequentially at each location during November 1997 (Kimbe Bay), December 1997 (One Tree Island) and January 1998 (Lizard Island). Fish were removed from the corals following anaesthetisation with clove oil (Munday and Wilson 1997). So that coral colonies could be located in subsequent censuses, each colony was tagged with an individually coded metal washer secured to a branch of the coral colony with a plastic cable-tie. At each location a similar number of coral colonies occupied by *G. histrio* and *G. quinquestrigatus* were haphazardly selected as control colonies. Each control colony was tagged but the resident fish were not removed. Both control and experimental removal colonies were censused after 3 months and then again after 7-10 months.

I used log linear models to determine, (1) whether the relative frequency of recruitment by *G. histrio*, *G. quinquestrigatus* and other species of *Gobiodon* varied between coral colonies previously occupied by *G. histrio* and *G. quinquestrigatus* and, (2) whether patterns of recruitment to coral colonies previously occupied by *G. histrio* or *G. quinquestrigatus* varied among locations. I used backwards elimination starting from a saturated model to examine the relationship among (1) the relative frequency of recruitment by each species of *Gobiodon*, (2) geographic location and, (3) coral colonies previously occupied by *G. histrio* and *G. quinquestrigatus*. Starting with the highest order interactions, each combination of factors was dropped from the model until no more factors could be removed without a significant increase in the deviance from one model to the next. The best fitting model was assumed to be the model with the least number of factors and the smallest deviance between the fitted model and the saturated model.

If a competitive hierarchy influences the relative abundances of *G. histrio* and *G. quinquestrigatus* following recruitment then the competitively dominant, *G. histrio*, should increase in abundance while the competitively subordinate species, *G. quinquestrigatus*, should decrease in abundance. I compared the frequencies of these two species present at the first census (3 months) with those observed at the second census (7-10 months). Changes in relative abundance of *G. histrio* and *G. quinquestrigatus* between the first and second census in treatment colonies were also examined in control corals during the same time interval. At each location, coral colonies previously occupied by *G. histrio* were analysed separately from coral colonies previously occupied by *G. quinquestrigatus*. I used a Fisher's exact test where the first column of the 2x2 table contained the number of coral colonies occupied by *G. histrio* and *G. quinquestrigatus* at the first census and the second column contained the frequencies of the species at the second census.

Growth and habitat type

G. histrio usually inhabits *A. nasuta* and *G. brochus* usually inhabits *A. loripes* at both Lizard Island and One Tree Island on the Great Barrier Reef (Chapter 3). At Lizard Island both *G. histrio* and *G. brochus* grow faster in *A. nasuta* compared to *A. loripes* (Chapter 5). However, *G. brochus* is usually excluded from *A. nasuta* due to competition with *G. histrio* (Chapter 4). To determine if the fitness benefits detected for both species of *Gobiodon* inhabiting *A. nasuta* at Lizard Island are also present at other locations I transplanted *G. histrio* and *G. brochus* to both *A. nasuta* and *A. loripes* at One Tree Island. *G. brochus* and *A. loripes* do not occur in Kimbe Bay, PNG, therefore, I was only able to examine growth of *G. histrio* in *A. nasuta* at this location.

Colonies of *A. nasuta* and *A. loripes* near the main entrance within the lagoon at One Tree Island and colonies of *A. nasuta* on Crater Reef and adjacent reefs in Kimbe Bay were cleared of resident fish and other infauna during November (Kimbe Bay) and December 1997 (One Tree Island). Each coral was individually tagged with a coded metal-washer secured to a branch of the colony with a plastic cable-tie and the locations of all tagged corals were mapped. Juvenile *G. histrio* and *G. brochus* were collected from colonies of the corals they usually inhabit (*A. nasuta* and *A. loripes* respectively) by anaesthetising the fish with clove-oil. I did not distinguish between the two forms of *G. histrio* (spotted and striped forms) because they have identical patterns of habitat use (Munday et al. 1999). Fish were collected from reefs other than the ones used in this experiment to prevent the possibility that they would move back to their original coral colonies following release. Fish were transported to the laboratory, re-anaesthetised, measured (standard length (SL) to 0.1mm) and individually marked with a small fluorescent-elastomer tag injected into the dorsal musculature (North-West Technologies). The use of two tagging colours and three locations on two sides of the body allowed a sufficient number of tagging combinations for individual identification. The use of micro-tagging techniques has been shown to have little effect on the mortality rates of coral-reef fish (Beukers et al. 1995) and tag loss is infrequent when fluorescent-elastomer tagging is used on coral-dwelling gobies (personal observations). Moreover, any potential mortality or tag loss is expected to be spread equally among the treatment fish and, therefore, would not affect the comparisons in this study. One tagged fish was released on each of the marked coral colonies. Each fish was observed for several minutes following release to ensure it had successfully colonised the new coral colony.

The mean size of fish transplanted to coral colonies at Lizard Island and One Tree Island was 22.03 mm SL. The growth of transplanted fish on each species of coral was estimated after approximately 100 days at each location (range 93-108 days). Fish were collected from each marked coral colony by anaesthetisation with clove oil and the SL of each tagged fish was measured to the nearest 0.1mm. I used ANCOVA to compare the mean growth of fish (increase in SL) in different species of coral at each location standardised to 100 days. Initial size was included as a covariate in each analysis. Because the combination of *G. histrio* and *G. brochus* transplanted to *A. nasuta* and *A. loripes* was conducted at both Lizard Island and One Tree Island I used ANCOVA to investigate the relationship between mean growth per 100 days of both species of fish in both species of coral at both geographic locations. Because *G. histrio* and *A. nasuta* were present at all the three locations I then used ANCOVA to compare the mean growth per 100days of *G. histrio* in *A. nasuta* among all geographic locations. Data were square root transformed to achieve homogeneity of variances where a Cochran's test indicated significant heterogeneity of the variances.

Habitat structure

The growth and survival of coral-dwelling gobies might be closely associated with the structure of the corals they inhabit. In particular, individual growth might be constrained by the space available between coral branches. Therefore, I examined the relationship between interbranch space of *A. nasuta* and *A. loripes* and the growth rates of *G. histrio* and *G. brochus* in these corals estimated in the growth experiment (above). I used a water-displacement method to estimate the interbranch space of approximately 10 equally sized colonies (20 cm maximum diameter) of each species of coral at each location. Coral colonies were carefully removed from the reef and transported to the laboratory. Each colony was tightly wrapped in thin plastic film ("cling wrap") and then completely submerged in a predetermined volume of water in a 20 l plastic container. The new meniscus level was marked on the container and the coral colony removed. The volume of water required to fill the container from the original volume to the new meniscus mark was used as an estimate of the displacement volume of the wrapped coral. The plastic film was removed from the coral colony and the unwrapped displacement volume was determined in the same manner. The unwrapped volume was subtracted from the wrapped volume to estimate the total interbranch volume. I then divided the total interbranch volume by the number of branches in each coral colony to estimate the average interbranch space. All branches that reached the outer perimeter of the coral colony were counted regardless of their total length. A two-way ANOVA was used to compare mean interbranch space of *A. nasuta* and *A. loripes* at Lizard Island and One Tree Island. One-way ANOVA was used to compare interbranch space of *A. nasuta* among all three geographic locations.

