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Habitat specialisation, niche overlap and site fidelity in a vulnerable family of coral reef fishes – the cardinalfish (Apogonidae)

Thesis submitted by

Naomi Marcelle Gardiner

(BA, BSc, GDipResMeth)

in July 2010

for the degree of Doctor of Philosophy

in the School of Marine and Tropical Biology

James Cook University

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The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Human (*1999*), the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997)*, the *James Cook University Policy on Experimentation Ethics*. *Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001)*. The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A1028).

13th December 2010

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ACKNOWLEDGEMENTS

To my amazing parents, sisters and their families: you are incredible and your love, prayers, faith and general support have kept me going. Thank you for always calling, visiting, listening and encouraging me through the joys and trials of this great journey.

To the many, many other friends and family in Townsville and beyond – I love you, you're amazing, thanks for loving me so much, for helping me de-stress, refocus and for being nearby.

It is the glory of God to conceal a matter;
to search out a matter is the glory of kings.
Proverbs 25:2

I dedicate this PhD thesis to my grandfather, Dr. John W. Gardiner.
Your scientific curiosity and passion for knowledge is an inspiration to us all.

GENERAL ABSTRACT

Habitat degradation is viewed as the most imminent threat facing coral reef fish assemblages. Reef fishes may have a low resilience to habitat change as a result of key ecological and behavioural traits, including extreme habitat specialisation, high levels of co-occurrence and strong home site fidelity. This thesis explores the levels of specialisation, co-occurrence and site fidelity (including homing behaviour) and their interrelationships in a speciose family of coral reef fishes - the cardinalfish (Family Apogonidae). The vulnerability of this family to habitat loss and degradation is examined by addressing the following five questions: (1) Do cardinalfish communities exhibit strong associations with particular substrata or do species vary in their micro-habitat use? (2) Do cardinalfish species differentially specialise on particular types of coral colonies and on specific areas within coral colonies? (3) Is the observed degree of habitat specialisation and niche overlap a result of behavioural preferences for habitat types, conspecifics or a combination of these? (4) Do cardinalfish individuals move amongst adjacent resting sites and can they home between isolated reef platforms? (5) Are cardinalfish constrained to using particular resting sites or can they relocate following habitat disturbance?

Chapter 2 describes the degrees of habitat specialisation and spatial overlap among 10 common cardinalfish species in Kimbe Bay, Papua New Guinea (PNG). Nine of the 10 common species were strongly associated with live scleractinian corals and the majority of individuals were associated with a single species of branching coral (*Porites cylindrica*). Cardinalfish used this coral much more than would be expected given its availability, indicating a high degree of apparent habitat specialisation. In addition, the nine coral dwelling apogonids exhibited a high degree of spatial overlap using the same depth ranges, the same species of corals and the same individual colonies. The high level of both specialisation and overlap in habitat use suggests that this reef fish assemblage is particularly susceptible to the loss of a single coral species.

Evidence for fine-scale habitat use and partitioning of a single coral species (*Porites cylindrica*) was examined in **Chapter 3**. There was considerable evidence of fine-scale specialisation and partitioning among seven common cardinalfish species in Kimbe Bay (PNG), both among *Porites* colonies and on refuge positions within *Porites* colonies. All species preferentially inhabited large coral colonies, despite their limited availability. Strong conspecific aggregation observed in six of these species lead to a high proportion of unoccupied corals. Within coral heads, three cardinalfish species showed a high degree of specialisation, inhabiting a small

proportion of the available space. A high level of habitat partitioning among species was also observed within colonies. Species differentiated between refuge areas deep inside coral colonies, within interstitial spaces at the colony surface and positions on the vertical edges of coral colonies. There was a positive relationship between the breadth of fine scale habitat use and the degree of species overlap both amongst and within coral colonies. Only two of the rarer, specialist species shared coral colonies and refuge positions. This study confirms that there is fine-scale habitat specialisation and partitioning in this common reef fish guild. Biodiversity of this group will be particularly vulnerable to the loss of large *Porites* colonies.

Chapter 4 explores the degree to which habitat and social preferences explain the association that three common cardinalfish species have with coral substrata. Three-way choice experiments were conducted to test fishes habitat preferences for living coral over dead substrata, for particular coral species and the influence of gregarious behaviour on these habitat choices. The strength of preferences for live *P. cylindrica* coral differed among species. All species were attracted to conspecifics and for some species attraction resulted in stronger associations with live *P. cylindrica* colonies. Conversely social preferences weakened associations with *P. cylindrica* when conspecifics occurred on marginal habitat. This chapter's results indicate that in the field, habitat preferences and conspecific attraction combine to reinforce the association between cardinalfishes and the narrow range of coral substrata seen in **Chapters 2** and **3**.

Under conditions of widespread habitat loss, strong bonds with home sites may restrict population connectivity and limit resilience to habitat change. **Chapter 5** examines the extent of site fidelity and homing behaviour for cardinalfishes of Kimbe Bay. It focuses on four species that are typically restricted to resting in large *P. cylindrica* colonies after nocturnal foraging migrations. Tagged individuals of two species remained faithful to particular colonies and to specific areas within these colonies. In contrast two other species moved between nearby colonies and/or away from the home reef area. Displacement experiments showed that all species exhibited strong homing behaviour up to 500m across continuous reef and deep open-water channels. A remarkable ability to home over long distances (2 and 5km) was also observed for one species.

Chapter 6 investigated whether cardinalfish species relocate from disturbed home sites or persist in the degraded habitat. Home coral colonies of two species were experimentally disturbed by draping them in netting to exclude cardinalfish access. Patterns of site fidelity and relocation of tagged individuals were compared with controls, before and after the disturbance. Most individuals remained faithful to home sites prior to the manipulation and on control sites

throughout the experiment. However, when access to home sites was blocked, most individuals either died (40%) or emigrated to nearby aggregation sites (50%). The majority of individuals resisted moving from home sites more than four days before emigrating. 25% of displaced individuals returned home after the disturbance had ceased. Results suggest cardinalfish associations with home sites are based on strong traditions and while some species can relocate to new homes, increased mortality may result. If traditional aggregation sites are permanently lost, long-term population decline is predicted.

In conclusion, the combination of extreme habitat specialisation, high levels of co-occurrence and strong site fidelity and homing behaviour indicate many cardinalfish species will be severely impacted by habitat loss. Cardinalfish in the Australia/PNG region will be highly vulnerable to declines in the availability, of not just a single branching coral species, *Porites cylindrica*, but to the loss of large coral colonies and to the damage of particular colonies sites that host large resting aggregations. Species exhibit a high dependence on particular coral colonies due to interactive effects of habitat specialisation preferences, social attraction to other cardinalfish and a limited capacity to relocate following localized disturbances. The family-level dependence on a single coral species provides a sobering example of how declining coral health may threaten biodiversity and re-shape the taxonomic structure of reef fish communities.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: General Introduction

Animals are inherently dependent on their immediate habitat for protection, food and living space (Wiens and Rotenberry, 1981, Bell et al., 1991, McCoy and Bell, 1991). Identifying the degree of susceptibility to habitat change and extinction risk amongst species and communities is a central theme of conservation biology and ecology and underpins conservation efforts (McKinney, 1997, O'Grady et al., 2004). Degradation of habitat quality and availability as a result of anthropogenic disturbances has affected animal species, communities and whole ecosystems throughout the world (Vitousek et al., 1997, Hoekstra et al., 2005, Fischer and Lindenmayer, 2007, Boakes et al., 2010). Some species have benefited from habitat changes, increasing in abundance and expanding their geographic range (Wehtje, 2003, D'Amore et al., 2010, Davies et al., 2010). However the effect of habitat degradation is usually negative with many local and global declines in species abundance and extinctions of vulnerable species (Tilman et al., 1994, Brook et al., 2003, Dulvy et al., 2003, Kappel, 2005).

A species vulnerability to habitat loss is predicted by a suite of biological characteristics including their geographic range size and population density (Lawton, 1993, Gaston, 1994); life history traits (MacArthur and Wilson, 1967); dispersal capacity (Stork et al 2009); trophic level (Diamond, 1984, Crooks and Soule, 1999); body size (Cardillo et al., 2005, Olden et al., 2007); habitat specialisation (Owens and Bennett, 2000); and social behaviour (Courchamp et al., 1999, Reed, 1999). Vulnerability will be higher for species occupying habitat particularly susceptible to human impact (Reed, 1999, Roberts and Hawkins, 1999, Purvis et al., 2000) and those severely impacted by other factors such as over-exploitation (Diamond, 1984, Dulvy et al., 2003). The suite of characteristics possessed by a species and the manner in which these interact will determine the species response to habitat loss. Species with high habitat specificity, low vagility, low population density, aggregative behaviour, small body size and/or those utilising habitats susceptible to anthropogenic disturbances are typically the most vulnerable to habitat disturbances (McKinney, 1997, Reed, 1999, Swihart et al., 2003, Olden et al., 2007, Stork et al., 2009). In general, a combination of several risk factors increases the chances that habitat loss will seriously impact on a species (Davies et al., 2004, Olden et al., 2008). If similar or co-occurring species possess similar characteristics, whole communities also become vulnerable (e.g., Julliard et al., 2004, Helmus et al., 2010).

If a species or community associates with a habitat that is being disturbed, there are three behavioural traits that can act independently or in concert to affect the degree of vulnerability to
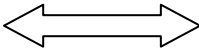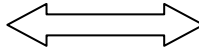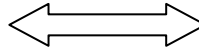
habitat change: (1) habitat dependency; (2) co-occurrence; and (3) site fidelity. For each of these traits, a species level of vulnerability to habitat disturbance can be characterised on an arbitrary scale of low to high (Table 1). Susceptibility to habitat loss will be highest for those species exhibiting combinations of traits.

Habitat dependency relates to each species degree of habitat specialisation or niche breadth. Species vary along a continuum of habitat dependency from extreme habitat specialists, restricted to a single habitat type, to extreme generalists that occupy many different habitats (Fox and Morrow, 1981, Futuyama and Moreno, 1988, MacNally, 1995). Habitat specialist species typically show greater susceptibility to habitat loss than habitat generalists (Warren et al., 2001, Fisher et al., 2003, Kotze and O'Hara, 2003).

Co-occurrence, or niche overlap, describes the degree to which individuals share living space. Within a guild of ecologically similar species, niche overlap occurs when different species share the same habitat resource. A community is vulnerable to habitat loss when multiple species rely on the same susceptible habitat type. For instance, several regional assemblages of cave-dwelling bats are currently threatened by anthropogenic disturbance. Large multispecific aggregations form in a limited number of large caves (Furman and Ozgul, 2004, Niu et al., 2007, Papadatou et al., 2009). Co-occurrence of individuals and species, in association with habitat specialisation on a susceptible habitat type thereby threatens species abundance and assemblage diversity.

Site fidelity is the repeated use of a particular area, such as a breeding site and often seen in the homing behaviour of migratory animals (Gerking, 1959, Switzer, 1993). Strong site fidelity restricts dispersal of individuals and limits species ability to move into new habitats following loss or degradation of home sites. Habitat threats and strong site fidelity currently endanger an array of animals including snakes (Webb and Shine, 1997, Brischoux et al., 2009); marine mammals (Parra et al., 2006, Wolf and Trillmich, 2007); and birds (Warkentin and Hernandez, 1996, Pichegru et al., 2010).

Table 1.1 The effect of three behavioural traits on species' vulnerability to habitat disturbances. For each trait a species (and/or guild) exists somewhere along the trait's continuum of low (left hand side) to high (right hand side). The strength of each trait acts independently and in combination with other traits to affect the species' overall degree of vulnerability to habitat changes. Species with a combination of high level traits will have greater absolute vulnerability than species with a combination of lower level traits.

Behavioural trait		Continuum	
1. Habitat dependence (degree of habitat specialisation)	Generalist	⟵⟶	Specialist
2. Co-occurrence on susceptible habitat (degree of dispersion)	Partitioned	⟵⟶	Overlap
3. Site fidelity (degree of reliance upon particular location/s)	Weak	⟵⟶	Strong
Vulnerability:	Low	⟵⟶	High

Marine communities have historically faced slower rates of habitat change and lower extinction risks than their terrestrial counterparts (Dulvy et al., 2003). In recent decades however anthropogenic impacts on the marine environment have escalated and habitat loss is a key driver of increasing extinction rates (Dulvy et al., 2003, Kappel, 2005). During the next 5-10 decades the frequency and intensity of marine habitat disturbances is predicted to increase because of human induced climate change (Brierley and Kingsford, 2009). Habitat loss and degradation is well-advanced for shallow water habitats such as mangroves, seagrass beds, kelp forests and coral reefs (Jackson et al., 2001, Pandolfi et al., 2003, Halpern et al., 2008). Coral reefs are particularly fragile and threatened ecosystems. Globally, many reefs have already declined in coral cover (Hoegh-Guldberg, 2004, Wilkinson, 2004, Graham et al., 2006).

Degradation of coral communities is the most imminent threat facing coral reef fish assemblages (Wilson et al., 2006, Pratchett et al., 2008b). Coral reef fishes are strongly dependent on the underlying reef habitat for food, shelter and other resources (Roberts and Ormond, 1987, Jones and Syms, 1998). There is increasing evidence of the role habitat specialisation has in determining reef fish community vulnerability to disturbances. Changes in the species composition and structural complexity of reef habitats has led to shifts in the community structure of many fish assemblages (Sano et al., 1984, Kokita and Nakazono, 2001, Halford et al., 2004, Jones et al., 2004, Munday, 2004b, Berumen and Pratchett, 2006, Garpe et al., 2006, Graham et al., 2006, Pratchett et al., 2006, Wilson et al., 2006, Graham, 2007, Cheal

et al., 2008, Bonin et al., 2009a). The magnitude of the shift is often correlated to the degree of habitat specialisation prevalent in a fish community and the effects disturbances have on habitat specialists (Caley and Munday, 2003, Jones et al., 2004, Munday, 2004b, Wilson et al., 2006, Feary, 2007, Feary et al., 2007b, Graham et al., 2007, Wilson et al., 2008, Coker et al., 2009, Graham et al., 2009). If habitat specialisation co-varies with niche overlap and site fidelity the vulnerability of fish communities may be greater and more extensive than currently appreciated. Alternatively broader spatial partitioning of individuals and species and a higher vagility amongst vulnerable habitat types and affected areas may buffer populations, species and communities against increased habitat disturbances and fragmentation. *This thesis explores the close relationship between a guild of common reef fish species and their underlying coral reef habitat. It investigates the mechanics of three 'high risk' traits (specialisation, co-occurrence and site fidelity) and how these behaviours interact to predict and determine the species' response to habitat disturbance*

Trait 1: Habitat dependence

Coral reefs are spatially complex environments offering an array of habitat types to fish assemblages. Small fish species dominate these environments, comprising 75% of most reef fish assemblages (Munday and Jones, 1998). They are differentially distributed amongst available habitats, with high degrees of habitat specialisation common both amongst and within reef areas (e.g., Clarke, 1977, Williams, 1991, Ormond et al., 1996, Depczynski and Bellwood, 2004). Many species are narrowly distributed among particular substrate types and some are specialised at the level of coral species (Munday et al., 1997, Pratchett, 2005). At finer scales at least several species differentiate amongst coral colonies of different sizes and amongst positions within colonies (Kuwamura et al., 1994, Holbrook et al., 2000, Hobbs and Munday, 2004, Limbourn et al., 2007, Schiemer et al., 2008).