6.4. RESULTS

Habitat availability

The abundance of *A. nasuta* colonies was significantly greater at One Tree Island than the more northern sites (Table 6.1). A total of 112 colonies of *A. nasuta* were recorded in transects at One Tree Island compared to 63 and 42 at Lizard Island and Kimbe Bay respectively. There was no significant difference in the abundance of *A. nasuta* colonies between Lizard Island and Kimbe Bay (Table 6.1). The frequency distribution of *Gobiodon* species occupying colonies of *A. nasuta* varied among all locations (chi-squared value = 28.7, df = 8, $p < 0.001$, critical value for replicated chi-squared test =18.633), with species distributions became more even from Kimbe Bay to One Tree Island (Fig. 6.1). There was no significant difference in the number of vacant colonies of *A. nasuta* among locations (chi-square = 4.036, df = 2, p = 0.13). There were no vacant colonies of A. nasuta in Kimbe Bay and only 6% of colonies were vacant at Lizard Island and 9% at One Tree Island.

Recruitment and competition for vacant coral colonies

All coral colonies cleared of fish were reoccupied after 3 months at Lizard Island and only 1 colony remained vacant at both One Tree Island and Kimbe Bay (Figs 6.2 and 6.3). Because corals were censused 3 months after becoming vacant it was difficult to distinguish between recruits that had grown since settlement and immigrants, therefore, recolonisation may include some component of movement. The relative frequencies of *Gobiodon* species recruiting to colonies of *A. nasuta* varied between coral colonies previously occupied by either *G. histrio* or *G. quinquestrigatus* and among geographic locations (Table 6.2.) At Kimbe Bay and Lizard Island, coral colonies previously occupied by *G. histrio* were mostly reoccupied by *G. histrio* (Fig 6.2). Similarly, coral colonies previously occupied by *G. quinquestrigatus* at these two locations were mostly reoccupied by *G. quinquestrigatus* (Fig 6.3). At One Tree Island the pattern of recruitment was more even for coral colonies previously occupied by both *G. histrio* and *G. quinquestrigatus* (Figs 6.2 and 6.3). At this locations, coral colonies previously occupied by *G. histrio* were reoccupied approximately equally by *G. histrio, G. quinquestrigatus* and *G. axillaris* (Fig 6.2). Although coral colonies previously occupied by *G. quinquestrigatus* were reoccupied by a range of species, they were infrequently reoccupied by *G. histrio* (Fig 6.3).

The frequency distribution of *G. histrio* and *G. quinquestrigatus* did not change significantly between the first and second census in either the removal corals or the control corals at all locations (Table 6.3). Therefore, there was no evidence of a competitive hierarchy influencing the relative abundances of *G. histrio and G. quinquestrigatus* following recruitment into coral colonies previously occupied by either of these two species

Growth and habitat type

Very similar patterns of growth were observed for *G. histrio* and *G. brochus* transplanted to *A. nasuta* and *A. loripes* at Lizard Island and One Tree Island (Fig. 6.4). At both locations the mean growth of fish transplanted to *A. nasuta* was over twice that of fish transplanted to *A. loripes* (Fig. 6.4). Mean growth did not vary between the two species of fish but there was a significant interaction between species of coral and geographic location (Table 6.4). This interaction was due to the greater difference in growth between fish inhabiting *A. nasuta* and *A. loripes* at One Tree Island compared to fish inhabiting these corals at Lizard Island (Fig. 6.4).

The mean growth rate of *G. histrio* transplanted to colonies of *A. nasuta* did not vary among Kimbe Bay, Lizard Island and One Tree Island (Table 6.5). Although the mean growth of *G. histrio* at Kimbe Bay was greater than fish at other locations (Fig. 6.5), this was not significant when initial size was included as a covariate in the analysis. The mean size of fish transplanted to coral colonies at Kimbe Bay was 17.00mm SL compared to 21.98mm SL at Lizard Island and 22.89mm SL at One Tree Island.

Habitat structure

Mean interbranch space varied between *A. nasuta* and *A. loripes* and between Lizard Island and One Tree Island (Table 6.6). *A. nasuta* had a much larger interbranch space than *A. loripes* and the interbranch space of both species was smaller at One Tree Island compared to Lizard Island (Fig. 6.6). However, the difference in interbranch space between locations was most marked for *A. loripes* (Fig. 6.6). The mean interbranch space of *A. loripes* at One Tree Island was approximately 5 times smaller than the interbranch space of *A. loripes* at Lizard Island (1.54ml/branch and 7.98ml/branch respectively). The mean interbranch space of *A. nasuta* also varied among locations (Table 6.7) but only from 15.28ml/branch at Lizard Island, to 11.58ml/branch at One Tree Island and 10.13ml/branch at Kimbe Bay (Fig. 6.6). Mean growth rates of *G. histrio* and *G. brochus* at Lizard Island and One Tree Island were closely correlated with mean interbranch space of corals from each location (Pearson's correlation *G. histrio*; $R = 0.936$, $N = 4$, $P = 0.06$ and *G. brochus*; 0.934, $N = 4$, $P = 0.06$).

TABLE 6.1. Results of ANOVA and Tukey's multiple comparison test comparing the abundance of *A. nasuta* colonies on the reef flat at One Tree Island, Lizard Island and Kimbe Bay.

Source	MS	d.f.	*F*	*P*
geographic location	86.02	2	7.9	0.001
error	10.87	42		

	Cochran's C	d.f.	*P*
dependent variable	0.426	2	0.203

Tukey's multiple comparison	
One Tree Island vs Lizard Island	*P*=0.04
One Tree Island vs Kimbe Bay	*P*=<0.001
Lizard Island vs Kimbe Bay	*P*=0.33

TABLE 6.2. Results of log linear models comparing the relative frequency of recruitment by each species of *Gobiodon* (fish spp) at three geographic locations (location) in coral colonies previously occupied by *G. histrio* or *G. quinquestrigatus* (colony). *** = $P < 0.001$, ns = non significant. Model 3 (underlined) is the best fitting model. Lower order models are not shown because they all gave a significant increase in deviance from model 3.

Model	Deviance	d.f.	Difference between models	d.f.
1. fish spp x location x colony	0			
2. fish spp x colony + fish spp x location + location x colony	11.07 ns	6	(1&2) 11.07 ns	6
3. fish spp x colony + fish spp x location	13.32 ns	8	(2&3) 2.25 ns	2
4. fish spp x location + location x colony	39.53***	12	(2&4) 28.47***	6
5. fish spp x colony + location x colony	67.63***	9	(2&5) 56.56 ***	3

TABLE 6.3. Results of Fisher's exact tests comparing the frequency distribution of *G. histrio* and *G. quinquestrigatus* between census periods in colonies of *A. nasuta*. Resident fish were removed from the treatment corals at the start of the experiment. Resident fish were not removed from control corals. Because there was an *a priori* assumption regarding the direction of any change in abundance (ie *G. histrio* increases, while *G. quinquestrigatus* decreases), one-tailed probabilities are shown. Nd = no data.

Location	Species	Removals	Control
Kimbe Bay	*G. histrio*	0.17	0.26
	G. quinquestrigatus	0.39	0.35
Lizard Island	*G. histrio*	nd	1.00
	G. quinquestrigatus	0.59	0.47
One Tree	*G. histrio*	0.58	0.63
	G. quinquestrigatus	0.24	0.40

TABLE 6.4. Results of ANCOVA comparing growth (mm SL) of *G. histrio* and *G. brochus* (fish species) transplanted to colonies of *A. nasuta* and *A. loripes* (coral species) at both Lizard Island and One Tree Island (geographic location). Initial size (mm SL) is the covariate. Growth data were square root transformed to achieve homogeneity of variances.

Source	MS	d.f.	*F*	*P*
location	0.879	1	4.173	0.045
fish species	0.00003	1	0.00014	0.991
coral species	17.551	1	83.32	<0.0001
location*fish species	0.035	1	0.166	0.685
location*coral species	0.927	1	4.402	0.04
fish*coral species	0.210	1	0.998	0.321
location*fish*coral species	0.209	1	0.990	0.323
error	0.211	66		

	Cochran's C	d.f.	*P*
dependent variable	0.235	6	0.312
covariate	0.331	6	0.345

TABLE 6.5. Results of ANCOVA comparing growth (mm SL) of *G. histrio* transplanted to colonies of *A. nasuta* at Lizard Island, One Tree Island and Kimbe Bay. Initial size (mm SL) is the covariate.

Source	MS	d.f.	*F*	*P*
geographic location	0.262	2	0.061	0.941
error	4.299	24		

	Cochran's C	d.f.	*P*
dependent variable	0.641	3	0.07
covariate	0.669	3	0.08

TABLE 6.6. Results of ANOVA of interbranch volume of *A. nasuta* and *A. loripes* at Lizard Island and One Tree Island.

Source	MS	d.f.	*F*	*P*
location	235.91	1	37.69	<0.001
coral species	689.13	1	110.10	<0.0001
location *coral species	17.03	1	2.72	0.11
error	6.25	33		

TABLE 6.7. Results of ANOVA of interbranch volume of *A. nasuta* at Lizard Island, One Tree Island and Kimbe Bay.

Source	MS	d.f.	*F*	*P*
geographic location	69.99	2	8.85	0.001
error	7.91	25		

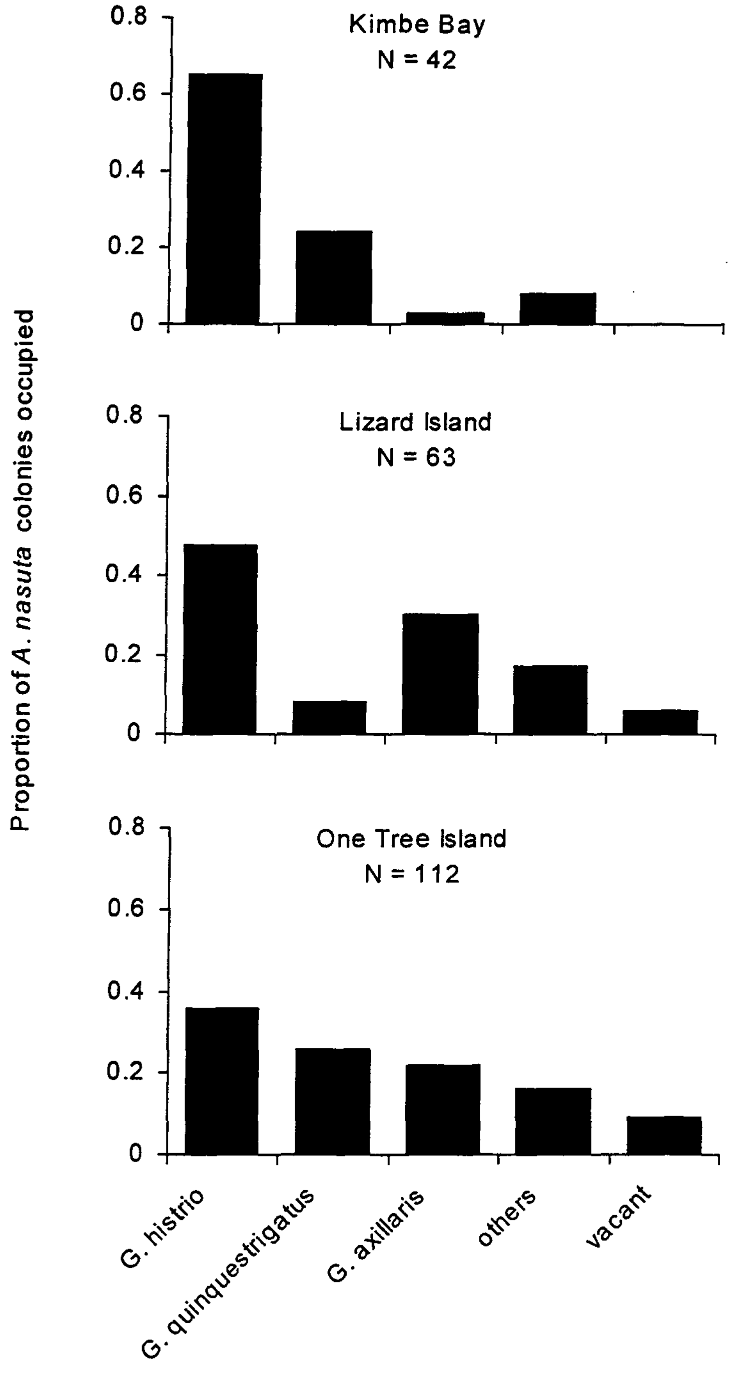

Fig 6.1. Proportion of *A. nasuta* colonies occupied by *G. histrio*, *G. quinquestrigatus* and other species of *Gobiodon* on sheltered reefs at One Tree Island, Lizard Island, and Kimbe Bay. N = total number of *A. nasuta* colonies recorded in 15 transects at each location.