Species with high degrees of habitat specialisation are typically more vulnerable to habitat disturbances (McKinney, 1997, Vazquez and Simberloff, 2002, Swihart et al., 2003). Because populations of generalist species utilise a broad array of habitats they are often less susceptible to variations in habitat availability and quality than specialists that are dependent on a single habitat (McKinney, 1997, Swihart et al., 2003). Within coral reef fish assemblages habitat changes have caused greater population declines in specialist species than in generalist species (Clarke, 1996, Munday, 2004b, Wilson et al., 2008).

Trait 2: Co-occurrence and niche overlap

Reef fish species are often partitioned amongst reef zones, depths and substrate types (e.g., Itzkowitz, 1977, Bouchon-Navaro, 1986, Williams, 1991, Clarke, 1994, Ormond et al., 1996). Some species partition living space at finer levels amongst coral species and amongst areas within colonies areas (Munday et al., 1997, Munday, 2004a, Dirnwöeber and Herler, 2007, Limbourn et al., 2007). The partitioned dispersion of reef fish individuals and species in this manner can be a consequence of distinct habitat preferences, territorial behaviour, or from an interaction of the two (Robertson and Gaines, 1986, Robertson, 1996, Bay et al., 2001, Munday et al., 2001, Clarke and Tyler, 2003, Bonin et al., 2009b, Kane et al., 2009).

Niche overlap of reef fish is also common. Numerically, aggregations of reef fish in particular places can dominate local assemblages. Heterospecific aggregations predominantly occur in foraging situations (e.g., Ogden and Buckman, 1973, Jones, 1984, Overholtzer and Motta, 1999, Sazima et al., 2007). Conspecific aggregations are particularly obvious in spawning and settlement phases (Booth, 1992, Warner, 1995, Öhman et al., 1998, Claydon, 2005, Lecchini et al., 2007). Coral colonies often host heterospecific and/or conspecific aggregations of small planktivorous fish (Smith and Tyler, 1972, Sale and Dybdahl, 1975). For most aggregating reef fish whether individuals form groups due to active social choices, limited habitat availability, an interaction of these or whether partitioning just occurs at finer unexplored scales is not known. Species that have a high degree of conspecific co-occurrence use fewer areas of preferred habitat and appear more vulnerable to localised habitat loss than individuals dispersed among multiple areas. If a whole community of species have high niche overlap and rely on the same vulnerable habitats, their vulnerability to disturbance will be increased.

Niche overlap and niche breadth can be inextricably linked. Similar species can theoretically co-exist because of interactions between their degree of specialisation and their degree of co-occurrence (Schoener, 1974, Schluter and Ricklefs, 1993). For any guild of species, interspecific variation in the degree of specialisation and in the degree of spatial overlap should act to minimise the effects of habitat loss on the whole guild. However if several species are specialised on the same habitat type the vulnerability of the whole community to habitat loss will be high.

Trait 3: Site fidelity and homing behaviour

Coral reef fish generally exhibit strong site fidelity, with individuals of small reef fish often confined to living in single coral colonies or anemones (Sale, 1971, Fautin and Allen, 1997). More mobile individuals show strong tendencies to favour particular areas within their home ranges or persistently utilise particular spawning, foraging or resting sites (Ogden and

Buckman, 1973, Zeller, 1997, Chapman and Kramer, 2000, Marnane, 2000, Jones, 2005, Afonso et al., 2009). These mobile species often also display homing behaviour, in which they return to particular sites after substantial daily or seasonal migrations (Papi, 1992, Dingle, 1996). Experimental displacement of individuals into non-familiar areas has resulted in high numbers of individuals homing back to the original site of capture (Ogden and Buckman, 1973, Ogden and Ehrlich, 1977, Buchheim and Hixon, 1992, Beets and Hixon, 1994, Marnane, 2000, Kolm et al., 2005, Wall and Herler, 2009).

Vulnerability to habitat loss depends on whether individuals affected by habitat changes can move between suitable areas of preferred habitat. Strong site fidelity and homing behaviour indicates a strong reliance on particular places and a very limited capacity to relocate should habitat loss occur (McKinney, 1997, Webb and Shine, 1997, Laidre and Heide-Jorgensen, 2005). Homing animals also tend to exhibit discrete populations with more limited connectivity than the scale of their migratory movements suggests (Bowen and Karl, 2007, Rooker et al., 2008). Strong site reliance, homing behaviour and low population connectivity combine to increase species' vulnerability to habitat loss and limit population recovery. Despite the apparent strength of site fidelity and homing behaviour in coral reef fish communities very little work has been done investigating the mechanisms and implications of this behaviour.

Site fidelity and homing behaviour feasibly interact with habitat specialisation and co-occurrence traits in many coral reef fish. Numerous studies investigating the mechanisms of coral reef fish habitat distributions have shown strong interactions between two out of three of these traits: habitat specialisation and social interactions (Booth, 1992, Clarke, 1996, Öhman et al., 1998, Bay et al., 2001, Elliott and Mariscal, 2001, Schofield, 2003, Whiteman and Côté, 2004, Lecchini et al., 2007, Kane et al., 2009); habitat specialisation and site fidelity/movement (Depczynski and Bellwood, 2004, Feary, 2007, Bonin et al., 2009a); social interactions and site fidelity/movement (Zeller, 1998, Bolden, 2000, Morgan and Kramer, 2004, Kolm et al., 2005, Afonso et al., 2008, Wall and Herler, 2009). However no studies have examined the interactive role of all three traits. Understanding these three traits and their interaction is necessary for predicting the response of a broader range of reef fish species to disturbance.

Study system: Cardinalfish (Family Apogonidae)
Research exploring the relationship between reef fish and coral distributions has predominantly focused on corallivores and obligate coral dwelling gobies (e.g., Munday et al., 1997, Munday, 2001, Pratchett, 2005). However, many other groups are dependent on the shelter corals provide (Jones et al., 2004, Munday et al., 2007). One group with very strong apparent dependence on live coral colonies for shelter is cardinalfish (Family: Apogonidae). On Indo-pacific reefs the

family ranks fifth in diversity and abundance, with most species < 100mm in average size (Munday and Jones, 1998, Allen, 2002). They dominate near-shore reef fish assemblages and are particularly abundant in shallow, sheltered reef zones such as lagoons and leeward slopes (Greenfield and Johnson, 1990, Finn and Kingsford, 1996, Marnane, 2001, Adams and Ebersole, 2002). Despite their dominance very little is known about this guild.

Cardinalfish are nocturnal planktivores that use branching corals and caves as diurnal resting sites (Vivien, 1975, Greenfield and Johnson, 1990, Marnane, 2001). Their foraging grounds are spatially partitioned but by day the group form large conspecific and multispecific aggregations (Greenfield and Johnson, 1990, Marnane and Bellwood, 2002). Strong site fidelity and homing to diurnal refugia has been shown for several species in a shallow lagoon habitat on the southern Great Barrier Reef, Australia (Marnane, 2000). If habitat dependency, co-occurrence and site fidelity occur and interact, the cardinalfish guild will be extremely vulnerable to habitat loss. Species-specific variation in the degree of habitat specialisation, niche overlap and capacity to relocate following disturbance will illustrate the guild's degree of resilience to habitat shifts as well as their actual response when changes occur.

This thesis explores the levels of specialisation, co-occurrence and site fidelity (including homing behaviour) and their inter-relationships in coral reef dwelling cardinalfish. The vulnerability of this family to habitat loss and degradation is examined by addressing the following five questions: (1) Do cardinalfish communities exhibit strong associations with particular substrata or do species vary in their micro-habitat use? (2) Do cardinalfish species differentially specialise on particular types of coral colonies and on specific areas within coral colonies? (3) Is the observed degree of habitat specialisation and niche overlap a result of behavioural preferences for habitat types, conspecifics or a combination of these? (4) Do cardinalfish individuals move amongst adjacent resting sites and can they home between isolated reef platforms? (5) Are cardinalfish constrained to using particular resting sites or can they relocate following habitat disturbance?

This thesis is constructed as a series of stand alone publications that are conceptually connected. **Chapter 2** investigates the degree of specialisation and overlap on live coral substrata among 10 common cardinalfish species on the inshore reefs of Kimbe Bay, Papua New Guinea. This study tests the following hypotheses (1) the cardinalfish family is not strictly dependent upon live coral; (2) species vary along a specialist - generalist continuum in micro-habitat associations; and (3) species partition their micro-habitat resources. Habitat associations and species co-occurrence are explored amongst broad categories of living and non-living reef substratum and amongst particular species of branching coral.

Fine-scale habitat use and partitioning of different coral colonies and positions within colonies is examined in **Chapter 3.** I hypothesise that specialisation and partitioning of diurnal refuge habitat by cardinalfish explains the coexistence of the speciose cardinalfish community on coral reefs. Cardinalfish are predicted to differentiate among coral colonies of variable size, complexity, health and isolation from neighbouring substrata. If multiple species share single coral colonies, interspecific partitioning of refuge space within the colony is predicted.

Spatial distributions of coral reef fish are potentially determined by habitat preferences and behavioural interactions. **Chapter 4** tests the hypotheses that the observed habitat associations of cardinalfish (Chapters 2 and 3) are due to strong preferences for living coral over dead substrata and for particular coral species. In addition the clumped dispersion of cardinalfish species is predicted to result from strong conspecific attraction which also reinforces habitat associations. The habitat and social preferences of three common cardinalfish were tested using a series of three-way choice experiments in large outdoor aquaria.

Under conditions of widespread habitat loss, strong bonds with home sites may restrict population connectivity and limit resilience to habitat change. A natural tendency to move among neighbouring areas of preferred habitat could buffer populations against localized habitat losses. Conversely strong homing behaviour will restrict the population's relocation capacity. In **Chapter 5** I therefore examine the extent of site fidelity and homing behaviour in the cardinalfishes of Kimbe Bay. I determine (1) whether individuals move amongst adjacent resting sites; (2) the relative homing ability of four species within and among isolated reef platforms; and (3) the long distances over which homing may occur. Given the vulnerability of open water passages for small reef fish, homing among reefs is not expected.

In the last data chapter (**Chapter 6**), the response of two abundant cardinalfish species to loss of their specific home sites is examined. I employed a small-scale habitat disturbance experiment to assess the strength of species site fidelity with particular resting sites. That is, to determine whether they have an obligate association with particular home sites or have the ability to relocate and establish new home sites. I predict strong preferences with the home site will result in high mortality while social behaviour will increase species' capacity to emigrate from degraded locations and resettle in neighbouring refugia.

CHAPTER 2: Habitat specialisation and overlap in a guild of coral reef cardinalfishes (family Apogonidae)

2.1. Abstract

The nocturnally foraging cardinalfish are known to exhibit a high degree of fidelity to their day-time resting sites. However, the micro-habitats chosen as resting sites, the degree of specialisation on live coral substrata and the degree of overlap among apogonid species have not been described. These patterns potentially affect how declining coral availability will affect the diversity and abundance of apogonid assemblages. Here, micro-habitat use, abundances and patterns of co-occurrence are examined for 10 common reef-dwelling apogonids in Kimbe Bay, Papua New Guinea. Nine of the 10 species were strongly associated with live scleractinian corals, with more than 80% of the individuals resting in branching forms. The exception was *Apogon nigrofasciatus*, a specialist on cave or crevice habitats. Among the available coral species, the vast majority of cardinalfish were associated with a single coral species (*Porites cylindrica*), although the degree of specialisation varied among species. *Zoramia leptacanthus* and *Sphaeramia nematoptera* were almost always only found on *P. cylindrica*, while *Apogon bandanensis, Apogon compressus, Zoramia fragilis, Archamia fucata, Archamia zosterophora, Cheilodipterus artus* and *Cheilodipterus quinquelineatus* also used a range of other corals. There was a positive relationship between the range of substratum types used and the number of groups of each species observed. The nine coral-dwelling apogonids exhibited a high degree of overlap in depth range and in the use of coral micro-habitats. Over 75% of aggregations were made up of more than one fish species. The high level of both specialisation and overlap in habitat use suggests that the future biodiversity of cardinalfishes in Kimbe Bay could be linked to the fate of a single coral species.

2.2. Introduction

Organisms vary in the range of habitats they use and the degree to which their patterns of habitat use overlap with one another. Knowledge of the range of variation in habitat use within and among species is necessary to understand how populations are regulated and ecological communities are structured (Morris, 1988, Begon et al., 1996, Fryxell and Lundberg, 1998). This information is also vital to predict how individual species and whole communities will

respond to the degradation of their habitats (Hawkins et al., 2000, Swihart et al., 2003, Jones et al., 2004). Species are known to vary along a continuum from extreme habitat specialists, restricted to a single habitat, to extreme generalists capable of living in many different habitats (Fox and Morrow, 1981, Futuyama and Moreno, 1988, MacNally, 1995). The degree of specialisation has important implications for a species' performance in different habitats and the influence of habitat availability on abundance (Rosenzweig, 1981, Brown, 1984). A specialist and a generalist can theoretically co-exist because each has a competitive advantage over the other in different habitats (Morris, 1996, Kassen, 2002). In addition, a specialist may co-exist with another specialist because, as a consequence of competition, each has become specialised on different habitats (MacArthur, 1958, Hardin, 1960, Schluter and Ricklefs, 1993). The validity of these ecological theories relies on a description of the relationship between the degree of specialisation and overlap in ecological communities, which is often unknown.