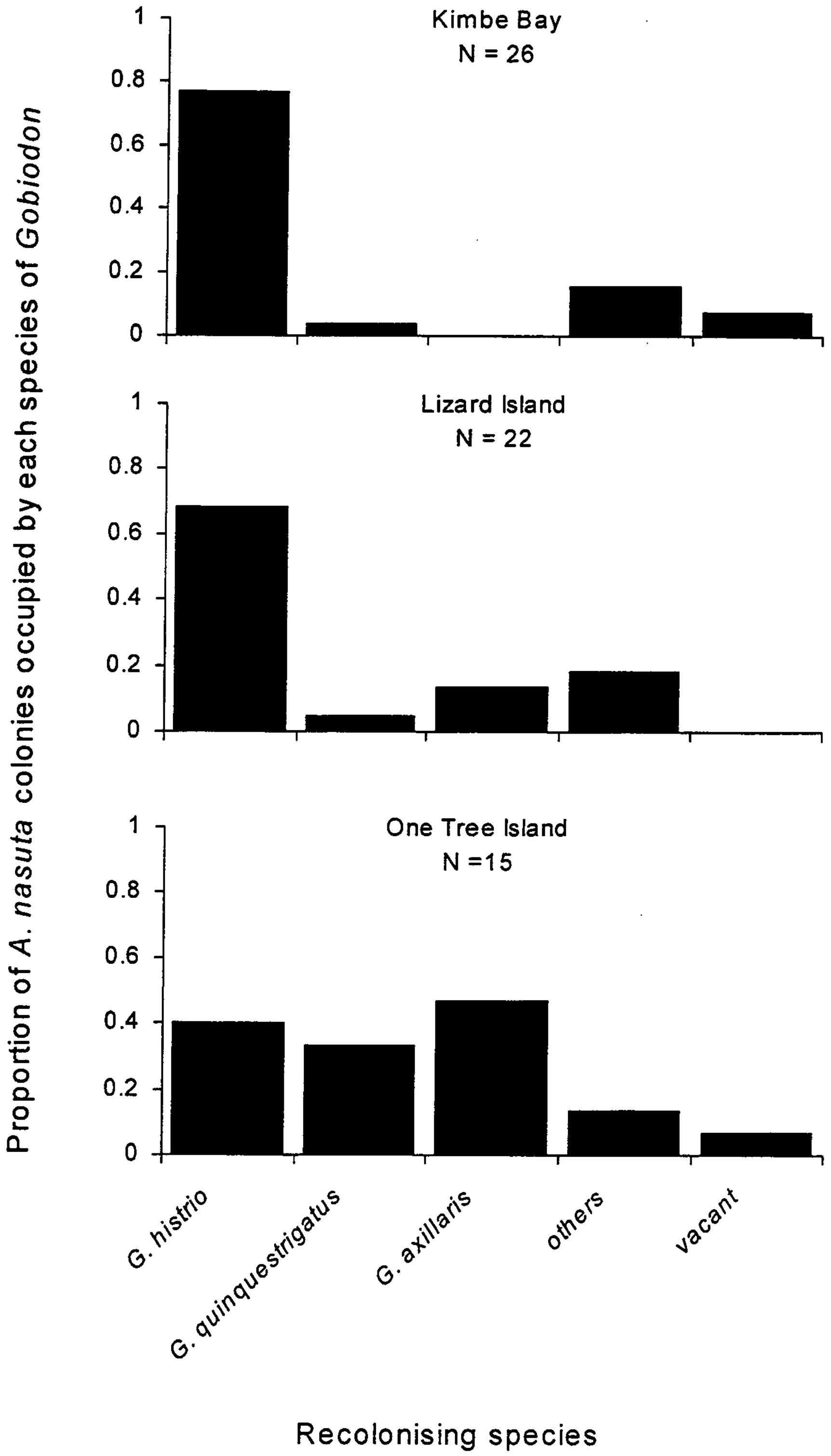

Fig 6.2. Proportion of coral colonies previously occupied by *G. histrio* that were recolonised by *G. histrio*, *G. quinquestrigatus* and other species of *Gobiodon* at Kimbe Bay, Lizard Island and One Tree Island. N = total number of coral colonies at each location.