Coral reef fishes are often dependent upon the underlying coral reef habitat for shelter and/or food. Reef fish ecologists have been divided over the degree of micro-habitat specialisation, the degree to which the available micro-habitats are partitioned amongst reef fish species and the degree to which the structure of reef fish communities is determined by habitat characteristics (Sale, 1991, Williams, 1991, Jones and Syms, 1998, Munday and Jones, 1998). Within any one family, reef fish species clearly vary both in the degree of micro-habitat specialisation (Munday et al., 1997, Munday, 2000, Bean et al., 2002) and in the degree to which they overlap with other fish species (Itzkowitz, 1977, Robertson and Lassig, 1980, Hourigan, 1989, Fowler, 1990, Clarke, 1994, Green, 1996, Öhman et al., 1998). If specialisation and overlap are linked, three broad patterns are possible. Firstly, communities may be composed primarily of generalists, which would inevitably overlap in habitat use. Secondly, communities may be composed primarily of specialists, but each species is specialised on different micro-habitats (as predicted from competition theory). Finally, communities may be composed primarily of specialists on the same micro-habitat, as might be expected if there is a single, highly preferred substrata for shelter or food. Which of these patterns best describes coral reef fish is unknown.

The degree of micro-habitat specialisation and overlap in reef fish assemblages and any linkage between them, has important ecological consequences (Jones et al., 2002). Firstly, theory predicts that among ecologically similar species, local abundance is positively related to the number of micro-habitats used (Brown, 1984, Hughes, 2000), which appears to apply to a number of reef fish groups (Meekan et al., 1995, Munday, 2000, Bean et al., 2002, Jones et al., 2002). Secondly, changes to habitat availability are predicted to affect habitat specialists more than habitat generalists (Swihart et al., 2003). Again a number of comparative studies have supported this conclusion (Clarke, 1996, Munday, 2004b). While specialists may be more

susceptible to habitat degradation, the ultimate effect on the whole community depends upon what proportion of species are specialised on micro-habitats that are under threat. Communities composed of species with a high degree of micro-habitat partitioning may be resistant to habitat degradation, provided that not all habitats are adversely affected. Conversely, if all species are specialised on the same micro-habitat undergoing degradation, the whole community will be threatened (McKinney, 1997). An understanding of these threats requires detailed knowledge of both niche breadth and overlap, which is lacking for most coral reef fish taxa.

Globally, many coral reefs are exhibiting a decline in coral cover due to a variety of anthropogenic sources (Hughes, 1994, Sebens, 1994, Wilkinson, 2002, Gardner et al., 2003, Hughes et al., 2003, Jones et al., 2004). The degree to which declining coral will affect fish communities will depend upon their reliance on susceptible coral species. While some taxa (e.g., butterflyfishes) appear to be particularly dependent upon live coral as a food source, many others are not. Recently, Jones et al. (2004) showed that the declining coral could affect a greater range of reef fish species than previously thought, because of an under-estimate of the species dependent upon coral at some stage in their life cycle. Many reef fish families have been neglected in studies of fish-habitat relationships, making it difficult to predict the community-wide effects of declining corals.

The cardinalfish (family Apogonidae) are one of the most abundant and diverse fish families on Indo-Pacific reefs (Munday and Jones, 1998, Allen, 2002). Despite their abundance, they are one of the least researched taxa and only limited information is available concerning their biology and ecology (Williams, 1991, Munday and Jones, 1998, Marnane and Bellwood, 2002). Apogonids are small in body size and predominantly nocturnal planktivores, a feeding mode that suggests they may have little reliance on the structure of reef habitats. However, during the day cardinalfish commonly form large, multispecific aggregations that are closely associated with the reef substratum, in particular with caves and branching corals (Vivien, 1975, Chave, 1978, Greenfield and Johnson, 1990, Marnane, 2001). A number of species exhibit strong fidelity to the same resting sites (Marnane, 2000), suggesting that specific features of the habitat may be important. However, the degree of habitat specificity and niche partitioning at this scale has not been examined for this group.

In this study I examine the degree of apparent micro-habitat specialisation and overlap in diurnal resting sites for common apogonid species in Papua New Guinea. The primary goal was to assess whether this community is primarily composed of habitat generalists, habitat specialists with little overlap among species or habitat specialists with substantial overlap among species. To examine the potential relationships between specialisation and overlap in the

use of coral substrata and predict changes in response to declining coral cover, I collected species-specific information on the types and range of coral species used as resting sites. Based on the literature, I predicted that: (1) the family as a whole would not be strictly dependent upon live coral; (2) species would vary along a specialist-generalist continuum in micro-habitat use; (3) species would show a high level of partitioning of micro-habitat resources; and (4) the degree of micro-habitat specialisation would be negatively correlated to the relative local abundance of species. The ultimate goal was to assess the likely consequences of habitat degradation on community dynamics in this little studied group of coral reef fishes.

2.3. Methods

2.3.1. Study site and species

The field study was conducted at Kimbe Bay, West New Britain province, Papua New Guinea (5°30'S: 150°05'E) in September 2003 (Fig. 2.1a). Kimbe Bay is a large, sheltered bay with little change in water temperature throughout the year ($31 \pm 1°C$). The bay's reefs have a large depth range, with many breaking the surface at low tide and extending to depths of > 200 m. Apogonid surveys were conducted at 17 study sites, 10 near the Mahonia Na Dari Conservation Centre and seven near Schumann Island (Fig. 2.1b). The family Apogonidae is the fifth most speciose reef fish family in the bay, with 36 species recently documented (Allen and Munday, 1996).
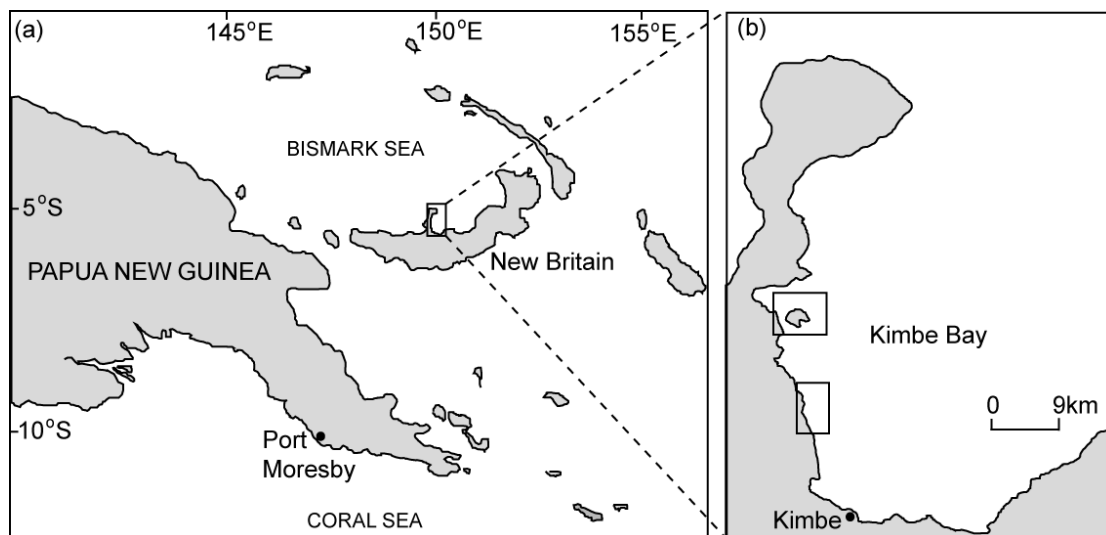
Figure 2.1 (a) Location of Kimbe Bay, New Britain Province, Papua New Guinea and (b) the two inshore areas where reefs were surveyed.

2.3.2. Apogonid surveys

Micro-habitat use by species was determined from surveys of back and fore-reef slopes as well as from a number of lagoons at each study site. Censusing across zones provided a cross-section of fish distribution and species diversity at each site. Due to the aggregated and often cryptic nature of apogonids a haphazard census method was used. Where the reef profile permitted, each census began at 15 to 20m with the diver swimming back and forth along the reef face in a zigzag fashion until reaching the reef flat, being careful not to survey the same area more than once. In lagoons or shallow reef slopes, census began from the reef base. All censuses took place between 09:00 and 17:00h when fish were generally observed at resting sites. Upon observation of a cardinalfish group or individual, records were taken as to the species present; number of individuals (per species) in the group (estimated if > 10); depth (to the nearest 0.5m); and micro-habitat use. To ensure sampling sizes had sufficient statistical power, a minimum of 18 groups per site were recorded. The habitat use data from each site was collated.

The micro-habitat used by individual cardinalfish was defined at two levels. The first level was a coarse classification that included a small number of both live and dead substrata. The categories were live hard coral, soft coral, gorgonians, other organisms (e.g., anemones), dead coral (with identifiable morphology), rubble, bare rock, algae (macro and turf), sand and caves (Table 2.1). Where live, hard coral was utilised, a second level of classification was applied, based on a combination of the coral genera and growth form (Table 2.1). This allowed the degree of specialisation on different corals to be assessed. Fish observed using rarer coral genera were recorded in 'other' categories based only on coral morphology. A total of eight coarse micro-habitat and 15 live, hard coral categories were distinguished (Table 2.1).

The micro-habitats used were recorded as those within which individual/s were first seen. Apogonids are relatively immobile on approach, making classification of micro-habitats straight forward. Individuals and aggregations were occasionally seen between or within two habitat types. In this case both habitat types were recorded. Apogonids observed within caves, rubble crevices or ledges under coral colonies (dead or alive) were recorded as primarily using a cave habitat, rather than the underlying substratum (eg. of sand, rubble or encrusting organisms) since the former clearly offered the dominant habitat structure.

2.3.3. Micro-habitat availability

Line transects were conducted at each site to assess the availability of each micro-habitat. Four 50m transects were laid randomly across the reef slope at depths of 0, 2, 6 and 10m. This depth range was sufficient as the majority of cardinalfish (97.6% of individuals) were observed at or

above 10m. Each tape was marked with 100 randomly allocated points and the substratum directly beneath each point recorded. Substrata were recorded to coarse micro-habitat and live, hard coral categories as per fish censuses (Table 2.1).

Table 2.1. Micro-habitat categories used in this study.

Coarse	Live, hard coral
Live, hard coral	*Acropora* – arborescent
Soft coral	*Acropora* – bottlebrush
Gorgonians	*Acropora* – bushy
Algae	*Acropora* – corymbose
Other organisms	*Anacropora* – branching
Dead coral[a]	*Montipora* – branching
Rubble[b]	*Pavona* – foliose branching
Bare rock	*Pocillopora* – branching
Sand	*Porites cylindrica*
Caves	*Porites* – digitate branching
	Seriatopora – branching
	Millepora – branched plates
	Other branching corals
	Plating corals
	Mound corals

[a] Coral genera and morphology identifiable.
[b] Dead coral unidentifiable to taxonomic or morphological level.

2.3.4. Micro-habitat specialisation

The relative specialisation of each cardinalfish species was assessed by comparing the absolute number of substrata used, both in terms of coarse micro-habitat categories and of live, hard coral substrata. Only species for which > 50 individuals and > 10 groups were recorded were used for comparisons of micro-habitat associations. Proportional use of micro-habitat categories by these species was calculated using the total number of observed individuals.

Chi-square goodness of fit statistics were applied to test the frequencies of habitat use against habitat availability. Use of live, hard corals was only examined when species showed > 10% proportional use of this coarse micro-habitat category. In order to meet assumptions of chi-square methodology a number of live coral categories were pooled to ensure that no more than 20% of expected counts were less than five and all were above one (Zar, 1999). Frequencies of cave use were not included because availability of this coarse micro-habitat substrate could not be measured. Chi-square goodness of fit statistics requires that each individual's resource use is independent of other animals. Because apogonids aggregate, I used the proportion of groups

using particular habitats, rather than the proportion of individuals, to compare with habitat availability.

Resource selection ratios quantified each species' degree of specialisation on different micro-habitats. Manly et al.'s (2002) resource selection Sampling Protocol A, Design I, was followed because it allowed for random sampling of used resource units and available resource units at the population level. The formula to calculate resource selection ratios was:

$$\hat{w}_i = o_i / \pi_i$$

where $\hat{w}_i$ is the resource selection probability function, o_i is the proportion of coarse micro-habitat i or coral i used and π_i is the proportion of resource unit i available to the fish population (Manly et al. 2002). Because of multiple comparisons, Bonferroni Z-corrections were used to calculate 95 % confidence intervals (CI) for each ratio, following the formula:

$$Z_{\alpha/2k} \surd [o_i (1 - o_i) / (U_+ \pi_i{}^2)]$$

where $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $a/2k$, $a = 0.05$, $k =$ the number of habitats used and U_+ is the estimated number of groups (per species) observed using that habitat type and π_i is the proportion of resource unit i available to the fish population. Selection indices (± 95% CI) above the value of one indicate significantly positive habitat use, while those below one indicate negatively significant use and those encompassing one show that habitat use is in proportion to habitat availability (not significant).

2.3.5. Niche overlap

The horizontal distribution of cardinalfish species were assessed using the percentage similarity measure (Krebs, 1999). In this manner the composition of each zone was compared to that in other zones. Niche overlap between each species on coarse and live coral micro-habitats were also calculated using the percentage similarity measure. The percentage of overlap on micro-habitats is calculated by:

$$P_{jk} = [\sum_{i=1}^{n} (\text{minimum } p_{ij}, p_{ik})] \times 100$$

where P_{jk} is the percentage overlap between species j and species k, p_{ij} is the proportion micro-habitat i is of the total micro-habitats used by species j, p_{ik} is the proportion micro-habitat i is of the total micro-habitats used by species k and n is the total number of micro-habitat categories

(Krebs 1999). The degree of habitat partitioning on coral substrata was further examined by evaluating the frequency of multispecific colony formations. Aggregations were defined apriori as groups with > 10 individuals occupying the same coral head.