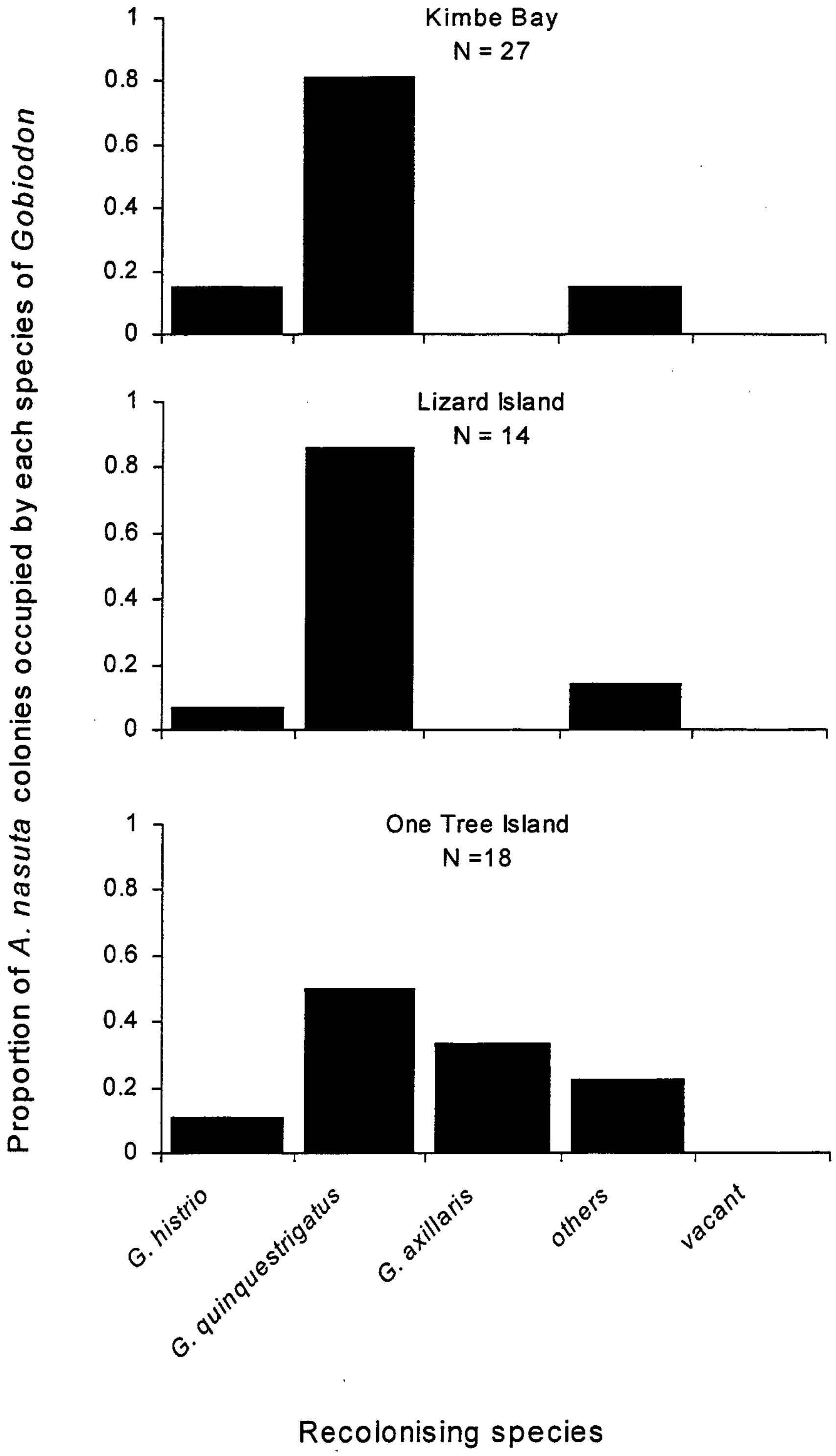

Fig 6.3. Proportion of coral colonies previously occupied by *G. quinquestrigatus* that were recolonised by *G. histrio*, *G. quinquestrigatus* and other species of *Gobiodon* at Kimbe Bay, Lizard Island and One Tree Island. N = total number of coral colonies at each location.

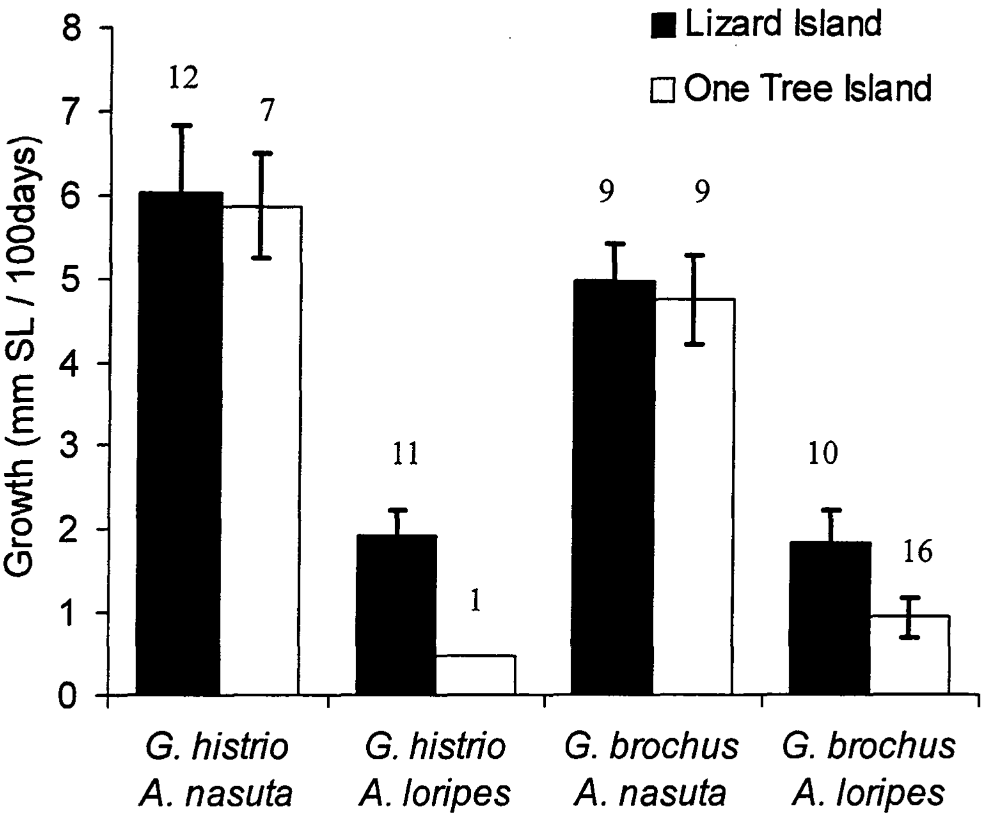

Fig 6.4. Mean increase in standard length (SL) ± SE of *G. histrio* and *G. brochus* transplanted to colonies of *A. nasuta* and *A. loripes* at Lizard Island and One Tree Island. Sample size is shown above bars.

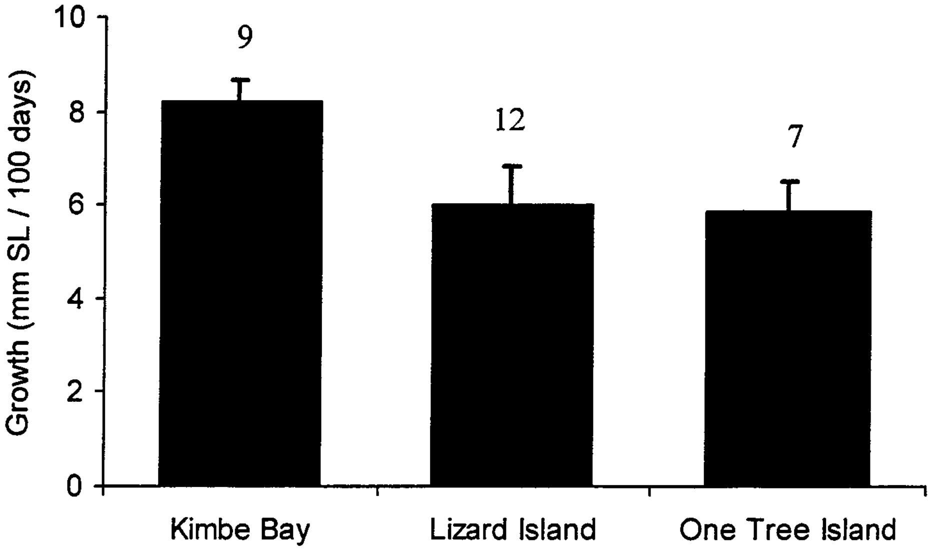

Fig 6.5. Mean increase in standard length (SL) ± SE for *G. histrio* transplanted to *A. nasuta* at Kimbe Bay, Lizard Island and One Tree Island. Sample size shown above bars.