2.3.6. Specialisation – abundance relationship

Linear regression was applied to test the relationship between micro-habitat specialisation and local abundance. The relative degrees of specialisation on both coarse micro-habitats and live coral substrata were compared using the number of micro-habitats used. The relative local abundance of each species was based both on the estimated number of individuals and on the number of groups per species.

2.4. Results

2.4.1. General Patterns

A total of 25 species, five genera and approximately 12,500 individual cardinalfish were observed on Kimbe Bay coral reefs (Table 2.2). The community was clearly dependent on live, hard coral as the primary resting habitat. Only three of 25 species were not observed in live coral and less than half the species were ever observed on non-living coral substrata (Table 2.2). I observed 10 species from four genera with sufficient individual (> 50) and group (> 10) abundance to carry out detailed analyses of habitat associations (Table 2.2). Rarer species were usually resting in either live, branching corals or in rubble crevices. Species that were only observed in non-living coral substrata were also rare (e.g., *Apogon taeniophorus*, *Apogon trimaculatus* and *Foa brachygamma*).

Table 2.2. Observed apogonid species and relative abundance.

Apogonid species	Number of individuals	Number of groups	% live coral use (individuals)
*Zoramia fragilis**	2721	23	94.5
*Cheilodipterus quinquelineatus**	2614	311	81.5
*Archamia zosterophora**	2415	60	100
*Zoramia leptacanthus**	1609	19	100
*Apogon compressus**	840	111	96.7
*Cheilodipterus artus**	800	65	81.9
Apogon cyanosoma	408	7	2
*Apogon nigrofasciatus**	383	124	6.3
*Apogon bandanensis**	154	22	96.1
*Archamia fucata**	140	11	100
*Sphaeramia nematoptera**	59	14	100
Apogon fraenatus	38	11	26.3
Apogon novemfasciatus	35	10	62.9
Apogon moluccensis	30	1	100
Apogon ventrifasciatus	30	1	100
Apogon multilineatus	26	20	15.4
Archamia biguttata	20	4	100
Archamia macroptera	20	1	100
Apogon taeniophorus	19	15	0
Apogon kallopterus	10	7	30
Cheilodipterus alleni	4	3	0
Apogon fuscus	4	2	100
Apogon trimaculatus	3	3	66.7
Foa brachygamma	2	3	0
Cheilodipterus macrodon	1	1	100

* indicates 10 species used in micro-habitat analyses

2.4.2. Degree of specialisation on coarse micro-habitats

Species varied in the number of coarse micro-habitats occupied (Fig. 2.2). Nine of the 10 relatively common species (*Apogon nigrofasciatus* excluded) occupied live hard coral with > 75% frequency, while soft coral, gorgonians, other organisms, dead coral, rubble and sand micro-habitats were utilised in less than 18% of observations (Fig. 2.2). Live coral cover made up less than 25% of the substrata (Fig. 2.3a). No species was distributed according to availability of coarse micro-habitats (Chi square goodness of fit test: $\chi^2 > 11.070$, d.f. = 5, $p < 0.05$). Apart from *A. nigrofasciatus*, all species occupied live hard coral more frequently than expected from substrata availability (Table 2.3a). This substratum was the only habitat ever utilised significantly more than availability predicted (Table 2.3a).

Although most species were to a large degree specialised on live coral, individual species did vary in the degree of specialisation. *Archamia fucata*, *Archamia zosterophora*, *Zoramia leptacanthus* and *Sphaeramia nematoptera* exhibited the highest degree of specialisation at the level of coarse micro-habitats, occupying 1-2 substrata each (Fig. 2.2). When two substrata were used, one was always live, hard coral and the other an adjacent micro-habitat. *Apogon bandanensis* and *Zoramia fragilis* both utilised four categories (Fig. 2.2). Dead coral, rubble and gorgonians (*Z. fragilis* only) were occupied in proportion to their availability (Table 2.3a). *Apogon compressus*, *Cheilodipterus artus* and *Cheilodipterus quinquelineatus* were the less specialised species of the group. Other than live coral use, *A. compressus* and *C. artus* utilised 2-3 other habitats in accordance to availability and one less frequently than expected (Table 3a). *C. quinquelineatus* occupied seven coarse substrata categories. It occupied all non-living coral substrata in proportion to their availabilities (Table 2.3a). The remaining species *A. nigrofasciatus* predominantly used cave habitats (Fig. 2.2). Unlike other common species it occupied live, hard coral less frequently than expected on the basis of availability (Table 2.3). Gorgonians were the only coarse micro-habitat it used in proportion to its availability.
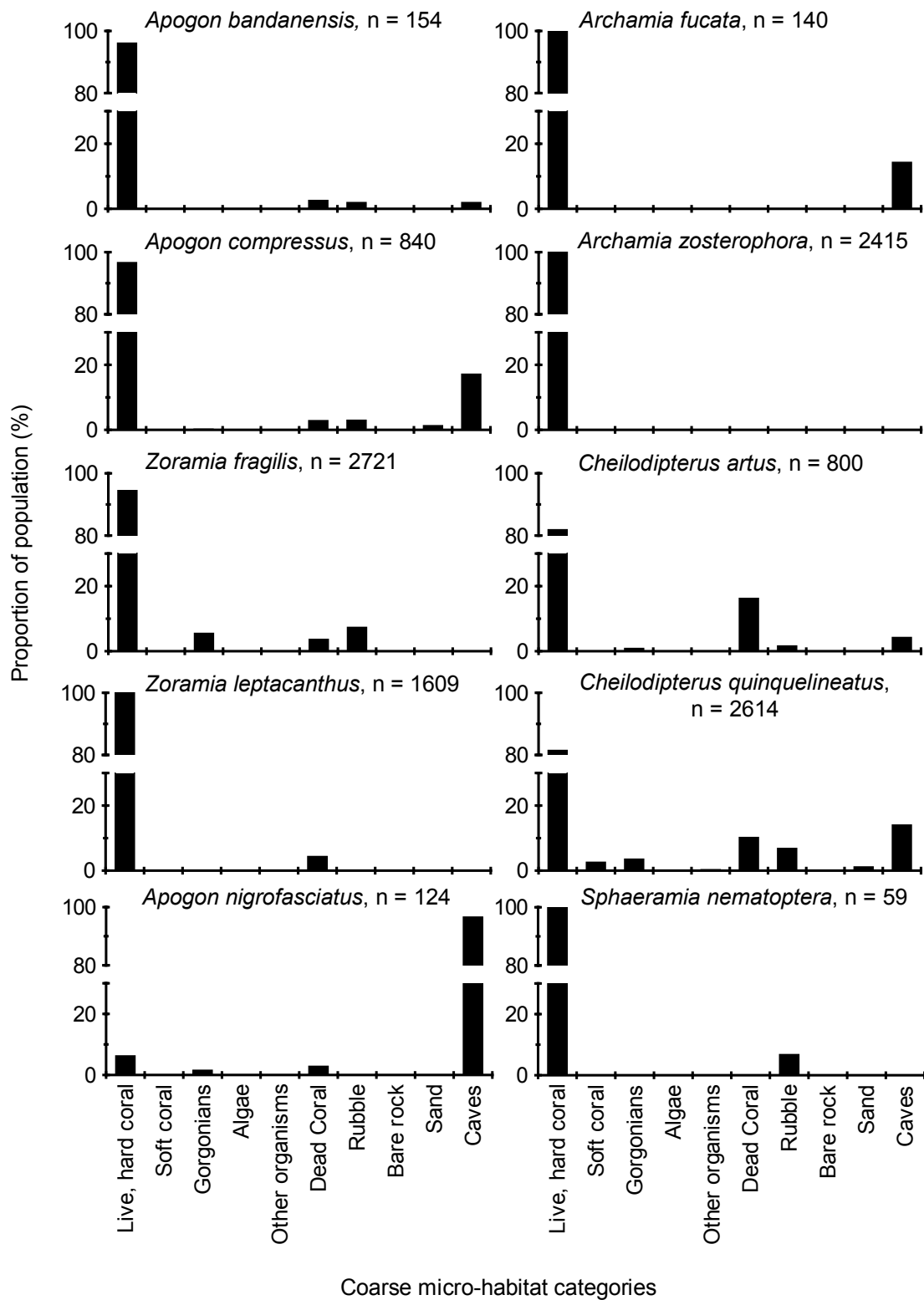
Figure 2.2 Relative proportions of populations of 10 common apogonid species associated with the different coarse micro-habitats, including living and non-living substrata (n = estimated no. of individuals sampled per species)

Table 2.3 Significance of habitat use by 10 common Apogonid species in Kimbe Bay using resource selection ratios and Bonferroni corrected 95% confidence intervals (Manly et al. 2002). (a) Use of coarse micro-habitat substrata. (b) Use of live, hard coral substrata (*Apogon nigrofasciatus* excluded). (=) Habitat used in proportion to availability (+) habitat used significantly more than expected, (−) habitat used significantly less than expected, (U) habitat not used

	Micro-habitat	*Apogon bandanensis*	*Apogon compressus*	*Zoramia fragilis*	*Zoramia leptacanthus*	*Apogon nigrofasciatus*	*Archamia fucata*	*Archamia zosterophora*	*Cheilodipterus artus*	*Cheilodipterus quinquelineatus*	*Sphaeramia nematoptera*
(a)	Live, hard coral	+	+	+	+	−	+	+	+	+	+
	Soft coral	U	U	U	U	U	U	U	U	=	U
	Gorgonians	U	=	=	U	=	U	U	=	=	U
	Other organisms	U	U	U	U	U	U	U	U	=	U
	Dead coral	=	=	=	=	−	U	U	−	=	U
	Rubble	=	=	=	U	U	U	U	=	=	=
	Sand	U	−	U	U	U	U	U	U	=	U
	Algae	U	U	U	U	U	U	U	U	U	U
	Bare rock	U	U	U	U	U	U	U	U	U	U
(b)	*Acropora* - arborescent	=	=	=	=		U	U	=	+	U
	Acropora - other branching	U	=	U	U		=	U	=	=	=
	Anacropora - branching	=	+	=	U		U	+	=	+	=
	Pavona - foliose branching	=	=	U	U		=	=	=	=	U
	Porites cylindrica	+	+	+	+		+	+	+	+	+
	Porites - digitate branching	=	+	U	U		U	=	=	=	U
	Other branching [1]	=	=	=	U		U	=	=	=	U
	Plating	U	−	U	U		=	−	U	−	U
	Mounds, encrusting and other	−	−	U	U		−	U	=	−	U

[1] includes *Millepora*, *Montipora*, *Pocillopora*, *Seriatopora* and other branching corals

2.4.3. Degree of specialisation on live coral substrata

The nine cardinalfish species associated with live coral exhibited an apparent selection for *Porites cylindrica* outcrops (*c.f.* Fig. 2.3 and Fig. 2.4). The proportion of individuals associated with this single coral species ranged from 24% in *C. quinquelineatus* to 94% in *Z. leptacanthus*. Branching corals accounted for less than 21% of the available live coral cover and *P. cylindrica* accounted for less than 5% (Fig. 2.3b). Although all fish species varied in the range of live hard corals occupied, none of these nine species were distributed according to the availability of

coral substrata (Chi-square goodness of fit test: $\chi^2 > 15.5$, d.f. = 8, $p < 0.05$). Of all the coral species used, only branching forms were ever occupied more frequently than expected on the basis of availability (Table 2.3b). Of these, *P. cylindrica* was always occupied more frequently than expected.

Cardinalfish species varied in their degree of specialisation on particular coral genera and growth forms. *Z. leptacanthus* and *S. nematoptera* exhibited the highest degree of apparent specialisation on live, coral taxa, utilising two and three categories respectively (Fig. 2.4). Over 90% of individuals in these species used *P. cylindrica*. *Acropora* and *Anacropora* (*S. nematoptera* only) branching corals were occupied in proportion to their availability (Table 2.3b). *Z. fragilis* was found in four branching coral categories, but only *P. cylindrica* was used more frequently than expected (Fig. 2.4, Table 2.3b). *A. fucata, A. zosterophora, A. bandanensis, A. compressus* and *C. artus* utilised a wider range of coral categories. However, 39-66% of groups were in *P. cylindrica*, far above that expected on the basis of availability. *A. compressus* and *A. zosterophora* also occupied *Anacropora* and digitate *Porites* (*A. compressus* only) more than predicted by habitat availabilities (Table 2.3b). *C. quinquelineatus* was clearly the least specialised apogonid species, using all 15 live, hard corals (Fig. 2.4). Like other species it occupied *P. cylindrica* more than any of the other corals. Of the nine pooled coral categories, *P. cylindrica*, arborescent *Acropora* and *Anacropora* were occupied more frequently than expected and non-branching corals less frequently than expected if this species was a complete generalist (Table 2.3b).
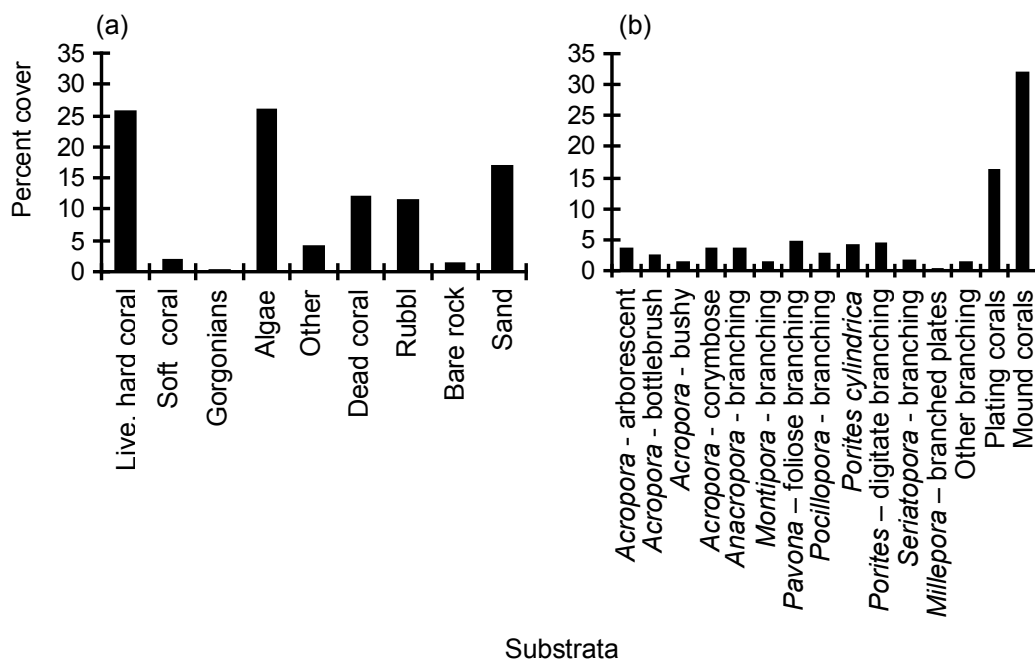
Figure 2.3 Relative cover of different micro-habitat types based on field estimates of (a) coarse micro-habitat categories, including living and non-living substrata; and (b) live coral substrata.
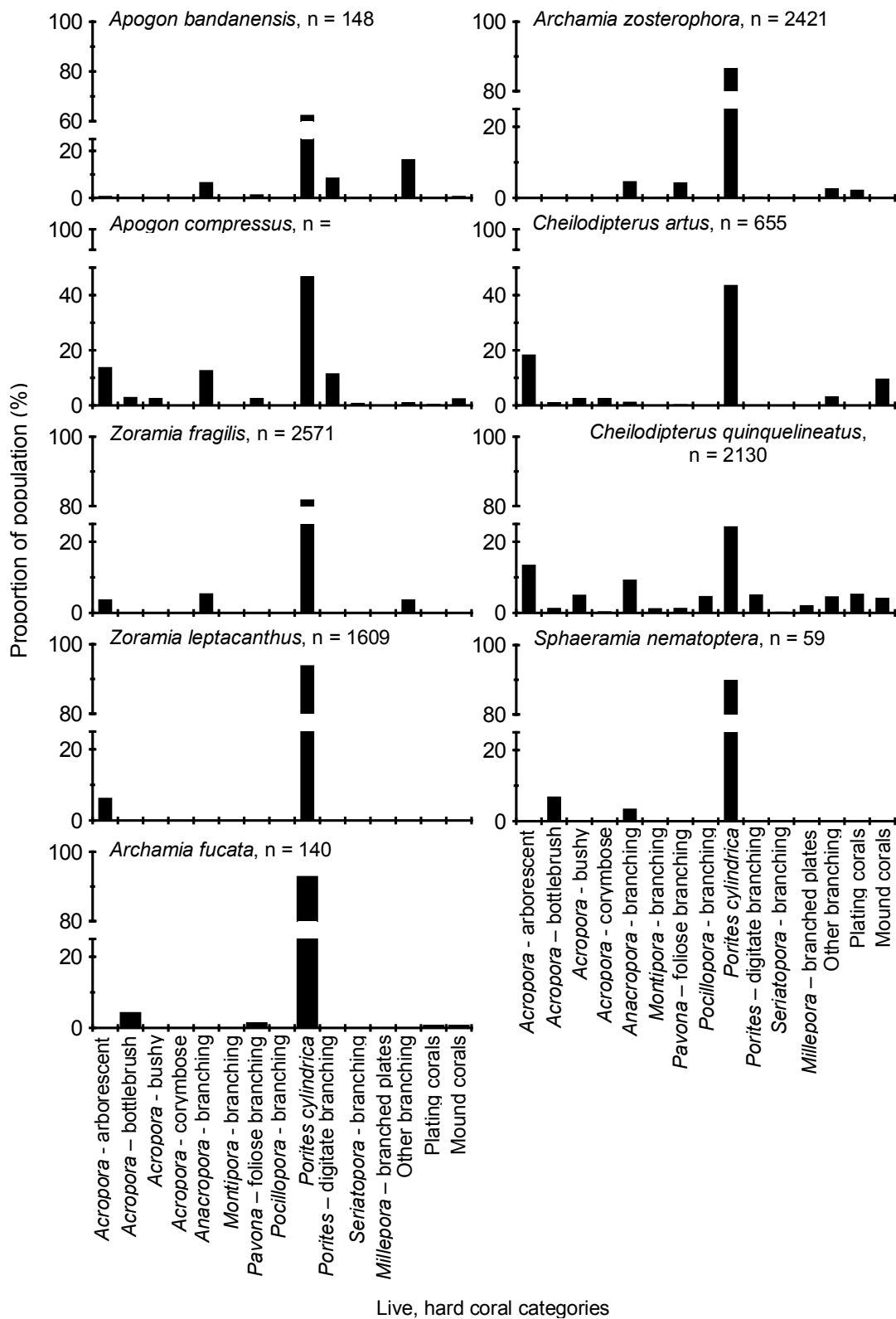
Figure 2.4 Relative proportions of populations of nine common apogonid species associated with different live coral substrata (n = estimated no. of individuals sampled per species)

2.4.4. Niche overlap

The ten common cardinalfish species exhibited very high levels of overlap in their use of habitats, in respect to zonation, depth and micro-habitat use. The communities of cardinalfish species observed within back-reef, fore-reef and lagoons were highly similar with pair-wise percentage similarities each greater than 66% (Fore-reef: Back-reef 89.76%, Fore-reef: Lagoon 66.14%, Back-reef: Lagoon 71.41%). There was a significant difference in observed mean depths ($F = 2.60$, $p < 0.01$), however the depth range of species broadly overlapped in shallow water (Fig. 2.5). There were strong positive relationships between the depth ranges of species and the ranges of coarse substrata ($r = 0.86$, $p < 0.01$) and coral types used ($r = 0.96$, $p < 0.001$). That is, species with the widest depth distributions tended to be less specialised in terms of substratum use.
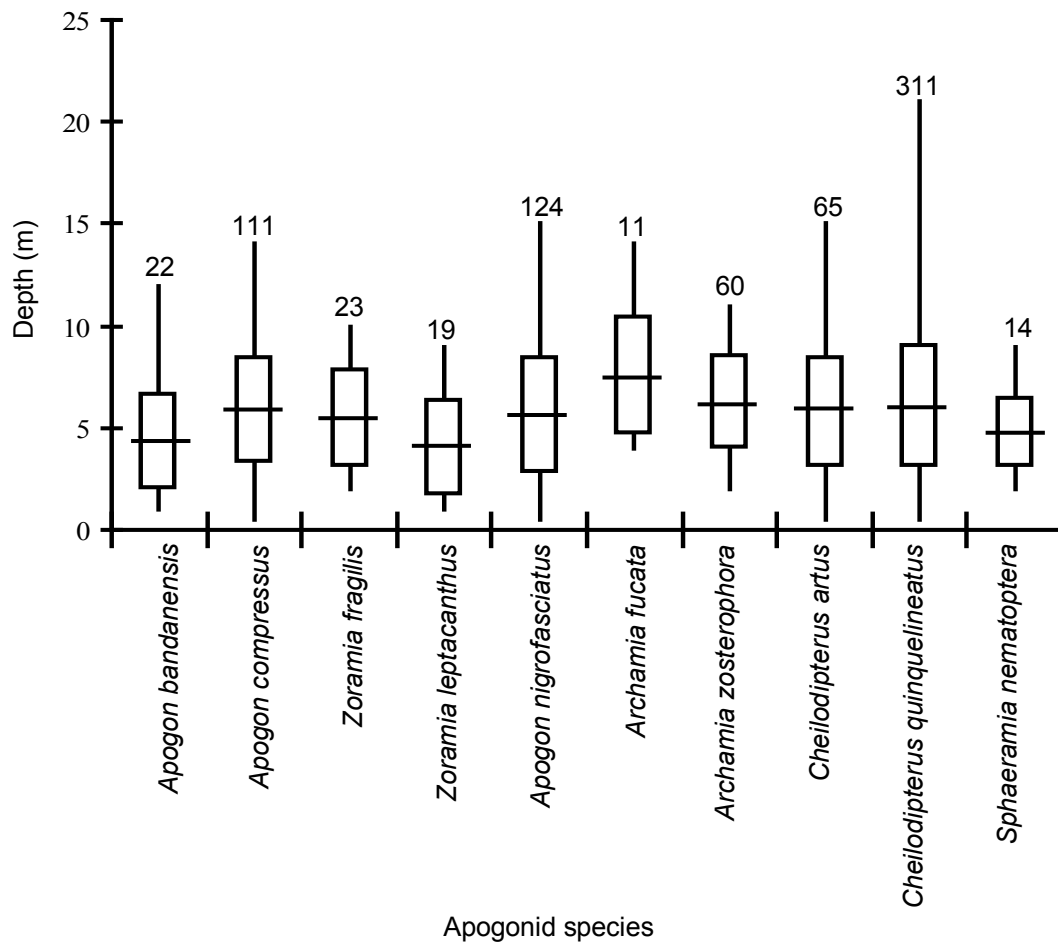
Figure 2.5 Depth distributions of 10 common apogonid species, including mean depth (horizontal line), standard error (vertical rectangle), total depth range (vertical line) and no. of groups per species

With the exception of the cave-dweller *A. nigrofasciatus*, niche overlap on coarse micro-habitat subdivisions was always higher than 80% (Table 2.4). This reflects the high level of use of live coral in nine of the 10 most abundant species. The lowest pair-wise overlap generally occurred between species that contrasted in their degree of apparent specialisation (e.g., 81.5% overlap between *A. fucata* and *C. artus*; and 81.9% overlap between *A. zosterophora* and *Cheilodipterus quinquelineatus*). *A. nigrofasciatus* clearly utilised different niche space to other apogonids, its highest overlap being with the less specialised *C. quinquelineatus* (10.7%).

Niche overlap estimates were also high on live coral subdivisions, reflecting the high level of use of a single coral species (*P. cylindrica*) (Table 2.4). Generally, the more specialised on this coral type the two species being compared were, the higher their overlap. Similarly, the least specialised species exhibited highest overlap with each other (eg. 71.5% between *C. quinquelineatus*, *C. artus* and *A. compressus*). The lowest niche overlap values occurred between the most and least specialised species. For example, 35.9% between *Z. leptacanthus* and *C. quinquelineatus*; 34.6% between *S. nematoptera* and *C. quinquelineatus*; and 33.3 % between *A. fucata* and *C. quinquelineatus*.

Table 2.4 Niche overlap of 10 cardinalfish species using percentage overlap method (Krebs 1999) on (a) coarse micro-habitats and (b) live coral substrata (*Apogon nigrofasciatus* excluded).

		Apogon compressus	*Zoramia fragilis*	*Zoramia leptacanthus*	*Apogon nigrofasciatus*	*Archamia fucata*	*Archamia zosterophora*	*Cheilodipterus artus*	*Cheilodipterus quinquelineatus*	*Sphaeramia nematoptera*
(a)	*A. bandanensis*	100	99	98.7	8.9	96.1	96.1	86.1	86	98.1
	A. compressus		100	99.5	9.4	96.7	96.7	86.6	88.7	99.6
	Z. fragilis			98.2	10.7	94.5	94.5	88.1	95.6	100
	Z. leptacanthus				9.1	100	100	86.2	85.8	100
	A. nigrofasciatus					6.3	6.3	10	10.7	6.3
	A. fucata						100	81.9	81.5	100
	A. zosterophora							81.9	81.5	100
	C. artus								94.2	86.2
	C. quinquelineatus									85.8
(b)	*A. bandanensis*	66.8	75.1	65.5		67	75.7	59.5	50.2	68.3
	A. compressus		58.8	71.1		53	57	71.5	71.5	54.6
	Z. fragilis			90.4		86.5	93.4	62.2	43.1	89.9
	Z. leptacanthus					92.9	86.3	59.3	35.9	89.8
	A. fucata						88.4	54.7	33.3	94.1
	A. zosterophora							57.5	39.1	89.7
	C. artus								59	55.9
	C. quinquelineatus									34.6

Apogonids not only exhibited a high degree of overlap in habitat use, they also frequently co-occurred in the same coral. Multispecific aggregations of cardinalfish accounted for > 75% of 74 aggregations on *P. cylindrica* of > 10 individuals (Fig. 2.6). There were usually 1-4 species per aggregation (16-27% occurrence) with three the most frequent number of species recorded (27%). The highest species richness in a single aggregation was seven species, but this was rare (2.7% frequency).
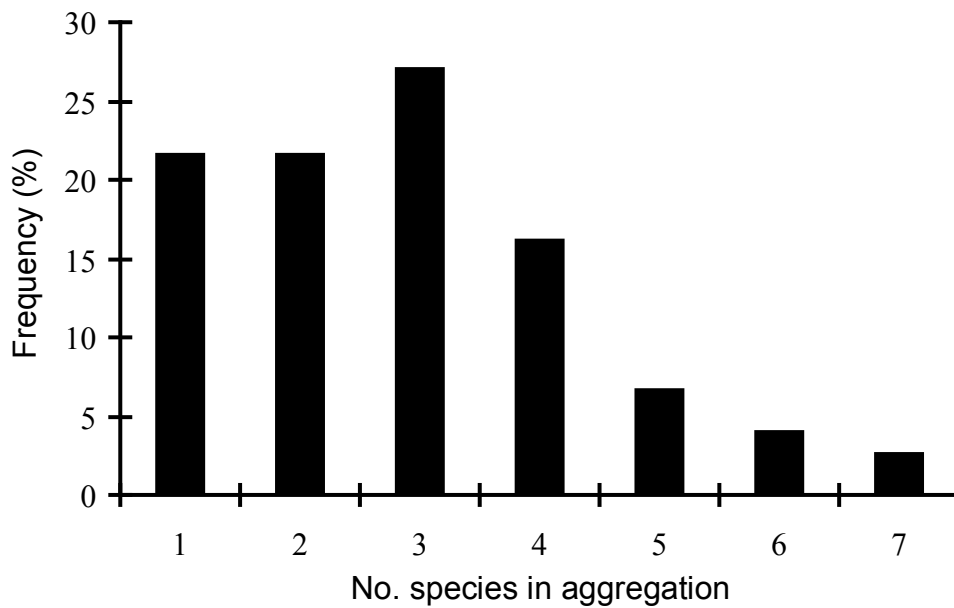
Figure 2.6 Frequency distribution of multispecific aggregations of cardinalfish associated with *Porites cylindrica* outcrops (based on 74 observed aggregations). An aggregation was defined as more than 10 individuals resting together in the same coral head.