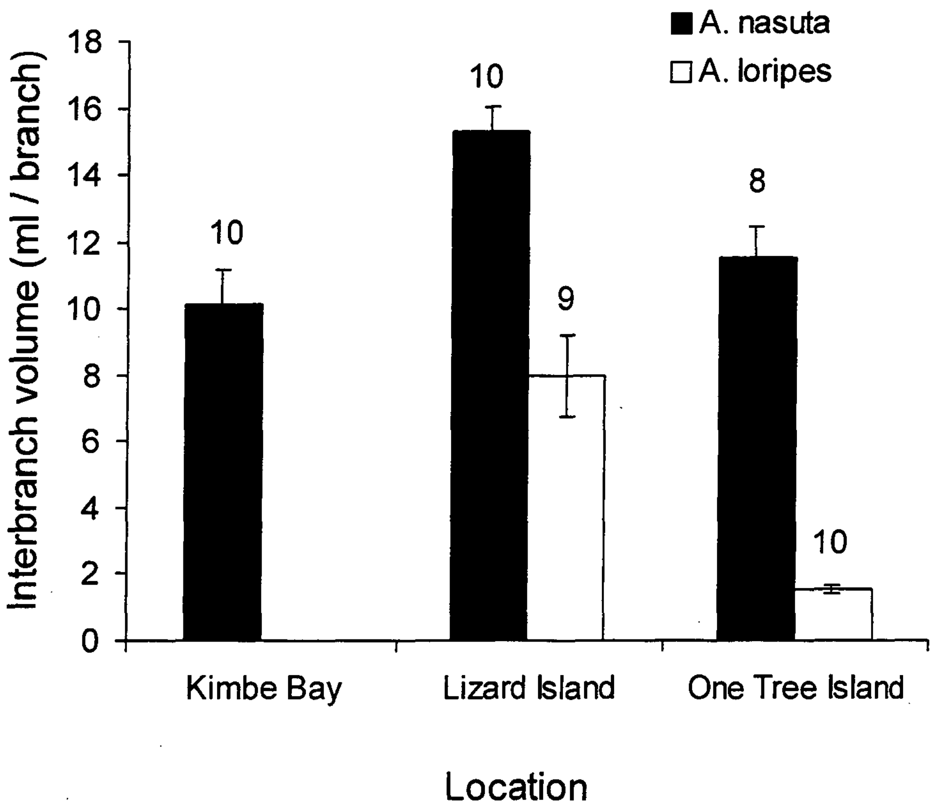

Fig 6.6. Mean interbranch volume of *A. nasuta* and *A. loripes* colonies at Kimbe Bay, Lizard Island and One Tree Island. Number of colonies sampled is shown above bars.

6.5. DISCUSSION

Identical experiments conducted at multiple locations provide a unique opportunity to test the generality of factors influencing important demographic parameters. However, rarely have such experimental comparisons been conducted across geographic spatial scales (Caley 1995a,b). In this study, patterns of recruitment by one superior competitor and one subordinate competitor were broadly similar among locations separated from each other by at least 1000km. In general, coral colonies were reoccupied by the same species that were previous residents. This pattern of recolonisation suggests that either, 1) recruiting gobies could detect previous residents and preferred to recruit to corals that previously contained conspecifics, or 2) there were predictable differences among coral colonies that were selected for by new recruits of each species. Preferential settlement of larvae into habitats occupied by conspecifics has been demonstrated for a number of coral-reef fish species (Sweatman 1983, 1985, 1988, Eckert 1985, Fowler 1990, Booth 1992, 1995, Ohman et al. 1998). However, in the experiments conducted here there were no resident fish present at the time of recruitment. The mechanism whereby settling larvae or new recruits might detect the past presence of conspecifics is not clear. The observed patterns of recruitment are more likely to be the result of subtle differences in the coral colonies that were easily distinguished by recruiting fish. Indeed, many coral reef fish are able to distinguish microhabitat types at settlement or recruitment (Sale et al. 1984, Sale 1991a, Booth and Beretta 1994, Elliott et al. 1995, Tolimieri 1995, Danilowicz 1996, Gutierrez 1998, Öhman et al. 1998).

Coral colonies previously occupied by *G. quinquestrigatus* were rarely recolonised by *G. histrio* at any location. In laboratory experiments *G. histrio* was found to be a superior competitor for *A. nasuta* colonies (Chapter 4) and is not expected to be excluded from preferred habitats by *G. quinquestrigatus*. Therefore it appears that *G. quinquestrigatus* occupies a distinct subset of the *A. nasuta* population (or a cryptic species) that is not used by *G. histrio*. The distribution patterns established at recruitment were not modified in the six months following the first census at any location. Therefore, patterns of recruitment and persistence to colonies of *A. nasuta* did not support a competitive hierarchy hypothesis where both *G. histrio* and *G. quinquestrigatus* recruit to the same preferred species of coral and the dominant species (*G. histrio*) subsequently excludes the subordinate species (*G. quinquestrigatus*). Rather, *G. quinquestrigatus* appears to recruit directly to a subset of *A. nasuta* colonies where it does not compete directly with *G. histrio*.

Increased availability of preferred habitats is expected to reduce the frequency or intensity of interspecific competition for space. At Kimbe Bay and Lizard Island, coral colonies previously occupied by *G. histrio* were mostly reoccupied by *G. histrio*. This might occur because the competitive dominant, *G. histrio*, excludes other species from its preferred species of coral. However, at One Tree Island, recolonisation of coral colonies previously occupied by *G. histrio* was more evenly spread among the suite of species present. This indicates that interspecific competition during the recruitment and early post-recruitment phase does not strongly influence patterns of habitat use by species of *Gobiodon* at One Tree Island. This might occur because *A. nasuta* is more abundant at One Tree Island than other locations and, therefore, *G. histrio* does not need to compete strongly for access to vacant colonies of *A. nasuta*.