2.4.5. Relationship between specialisation and abundance

The abundance per species was positively related to the range of coarse and live coral micro-habitats used, but only when measured as the number of groups per species (Fig. 2.7). That is, the more specialised a species was, the rarer groups were (Fig. 2.7a,c). For example, only 19 *Z. leptacanthus* groups and 14 *S. nematoptera* groups were found compared to 313 groups of the less specialised *C. quinquelineatus* (Table 2.2). The number of individuals per species was not correlated to the number of habitats they occupied (Fig. 2.7b,d). There was a poor relationship between the number of groups and the number of individuals ($r = 0.36$, $p > 0.05$), which explains the lack of correspondence between the two levels of examining specialisation/abundance relationships.
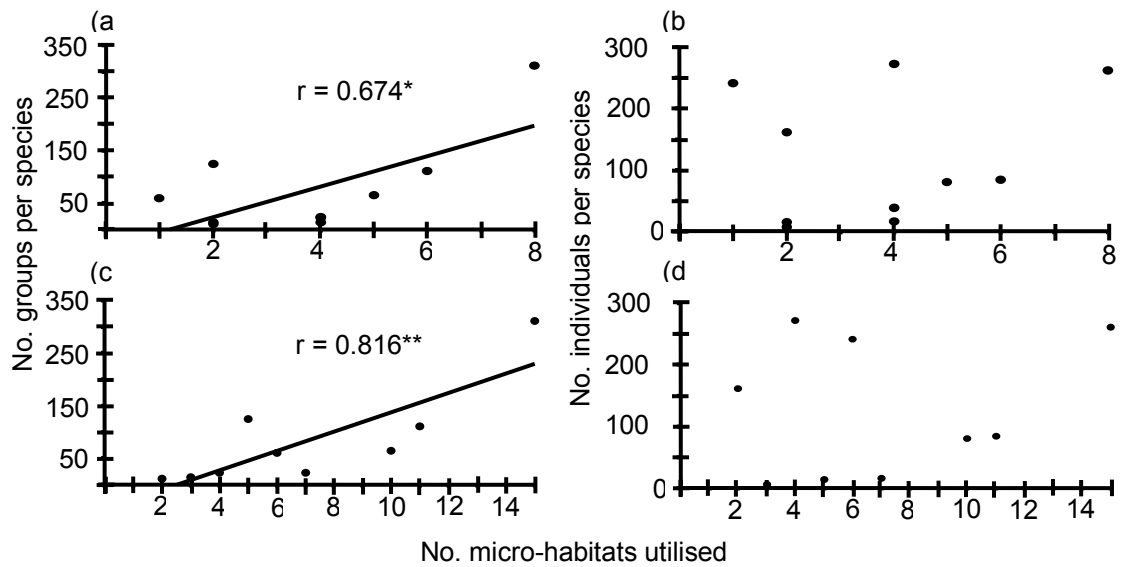
Figure 2.7 Relationship between micro-habitat specialisation and abundance of 10 common cardinalfish species. Habitat specialisation is defined as the number of habitats utilised. Abundance measured both by no. groups and no. individuals per species. (a) Coarse substrata and total no. of groups. (b) Coarse substrata and total no. of individuals. (c) Live coral substrata and total no. of groups. (d) Live coral substrata and total no. of individuals.
** $p < 0.01$, * $p < 0.05$

2.5. Discussion

The strong association between the common apogonids and living corals in Kimbe Bay was much greater than expected. Previous descriptions of habitat use in cardinalfishes have emphasized either their generalist nature (Greenfield & Johnson 1990) or use of other specialised habitats on coral reefs, such as caves or rubble areas (Chave 1978, Allen 2002). The fact that many cardinalfishes favour complex coral cover has been reported (Vivien 1975), however, few studies have quantified the proportion of individuals associated with coral substrata. My study extends this previous work, showing that the apparent selection for live coral is extreme, with over 80% of individuals found associated with live corals. The strong association with live-coral as a day-time resting site rivals that of other taxa more traditionally recognised as coral-associates, such as corallivores (Anderson et al., 1981, Bell et al., 1985, Bouchon-Navaro and Bouchon, 1989) and obligate coral-dwelling gobies (Munday et al., 1997, Munday, 2000) .

The degree of habitat specialisation was even higher than indicated by the composite measure of coral cover. Apogonids were most often associated with branching corals, most notably a single species (*Porites cylindrica*). Approximately 60% of all individuals were observed in this single coral species and all cardinalfish species were positively associated with it. A number of factors could explain the convergence in apparent selection for branching corals and this

27

particular species. Firstly the quality of shelter has a strong influence on coral reef fish survivorship (e.g Beukers and Jones, 1997, Nemeth, 1998). Apogonids would be expected to shelter in the coral species with architecture that offers them the maximum protection from predators (Shulman, 1985, Hixon and Beets, 1989, 1993). The higher use of branching corals over plating and mound corals probably reflects differences in refuge space dimensions and subsequent survivorship. Pomacentrid reef fish species settling into *P. cylindrica* appear to show higher survivorship than those settling into other coral habitats (Jones, 1988). This may be true for apogonids, however settlers appear less associated with substrata than adults. They frequently hover above coral heads and suffer from relatively high post-settlement mortality compared to other reef fish groups (Beukers-Stewart and Jones, 2004). Secondly the apparent selection of complex branching corals may reflect favourable hydrodynamic conditions. Apogonids are primarily nocturnal foragers but can also supplement their diet by day (Marnane and Bellwood, 2002). Small eddies could concentrate availability of plankton within branching corals as well as minimise the energy fish expend in maintaining resting positions.

My results suggest that although the common cardinalfish species present in Kimbe Bay vary in their degree of specialisation on live coral, most would be considered closer to the "specialist" end of the scale. No species could be described as extreme generalists, occupying all substrata in accordance with their availability. The degree of habitat specialisation recorded here exceeds that described for cardinalfish assemblages in other locations (e.g., Greenfield and Johnson 1990). However, patterns described for particular species are supported by the literature where they are known. For example, Marnane (2001) and Nanami and Nishihira (2003) describe a similarly broad use of micro-habitat types by *Cheilodipterus quinquelineatus* and the similarity in micro-habitat associations between it and *Cheilodipterus artus* (Marnane and Bellwood 2002).

It is not known to what degree patterns in Kimbe Bay represent true habitat specialisation or an apparent specialisation that reflects historic changes in the availability of preferred corals. In this study, *Porites cylindrica* appeared to be the only consistently available large coral colonies with a growth form that supported large aggregations of cardinalfishes. Coral cover in the inner part of Kimbe Bay is known to have undergone a massive decline over the last decade, due to a variety of factors (Jones et al. 2004, Munday 2004b). The limited availability of other appropriately sized branching corals (e.g., *Acropora spp.*) could partially explain the low level of their utilisation by apogonids. Nevertheless, the current use of *P. cylindrica* by apogonids far exceeds its' current availability. The actual degree of specialisation may be lower at locations supporting a much higher cover and diversity of corals, but this needs to be examined further.

The other unexpected finding in this study was that the high level of apparent specialisation on day-time resting sites was associated with a high overlap among species. Previous studies have emphasized limited diurnal segregation amongst reef zones (Greenfield and Johnson 1990, Marnane 2001, Marnane and Bellwood 2002), but here I show this extends to depths and micro-habitats within zones. This low level of habitat partitioning does not follow from competition theory (Hutchinson, 1957, Hardin, 1960, MacArthur and Levins, 1967), suggesting that the high level of specialisation on resting habitat is governed by other factors. However, competition may explain the partitioning of other resources such as food. Marnane and Bellwood (2002) have suggested that interspecific competition may be a causative factor in the division of apogonid nocturnal foraging habitats and prey.

The most likely potential source of competition during the day is for shelter sites. However, while coral species appear to vary in terms of the quality of the shelter they provide, the large number of outcrops of *Porites cylindrica* that were not occupied, the lack of micro-habitat partitioning among fish species and the high frequency of multispecific colony formation all suggest that competition for shelter may be minimal (see also Greenfield and Johnson 1990). Any costs of competition for shelter in large aggregations may be offset by the advantages of living in mixed species groups. The typical reason given for fish shoaling behaviour is predator deterrence, by means of increasing predator detection, predator confusion, predator evasion and diluting the individual's mortality risk (Pitcher, 1986). However, coral reef piscivores prey heavily on apogonids (Kingsford, 1992, Beukers-Stewart and Jones, 2004) and their aggregative behaviour (and large shoal sizes) may actually lead to density dependent mortality (Connell, 2000). Investigating group sizes, predation rates and other prey-predator interactions within apogonid aggregations will serve to expand our current understanding of ecological mechanisms and coral reef fish shoaling behaviour.

In theory, the competitive costs of specialising on a single habitat can be offset in patchy habitats by intra-specific aggregative behaviour, as this leaves space available to weak competitors (Atkinson and Shorrocks, 1981). This model could apply to the apogonid assemblages in Kimbe Bay, if species that are weaker space competitors occupy different coral colonies to dominant competitor species. It could explain the lower niche overlap values found between the most and least specialised species. Further evaluation of the importance of competitive processes will require density and diversity manipulations of cardinalfish aggregations on *Porites cylindrica* colonies. While the spatial scale of habitat examined here was considered relevant to the family's usual body size, partitioning may occur at a finer level of positioning within or around coral heads. For example, cave dwelling apogonids appear to partition space along gradients of light intensity and distance from cave entrances (Chave

1978). Also, different relative distances above/within protective habitat structures were observed for apogonid assemblages in Southern Japan (Ida and Moyer, 1974). Where multispecific use of one habitat type was evident, species appeared to segregate themselves by relative positions within coral colonies. For example, *Cheilodipterus* species were generally found beneath structures, while *Rhabdamia* species were found above structures in the water column, *Siphamia* species were deep inside them and *Zoramia leptacanthus* were found in branch tips (Ida and Moyer 1974). Further work is necessary to examine this fine-scale level of partitioning in Kimbe Bay apogonid assemblages.

This study provides partial support for the prediction that the more specialised species will be less abundant than those capable of occupying a variety of habitats (Brown, 1984). While this pattern has been observed for other coral reef fishes (Meekan et al., 1995, Munday, 2000, Bean et al., 2002), the absence of a strong relationship between absolute abundance and specialisation for the apogonids was not unexpected, given that they all appear to be at the specialised end of the scale. Variation in micro-habitat specialisation cannot be expected to explain differences in relative abundance when most species are specialised on the same coral species and aggregate together. Nevertheless, the number of groups was far greater in the less specialised species suggesting that they have a more ubiquitous distribution. The degree of specialisation is probably only one of many factors affecting the distribution and abundance of cardinalfishes.

These results have important implications for the resilience of apogonid communities to the declining coral cover in many tropical regions (Wilkinson, 2002, Gardner et al., 2003, Hughes et al., 2003), including Kimbe Bay (Jones et al., 2004, Munday, 2004b). The strong association with live, branching corals suggests that the biodiversity of cardinalfishes may be as threatened by habitat loss as many other typical reef fish families (Bouchon-Navaro et al., 1985, Jones et al., 2004, Munday, 2004b). *Porites cylindrica* appears to be more resistant than other branching corals to anthropogenic effects and global climate change (Marshall, 2000). The apogonid community's apparent reliance upon it may reflect a greater availability of this coral compared to other branching corals in the bay. However, the dominant use of *P. cylindrica* by most apogonid species (shown here) and high site fidelity to it (Marnane 2000), suggests that the family's vulnerability is comparable, if not greater than other coral associated families.

In order to understand and preserve apogonid diversity, the basic dynamics of their multispecific communities and their relationship with branching corals need to be more fully understood. The experimental evaluation of habitat selection, how it is modified by habitat availability and how habitat use interacts with ecological processes, such as competition and predation, will all further our understanding of the apogonid family's vulnerability to habitat

decline. The future of this fish guild in Kimbe Bay may now be dependent upon the fate of a single coral species, a likely remnant of branching coral cover.

CHAPTER 3: Fine-scale micro-habitat specialisation and partitioning in a guild of coral-dwelling cardinalfish

3.1. Abstract

It is commonly argued that species in diverse and complex tropical assemblages will exhibit fine-scale habitat specialisation and partitioning of resources. On coral reefs, many coral-associated fishes often exhibit distinct habitat preferences and strong behavioural interactions within and among species. However, fine-scale habitat use and partitioning of a single coral resource has not been examined. Here, I explore how seven common cardinalfish species (Family Apogonidae) exploit a single preferred branching coral species (*Porites cylindrica*) in Kimbe Bay, Papua New Guinea. I found fine-scale specialisation and partitioning among cardinalfish species, both among coral colonies and on refuge positions within colonies. All species preferentially inhabited large coral colonies, despite their limited availability. Strong conspecific aggregation observed in six of these species leads to a high proportion of unoccupied corals. A high level of habitat partitioning among species was observed within colonies, with a mean of 38% overlap in use of six arbitrary refuge positions. Within corals, three cardinalfish species showed high degree of specialisation inhabiting a small proportion of the available space, while others were found throughout most of the colony. Heterospecific partitioning within coral colonies was highest for those species occupying a narrow range of positions. Only two of the rarer specialist species (*Zoramia leptacanthus* and *Z. fragilis*) shared positions within coral colonies and frequently co-occurred on the same corals. This study confirms that there is fine-scale habitat specialisation and partitioning in this common reef fish guild. Biodiversity of this group will be particularly vulnerable to the loss of large Porites colonies.