The growth advantage of inhabiting *A. nasuta* appears to be a strong and general phenomenon for *G. histrio* and *G. brochus*. Growth of *G. histrio* inhabiting *A. nasuta* did not differ among locations, despite these locations being separated by several thousand kilometres. The consistent growth advantage of inhabiting *A. nasuta* might explain the strong preference for this coral exhibited by *G. histrio* at all the geographic locations studied here. At both Lizard Island and One Tree Island, *G. histrio* and *G. brochus* grew faster in *A. nasuta* compared to *A. loripes*. *G. brochus* mostly inhabits *A. loripes* at all locations, despite a slower growth rate in this species of coral. Therefore, it appears that *G. brochus* uses an inferior habitat at all locations (Chapter 3), probably because of the dominance of *G. histrio* in colonies of *A. nasuta* (Chapter 4). Specialisation on inferior resources provides a mechanism for coexistence of species with common resource preferences (Robinson and Wilson 1998).

Although competition for colonies of *A. nasuta* appears to be less intense at One tree Island, *G. brochus* is rarely found outside the lagoon, where the recolonisation experiment was conducted. The absence of *G. brochus* outside the lagoon might be associated with the rarity of *A. loripes* in this location. In contrast, *G. brochus* is abundant inside the lagoon where *A. loripes* is also abundant (pers obs). This suggests that *G. brochus* might always recruit to *A. loripes* and then move to *A. nasuta* when it reaches a larger size. In this way individuals of *G. brochus* would mostly avoid competition with *G. histrio* when small. Many of the *G. brochus* juveniles transplanted to *A. nasuta* colonies within the lagoon at One Tree were replaced by *G. histrio* during the course of the transplant experiment. Several of these fish were relocated in nearby colonies of *A. loripes* and their growth was found to be intermediate between individuals that had remained on *A. nasuta* and those originally transplanted to *A. loripes*. This further supports the role of habitat type in determining growth rates of coral-dwelling gobies.

Growth of fish is indeterminate and can be constrained by living space. For example, space constraints on growth can explain the common observation that a fish in a very small aquarium will grow more slowly than a fish in a large aquarium (Sebens 1987). Mean growth of both *G. histrio* and *G. brochus* was closely correlated with mean interbranch space of the coral species inhabited. The positive relationship between interbranch space and growth suggests that habitat structure is the underlying mechanism determining growth rates of coral-dwelling gobies in different species of coral. In particular, *A. loripes* has a fine branching structure that might constrain their growth, perhaps by reducing foraging efficiency. In contrast, *A. nasuta* has a complex, open branching structure that might provide sufficient room for rapid growth while still providing adequate protection from predation. Manipulative experiments that alter the interbranch space within each species of *Acropora* are now needed to test this hypothesis.

Differences in growth rates of coral-dwelling gobies between species of coral might also be influenced by other factors such as food availability. If coral-dwelling gobies feed on the tissue of the corals they inhabit, as suggested by Lassig (1981) and Patton (1994), then within and among species differences in the nutritional value of coral colonies could have significant effects on growth. However, Harold and Winterbottom (1999) found copepods, foraminifera and unidentified material in the guts of *G. brochus* and I found no evidence of nematocysts or zooxanthellae in the gut contents of 10 *G. histrio* and 10 *G. brochus* collected from Lizard Island (unpublished data). Therefore corallivory by *Gobiodon* appears to be facultative and may not be a major nutritional source. Moreover, growth of both *G. histrio* and *G. brochus* was similar in *A. nasuta* at both locations but lower in *A. loripes* at One Tree Island compared to Lizard Island. This suggests that it is not coral species *per se* that influences growth rates, but rather the branching structure of the corals inhabited.

CHAPTER 7: GENERAL DISCUSSION

Although resource limitation and competition are cornerstones of ecological theory, the role of competition in structuring animal communities remains controversial. In particular, the spatio-temporal scales over which resource availability and competition influence the distribution and abundance of animals is unclear. For coral reef fishes the role of habitat availability in determining local and larger scale patterns of abundance is still debated, while interspecific competition for space is often considered unimportant. If habitat availability and competition for space can influence the distribution and abundance of coral reef fishes then we might expect that the effects would be detected among habitat specialist species, such as obligate coral-dwelling gobies. This study demonstrates that; 1) Habitat availability and interspecific competition do have significant effects on the distribution, abundance and demographic parameters of coral-dwelling gobies. 2) Relationships between habitat availability and the distribution, abundance and demographics of coral-dwelling gobies are similar among widely separated locations and, therefore, appear to be of general importance and 3) Other processes interact with habitat availability to determine patterns of distribution and abundance, especially as spatial scale increases.

Coral-dwelling gobies mostly inhabit coral of the genus *Acropora*, however, the degree of specialisation varies among species of *Gobiodon*. Some are specialists on only one species of coral, others inhabit a range of coral species (Chapters 2 and 3). In general, patterns of habitat use are consistent within locations (Chapter 2) and for some species of *Gobiodon*, patterns of habitat use are also consistent among locations separated by thousands of kilometres (Chapter 3). For some species, such as *G. histrio*, these patterns of habitat use are clearly the result of habitat selection for preferred coral species (Chapter 4). For other species, such as *G. brochus*, patterns of habitat use are the result of interactions with superior competitors (Chapter 4 and 5). More generalist species, such as *G. quinquestrigatus* appear to change their patterns of habitat use to take advantage of new or abundant coral species at particular locations.

Determining the spatial scales at which various processes act has become a major focus for ecology. There is a close relationship between the abundance of most species of *Gobiodon* and the species of coral they usually inhabit (Chapter 2 and 3). This is consistent with the notion that habitat availability has a significant effect on patterns of distribution and abundance. However, the abundances of some species of *Gobiodon* are also associated with particular reef zones or reef types, independently of coral availability (Chapter 2 and 3). Multiscale habitat selection can most easily explain this hierarchical pattern of abundance. A model describing the major processes determining the distribution and abundance of coral-dwelling gobies within locations would include; 1) Broadscale habitat selection before settlement where larvae first select the general reef environment or select hydrodynamic conditions that transport them to these locations. 2) At the reef, species select particular reef zones and then settle into preferred corals within these zones. 3) Interspecific competition within reef zones results in superior competitors acquiring preferred corals and subordinate competitors being forced into inferior habitats. Habitat availability also appears to influence patterns of abundance among geographic locations (Chapter 3). However, at this scale, difference in patterns of larval supply and the physiological tolerances of species are also likely to help determine patterns of distribution and abundance.