3.2. Introduction

Coral reefs are spatially complex environments that provide a range of habitats that support diverse reef-associated fish assemblages (Luckhurst and Luckhurst, 1978, Williams, 1991). Fish communities closely associated with the reef substratum are numerically dominated by small fishes (<100mm in length) which typical comprise > 75% of the species present (Munday and Jones, 1998). There is increasing evidence, not only of high levels of habitat specialisation in such species, but also partitioning of habitats among ecologically similar species. Spatial

distributions of coral reef fish species are often biased towards particular reef zones (Alevizon et al., 1985, Williams, 1991, Meekan et al., 1995, Green, 1996, Bean et al., 2002, Depczynski and Bellwood, 2005), substratum types within reef zones (Clarke, 1977, Ormond et al., 1996, Depczynski and Bellwood, 2004) and towards particular coral species (Munday et al., 1997, Pratchett, 2005). In conjunction with habitat specialisation, there is often a high degree of habitat partitioning among sympatric species' use of reef zones, substratum types and coral species (Anderson et al., 1981, Bouchon-Navaro, 1986, Clarke, 1994, Ormond et al., 1996). Habitat specialisation and partitioning are often referred to as important in explaining the distribution and coexistence of species in speciose tropical assemblages, including coral reefs, due to the principles of competitive exclusion (Smith and Tyler, 1972, 1973, Schoener, 1974, Schluter and Ricklefs, 1993). Competitive exclusion theory predicts that species will vary along a continuum of specialist to generalist habitat users and specialists will partition their habitat use (Hardin, 1960, Fox and Morrow, 1981). Finer scaled differentiation of habitats in tropical communities than in temperate communities is purportedly a result of higher species diversity (Colwell, 1973b, Stevens, 1989, Rosenzweig, 1992). However, it remains unclear how fine spatial distributions among coral reef fish species can get.

The degree of habitat specialisation exhibited by small coral reef fishes may be at a much finer scale than currently appreciated. While specialisation on specific coral species is now widely recognized, particularly for coral dependent reef fish guilds, fish may also be selecting particular coral individuals or particular positions within individual corals. Within coral species some colonies appear to be better than others, hosting more individuals or having high occupancy rates than others, while other colonies appear to be avoided. Fish density and occupation is often positively related to coral size (Fricke, 1980, Kuwamura et al., 1994, Holbrook et al., 2000, Wong et al., 2005) and fish often exhibit strong habitat preferences for larger coral sizes (Hobbs and Munday, 2004, Thompson et al., 2007, Schiemer et al., 2008). Some species also select coral colonies with greater branching complexity (Tyler, 1971, Ebersole, 1985, Holbrook et al., 2000, Munday, 2001). Coral health and the proportion of live coral tissue can also affect colony use (Booth and Beretta, 2002, Feary et al., 2007b, Bonin et al., 2009a) as can the distance between colonies and alternate habitats (Ault and Johnson, 1998, Holbrook et al., 2002, Belmaker et al., 2005, Jordan et al., 2005). Host corals could also be selected on the basis of resident competitor and predator densities (Beukers and Jones, 1997, Öhman et al., 1998, Schofield, 2003). Individuals may also specialise on particular areas within colonies and partition these areas among co-occurring species (Limbourn et al., 2007).

Behavioural interactions of individuals may also play a leading role in determining the distribution of species across colonies of a single coral species. Aggregative behaviour of

conspecifics results in species with a clumped dispersion of individuals among habitats and can leave many apparently suitable habitat sites empty (Alonso et al., 2004, Grether and Donaldson, 2007, Campomizzi et al., 2008). This behaviour can potentially interact to increase associations with particular colony types resulting in higher degrees of habitat specialisation. Conversely, aggression between conspecifics results in broader dispersion of individuals among available colonies (Robertson and Gaines, 1986, Ormond et al., 1996, Bay et al., 2001). While behavioural interactions are potentially very important in explaining fine-scale patterns of resource use there are few studies which have addressed these issues.

A number of coral reef fish families characterised by small species, are either partially or completely dependent on living corals for habitat. In the Indo-Pacific, ~10% of species exhibit dependence on corals during at least part of their life cycle (Jones et al., 2004, Munday et al., 2007). To date, research on the habitat specialisation and partitioning of corals has predominantly focused on corallivores and obligate coral dwelling fish (Bouchon-Navaro, 1986, Munday et al., 1997, Munday, 2001, Zekeria et al., 2002, Munday, 2004b, Pratchett, 2005, Limbourn et al., 2007, Schiemer et al., 2008). Another speciose family, cardinalfish (Family: Apogonidae), also appears to have a strong dependence on live coral colonies. On Indo-pacific reefs the family ranks fifth in diversity and abundance, with the most species < 100mm in size (Munday and Jones, 1998, Allen, 2002). Common species have a very high degree of apparent habitat specialisation on one branching coral species, *Porites cylindrica*, with very little partitioning of diurnal refugia (Chapter 2). Large multispecific aggregations occur on particular coral colonies while others remain vacant. This apparent specialisation and co-occurrence raises the question as to the extent of fine-scale responses to habitat and species interactions occurring within a single host coral species.

The overall aim of this study was to examine patterns of habitat specialisation and partitioning within and among coral colonies of a single coral species. I hypothesised that cardinalfish would exhibit fine-scale specialisation and partitioning not evident at larger scales. Firstly, I examined how cardinalfish are distributed among different *Porites cylindrica* colonies, addressing (1) whether species disproportionately occupy colonies of larger sizes, greater isolation, better health and with less competitors or predators; (2) whether species share coral colonies with other cardinalfish or whether colonies are partitioned; and (3) whether conspecific individuals are evenly dispersed among colonies. Secondly, I addressed how cardinalfish are distributed within *P. cylindrica* coral colonies, examining (1) whether fine scale specialisation of refuge space within corals occurs; and (2) whether species partition space within the coral refuge. Among the guild I expected that variation in each species degree of specialisation would

follow a specialist - generalist continuum and that specialists would partition their fine-scale habitat use.

3.3. Methods

3.3.1. Study site and species

This study was conducted on coastal coral reefs in Kimbe Bay, Papua New Guinea (5°30'S; 150°05'E), in the vicinity of the Mahonia Na Dari Research and Conservation Centre (Fig. 3.1a). More than 43 species of cardinalfish have been recorded in Kimbe Bay (Allen & Munday 1996) and many of the common nearshore species are closely associated with outcrops of the coral *Porites cylindrica,* which serves as their diurnal resting habitat (Chapter 2). Here, I focused on habitat use in the seven most common species: *Apogon bandanensis, A. compressus, Archamia zosterophora, Zoramia fragilis, Z. leptacanthus, Cheilodipterus artus* and *C. quinquelineatus.*

The host coral species *Porites cylindrica* is a branching coral that typically inhabits sheltered locations such as reef slopes and lagoons forming both isolated coral colonies and large contiguous patches that can dominate sheltered reef habitat. Cardinalfish tend to aggregate among the fat finger-like projections that provide shelter. Data for this study were obtained from *P. cylindrica* colonies located on leeward reef slopes of five discrete reefs: Gava Gava, Garbuna, Malane Huva, Madaro and Limuka (Fig. 3.1b).
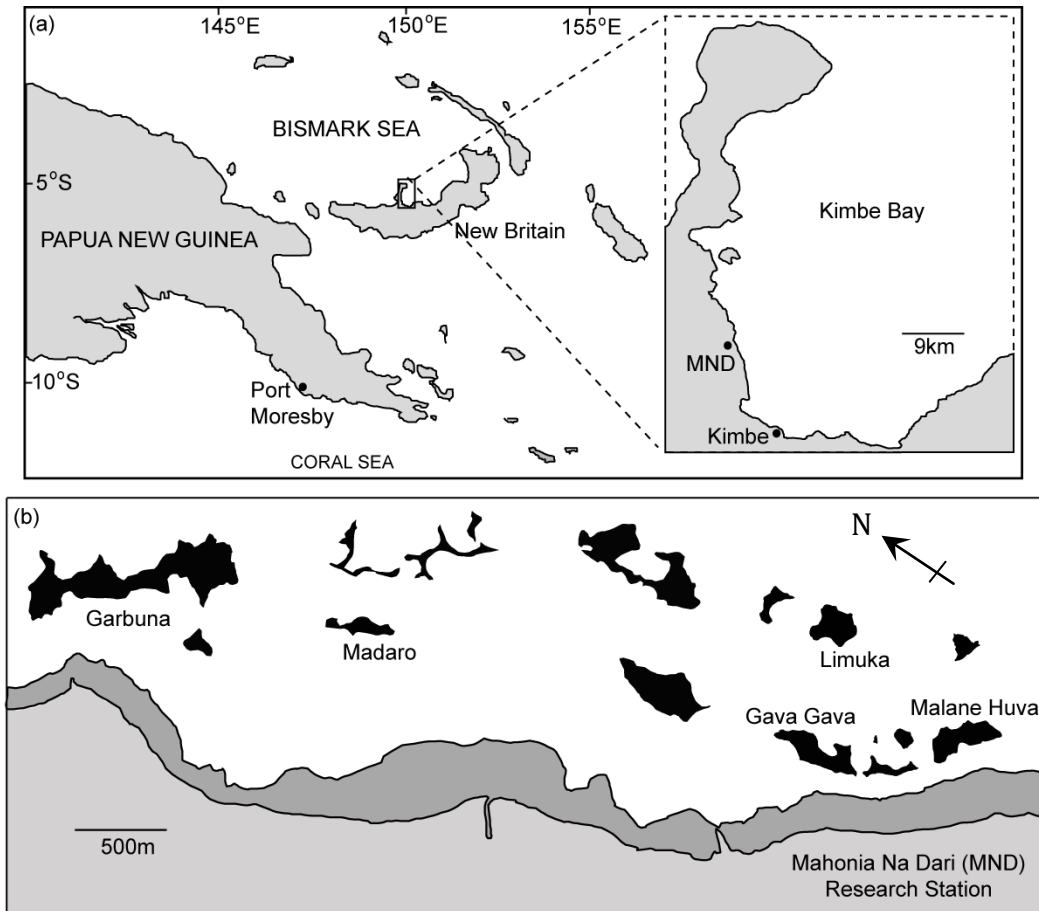
Figure 3.1 Location of (a) Kimbe Bay, Papua New Guinea and (b) inshore reefs in vicinity or Mahonia Na Dari Research Station (MND). Five study reefs are labeled. Scale is approximate.

3.3.2. Distribution among *P. cylindrica* coral colonies

3.3.2.1. *Associations with host coral attributes*

Two different approaches were used to determine whether distribution of cardinalfish among *P. cylindrica* colonies was influenced by variation in the attributes of individual corals. Firstly, coral size selectivity was examined. A transect-based survey compared the occupancy rates of different sized coral colonies with availability of these colonies. Secondly, a range of biological and physical attributes of coral characteristics were measured to determine what factors best explained use of particular corals.

In order to determine whether cardinalfish disproportionately occupy corals of larger sizes, the size frequency of *P. cylindrica* coral colonies and their occupancy by cardinalfish was determined. *P. cylindrica* corals were counted and measured using four replicate 50 × 2m belt transects on four reef slopes at two depths (4 and 7m). Colonies were classified into one of six size categories according to their maximum surface diameter; < 0.5m, 0.5-1m, 1-2m, 2-3m, >

36

3m and 'patch'. Patch corals were very large stands of *P. cylindrica* from which smaller, isolated colonies could not be distinguished. Cardinalfish presence or absence was recorded for each coral colony. Data from replicate transects was pooled. Size selectivity was quantified using Manly's resource selection indices and 95% Bonferroni confidence intervals (Manly et al., 2002). Resource selection ratio's above one indicated positive habitat preferences while those below one indicate avoidance.

To further compare whether cardinalfish differentiate among coral colonies, relationships between cardinalfish abundance and characteristics of *P. cylindrica* coral colonies were explored. Physical and biotic attributes of coral colonies were measured. Physical characteristics were colony size (maximum surface diameter, perpendicular surface diameter, coral height and surface area), isolation (distance from coral edge to nearest reef structure) and coral health (estimated percent of live tissue at colony surface). Maximum and perpendicular surface diameters were multiplied to approximate relative coral surface area. Biotic attributes were the abundance of non-familial refuge competitors (predominantly small damselfish species) and resident predators (predominantly small groupers). Cardinalfish abundance and colony attributes were recorded from 75 discrete coral colonies haphazardly located on four reef slopes (Gava Gava, Madaro, Malane Huva and Garbuna). Cardinalfish densities were estimated on a log 2 scale to minimize error in estimation of large aggregations.

Variance in cardinalfish abundance was compared to the host coral attributes with forward stepwise regression analysis. This was performed separately on total cardinalfish abundance and on the abundance of four common species. Coral size attributes were log 10 transformed and branch health percentages square-root transformed to improve normality and homogeneity of variances. Significance levels were set at $p < 0.05$. Semi-partial correlation co-efficients were used to determine the unique contribution of a variable to the predictor independent of multi-collinear effects with other variables.

To determine whether structural complexity of host corals affected colony use, inter-branch space measurements of eight occupied and seven unoccupied large coral colonies were compared. Within each colony branch tips on the colony surface were haphazardly selected and the space between 10 branch tip pairs measured. Statistical comparison of inter-branch space on occupied and unoccupied coral colonies was carried out with Students t-test.

3.3.2.2. Partitioning of coral colonies

I hypothesised that cardinalfish species would partition their use of coral. This was assessed by determining the degree to which each of the seven cardinalfish species shared colonies with other cardinalfish species. Conspecific densities and presence/absence data for each species was surveyed on all occupied *P. cylindrica* colonies on five reef slopes. The total number of colonies that each species shared was calculated. To discern whether particular pairs of species were strongly partitioned, the proportion of colonies occupied by both species was also determined. Values close to 0% indicated the two species rarely shared corals (partitioning of colonies) while values close to 100% indicated high interspecific overlap among coral colonies.

3.3.2.3. Dispersion of conspecific individuals among host corals

In order to determine whether social behaviour increases associations with particular coral colonies the dispersion of each cardinalfish species was measured. Morisita's index (MI) of dispersion was used to test the differences in conspecific densities among occupied coral colonies (Krebs 1999):

$$MI = \frac{S \sum (n^2 - N)}{N(N-1)}$$

where 'n' is the total number of conspecifics per colony, 'N' is the total number of individuals per species and 'S' is the number of occupied colonies. MI values greater than one indicate a clumped dispersion; equal to one indicate a random dispersion; and less than one indicate a even dispersion of individuals. Because Morisita's index assumes sample sizes are equal, conspecific abundance on each colony was standardized for coral size:

Standardized abundance (N) = actual abundance (n) / coral surface area (m^2)

Counts of conspecific densities on discrete coral colonies were recorded for each species across four reef slopes (Gava Gava, Madaro, Malane Huva and Garbuna). Cardinalfish aggregations on patches of *P. cylindrica* corals were excluded due to difficulties in determining distinct aggregations.