Interspecific competition for space was considered a significant force in early models of community structure of coral reef fishes. This paradigm has been significantly eroded and interspecific competition for space is often considered to be relatively unimportant to the ecology of reef fishes. This thesis demonstrates that interspecific competition does influence the distribution, abundance and fitness of coral dwelling gobies (Chapter 4 and 5). Moreover, the effects of competition are largely predictable from patterns of habitat use and an understanding of species' competitive abilities. Differences in growth and survival among habitats appear to explain the advantage of habitat selection and competition for habitats (Chapter 5). Differences in habitat structure between species of coral may be the mechanism underlying these habitat related differences in fitness (Chapter 6). There is now growing evidence that interspecific competition can influence the population ecology of habitat specialist fishes.

This study was conducted at multiple geographic locations to help establish the generality of processes influencing the distributions and abundances of coral-dwelling gobies. Within location distribution patterns were similar at multiple locations for most species of *Gobiodon* (Chapter 3), therefore the processes determining the distribution and abundance of these fish are likely to be similar at these locations. Patterns of recruitment to vacant corals were similar at two locations but differed at a location with a higher availability of preferred habitat. Patterns of growth in different species of corals were also similar between locations. Therefore, it appears that habitat availability helps determine the distribution, abundance and fitness of coral dwelling gobies in very similar ways at widely separated locations. Small scale differences in habitat structure, habitat availability and interspecific competitive abilities appear to be primary determinants of the population ecology of coral-dwelling gobies at local spatial scales.

The research described in this thesis provides the foundation for further study of important ecological and evolutionary questions. I have selected three areas in which further research is already underway, 1) predictive models of the distribution and abundance of competing species under different resource and recruitment regimes, 2) manipulative experiments to investigate the relationship between habitat specialisation, competitive ability and phenotypic plasticity and, 3) phylogenetic studies to consider the evolution of habitat specialisation and competitive abilities.

Because I have precise knowledge on the outcome of 1) competitive interactions between *G. histrio* and *G. brochus* and 2) growth and survival patterns of these fish in *A. nasuta* and *A. loripes*, I can model the effects of interspecific competition under different scenarios. In particular, I should be able to predict the spatial distribution of each species of *Gobiodon* among the two species of coral under different recruitment and habitat availability regimes. The theory of stochastic processes (Cox and Miller 1965) provide a useful mathematical framework for such models and has been recently used to incorporate spatial structure into models of population dynamics (Day and Possingham 1995). In conjunction with P. Armsworth (Department of Mathematics JCU) I am developing discrete-time Marcov Chains to model interspecific competition in a simple system, such as exists with *G. histrio* and *G.*

brochus inhabiting *A. nasuta* and *A. loripes*. Marcov Chains use transition matrices that describe the probabilities of movement from one state space to another. For example, consider the situation where at time *T* we have a state space consisting of one colony of *A. nasuta* inhabited by *G. histrio* and one colony of *A. loripes* inhabited by *G. brochus*. The state space occupied at time T_{+1} will depend on the competitive ability of each species and the probability of recruitment, movement and mortality. These probabilities are contained within the transition matrix. The probabilities of recruitment and mortality can be modelled as Poisson processes. Movement can depend on the availability of a vacant coral colony such that *G. brochus* will always move to *A. nasuta* if space is available but *G. histrio* will not move to *A. loripes*. Competitive ability is incorporated such that *G. histrio* can exclude *G. brochus* but not vice versa. Size structure can then be included in the model to accommodate a size specific competitive hierarchy (eg $H_i > H_j > B_i > B_j > H_k > H_l > B_k$......where H = *G. histrio* and B = *G. brochus* and *i,j,k,l* are size classes). The transition between size classes is based on the growth data for each species of fish from each species of coral. The population is then simulated using random numbers to pick a particular set of transitions for each time step and repeating the process many hundreds of times. Initial results are promising and the models are being refined.

Specialisation on a particular resource may limit a species ability to use other resources (Futuyma and Moreno 1988). Phenotypic plasticity will not be selectively advantageous where there is a phenotypic trade-off between performance in different environments. Consequently, the evolution of habitat specialisation is expected to result in reduced phenotypic plasticity (Holt 1997). Because coral-dwelling gobies exhibit a range of habitat specialisation and competitive ability and because they can be transplanted among coral types, they provide a great opportunity to test relationships between habitat specialisation, competitive ability and phenotypic plasticity. Comparisons of phenotypic traits such as growth rates between specialist and generalist species (eg *G. histrio* and *G. quinquestrigatus*) in different habitats provides an opportunity to test the relationship between phenotypic plasticity and habitat specialisation. Extending the comparisons to include a species that is similarly specialised to *G. histrio* but is a competitive subordinate (eg *G. brochus*) provides the opportunity to test the relationships between phenotypic plasticity and competitive ability. Extending the comparisons to include multiple populations provides the opportunity to estimate overall genetic variation in phenotypic plasticity between species with varying degrees of habitat specialisation and competitive ability. The norms of reaction for growth of *G. histrio* and *G. brochus* in *A. nasuta* and *A. loripes* at two locations considered here provide the basis for this analysis and can be expanded to include *G. quinquestrigatus* and other locations.

The range of suitable habitats must become increasingly limited with increasing habitat specialisation and consequently intraspecific competition should become more intense as specialisation increases (Rosenzweig and Lomolino 1997). Increased intraspecific competition could provide the mechanism for micro-allopatric speciation through the use of new habitat types. Development of a phylogeny for *Gobiodon* would enable questions related to the evolution of habitat specialisation and competitive ability to be considered. With a phylogeny for *Acropora* it would also be possible to determine whether patterns of habitat use by species of *Gobiodon* are a result of coevolution with species of *Acropora*. Construction of molecular phylogenies for *Gobiodon* and *Acropora* is already underway and when available these phylogenies will be used to test hypotheses about competition and speciation among *Gobiodon* and the evolution of the relationship between *Gobiodon* and the species of corals they inhabit.

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APPENDIX 1: GUIDE TO CORAL-DWELLING GOBIES, GENUS *GOBIODON* (GOBIIDAE), FROM PAPUA NEW GUINEA AND THE GREAT BARRIER REEF

Guide to coral-dwelling gobies, genus *Gobiodon* (Gobiidae), from Papua New Guinea and the Great Barrier Reef

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APPENDIX 2: THE ECOLOGICAL IMPLICATIONS OF SMALL BODY SIZE AMONG CORAL-REEF FISHES

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APPENDIX 3: COMPARATIVE EFFICACY OF CLOVE OIL AND OTHER CHEMICALS IN ANAESTHETIZATION OF *POMACENTRUS AMBOINENSIS*, A CORAL REEF FISH

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Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish

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APPENDIX 4: SETTLEMENT STRATEGIES AND DISTRIBUTION PATTERNS OF CORAL-REEF FISHES

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Settlement strategies and distribution patterns of coral-reef fishes

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