38

3.3.3. Fine-scale distribution within *P. cylindrica* coral colonies

3.3.3.1. Specialisation on refuge areas within coral colonies

The specialisation and partitioning of space within corals by cardinalfish was determined by measuring the use of six arbitrary refuge positions within host coral colonies (Fig. 3.2). Resting positions were recorded for all large coral colonies occupied by cardinalfish species on Limuka and Garbuna reefs (total n = 99). For each coral colony the position that the majority of individuals occupied was recorded for each species. The six possible refuge positions were: 1 - > 5cm above coral; 2 - amongst branch tips; 3 - below branch tips (cryptic); 4 - amongst side branches of coral colony; 5 - to the side of coral colony but > 5cm from branch edges; and 6 - beneath coral colony. Natural 'at rest' positions were recorded by divers at first keeping their distance from fish, noting obvious species and positions (i.e., position 1, 2 and 5) followed by closer searches for fish in cryptic positions (position 3 and 6).
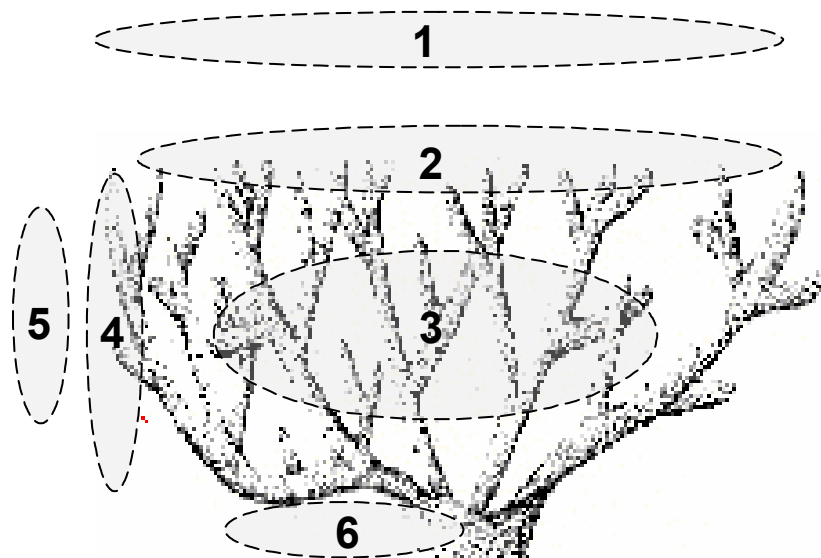
Figure 3.2 Designation of refuge areas within coral colonies that were occupied by cardinalfish. 1 - > 5cm above coral; 2 - amongst branch tips; 3 - below branch tips (cryptic); 4 - amongst side branches of coral colony; 5 - to the side of coral colony but > 5cm from branch edges; and 6 - beneath coral colony.

3.3.3.2. Partitioning of refuge areas within coral colonies

I hypothesised that species would partition refuge areas within colonies. This was assessed by comparing similarities in each species' use of colony space. Pair-wise percentage similarity measures were calculated and spatial distributions compared graphically (Krebs, 1999). Similarity values approaching 100% indicated high spatial overlap, while values near 0% indicate spatial partitioning.

A positive relationship between specialisation and partitioning was expected. Similarities in each species degree of specialisation on refuge areas within colonies were therefore compared graphically. Further tests were made by investigating differences in three species' use of refuge areas in the presence or absence of several secondary species with which the first appeared to overlap. Each species proportional use of refuge areas was recalculated and compared amongst colonies that were shared with the secondary species and colonies that were not. Differences in the species proportional use of refuge in shared versus not shared colonies were compared with chi-squared analysis.

3.4. Results

3.4.1. Distribution among *P. cylindrica* coral colonies

Cardinalfish in Kimbe Bay were not evenly distributed among *P. cylindrica* coral colonies. Species preferred large coral sizes. Coral colonies were not partitioned and species predominantly shared colonies. Conspecifics of each species were also not evenly dispersed among coral colonies, but highly aggregated. The distribution of cardinalfish among *P. cylindrica* coral colonies was therefore both highly specialised with very limited partitioning of colonies.

3.4.1.1. *Specialisation on host coral attributes*

Populations were not evenly distributed among available coral colonies. Only 25% of corals were occupied and these were predominantly larger coral colonies (> 2m in diameter; Fig. 3.3a). There was high discordance between the size distribution of colonies and cardinalfish use of each size category (Fig. 3.3b). On average, 65% of the available *P. cylindrica* colonies were smaller than 1m in diameter and less than 30% of these were occupied by cardinalfish. Resource selection indices showed these coral sizes are avoided by cardinalfish (Fig. 3.3c). Fish predominantly occupied corals larger than 1m in diameter, despite their limited availability (Fig. 3.3b,c). These corals were used in significantly greater proportions than their availability suggesting positive behavioural preferences for larger corals (Fig. 3.3c). The spatial distribution of cardinalfish on the study reefs was therefore strongly affected by the availability of large host corals on which there is high specialisation.
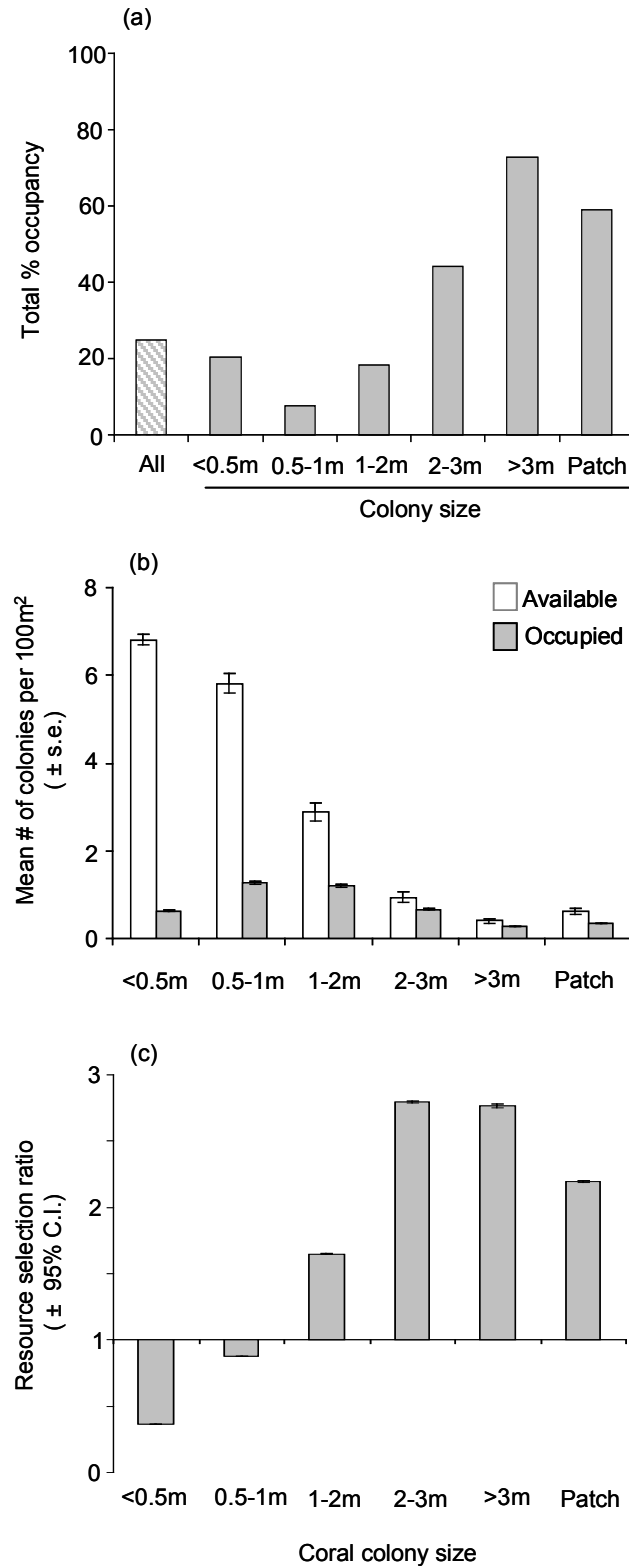
Figure 3.3 Diurnal distribution of cardinalfish among *Porites cylindrica* coral colonies. (a) Total percent occupancy of coral colonies according to colony size. Size was measured as maximum diameter of colony surface (m). (b) Average availability and occupancy of coral colony sizes on 100m² reef slope area. (c) Colony size selectivity: Resource selection ratios with 95% Bonferroni confidence intervals. Values > 1 indicate size preference and < 1 indicate avoidance of colony sizes. All data obtained from 32 replicate 50 × 2m belt transects on leeward reef slopes.

Comparison between total cardinalfish abundance and a range of host coral attributes further confirmed the importance of colony size to cardinalfish. 63% of total cardinalfish abundance was explained by the regression model incorporating six physical and biological attributes of *P. cylindrica* coral colonies. Colony surface area, however, was the only significant variable and explained 57% of variation in total cardinalfish abundance (Table 3.1). A seventh coral attribute, coral complexity was not important in explaining cardinalfish occupancy. Interstitial branch space measurements did not differ amongst occupied and un-occupied *P. cylindrica* corals ($T_{13} = 2.16$, $p = 0.81$).

Host coral attributes were only variably successful in predicting the abundance of four particular cardinalfish species (Table 3.1). Coral surface area remained the most important attribute for abundance of *A. zosterophora* densities, but was not statistically significant. Approximately 50% of variation in abundance of *A. compressus* was due to a negative relationship with resident predator density. However, very few resident predators were actually observed on coral colonies (total observed = 31). Host coral attributes did not significantly explain variation in the abundance of *C. quinquelineatus* or *C. artus* (full model: $p > 0.05$). However coral colonies with fewer competitors and corals with greater isolation did have more *C. artus* individuals.

Table 3.1 Summary of multiple forward stepwise regression analyses examining relationships of cardinalfish abundance to attributes of host colonies. Relationships were assessed for total cardinalfish abundance and for abundance of the 4 most common species. Regression co-efficient (R^2) is the total variation in the predictor explained by the model. *F*-stat and *p* indicate the overall significance of the regression. Total (Beta) and semi-partial correlation co-efficients of each variable per model are listed in order of significance. Non-significant variable contributions are not shown.

Predictor Host coral variables	Significance of regression analysis				Variable contribution to model		
	df [a]	R^2	*F*-stat	*p*	Beta co-efficient	Semi-partial correlation co-efficient	*p*
cardinalfish abundance	6, 68	0.627	19.052	< 0.001			
Surface area					0.567	0.340	< 0.001
Cheilodipterus quinquelineatus	6, 40	0.204	1.707	0.144			
					(no significant variables)		
Archamia zosterophora	6, 6	0.677	2.099	0.194			
Surface area					1.450	0.704	0.022
Cheilodipterus artus	6, 12	0.507	2.054	0.136			
Competitor abundance					- 0.614	- 0.509	0.027
Coral isolation					0.697	0.548	0.019
Apogon compressus	6, 16	0.446	2.144	0.104			
Predator abundance					- 0.522	- 0.488	0.018

[a] (regression, residual)

3.4.1.2. Partitioning of coral colonies

I hypothesised that cardinalfish species would partition their use of coral colonies in order to minimise the amount of shared refuge space. However, absolute partitioning of colonies was low. Of the 118 utilised colonies less than a third were occupied by only one species (n = 33). On average three cardinalfish species rested in each colony with 10 species observed in two of the corals.

Among species pairs the average proportion of shared colonies was 42 ± 4% (s.e.). No species pair had either 100% avoidance or 100% overlap (Table 3.2). *C. quinquelineatus* occupied the most colonies and subsequently most other species shared colonies with *C. quinquelineatus*. *A. bandanensis, Z. leptacanthus* and *C. artus* all shared around 80% of their host corals with *C. quinquelineatus*. Species overlap among colonies was consistently the lowest with *Z. leptacanthus*, averaging 12%. Despite very high total abundance of individuals in the study area (> 1000 fish) *Z. leptacanthus* only occurred on six colonies. Other species therefore had little opportunity to share colonies with this species. The diversity of cardinalfish aggregations on these 6 colonies was quite high such that *Z. leptacanthus* did not appear to avoid using coral colonies with other species (mean interspecific overlap = 61%). *Z. fragilis* displayed a very similar pattern of abundance and colony use to *Z. leptacanthus*, occupying 13 of the surveyed corals and always co-occurring with other species. *Z. leptacanthus* and *Z. fragilis* often shared their coral colonies. 30% of corals used by *Z. fragilis* contained *Z. leptacanthus* and 70% of corals used by *Z. leptacanthus* held *Z. fragilis*.

Table 3.2 Distribution of seven cardinalfish species among *Porites cylindrica* colonies. Values indicate percentage of observations in which species shared colonies with each other species. N is the total number of occurrences per species across 118 coral colonies. Bold and underlined values indicate strongest and weakest associations, respectively.

Cardinalfish species	% of shared colonies								Total % not shared	Total # of colonies used
	Ab	*Ac*	*Az*	*Ca*	*Cq*	*Zf*	*Zl*	Mean		
Apogon bandanensis (Ab)		48	24	40	**80**	24	16	39	4	25
A. compressus (Ac)	20		39	44	**75**	<u>8</u>	<u>5</u>	32	5	59
Archamia zosterophora (Az)	15	56		54	66	27	<u>10</u>	38	5	41
Cheilodipterus artus (Ca)	24	62	52		**76**	21	<u>5</u>	40	21	42
C. quinquelineatus (Cq)	22	48	30	35		<u>10</u>	<u>5</u>	25	20	91
Zoramia fragilis (Zf)	46	38	**85**	69	69		31	56	0	13
Z. leptacanthus (Zl)	67	50	67	33	**83**	67		61	0	6
Mean	32	50	49	46	75	26	12	42 ± 4 (s.e.)		

3.4.1.3. Dispersion of conspecific individuals among host corals

Aggregative behaviour by cardinalfish increased associations with particular coral colonies. Cardinalfish species were narrowly dispersed among *P. cylindrica* corals. Morisita's dispersion index values were greater than one for all species indicating highly clumped distributions (Fig. 3.4). *Z. fragilis* and *Z. leptacanthus* had the narrowest distribution among colonies, while *C. quinquelineatus* had the least. More than 1000 *Z. fragilis* individuals were distributed over only eight coral colonies (14% of total sample) while nearly 500 *C. quinquelineatus* individuals were dispersed over 48 colonies (84% of sampled colonies).
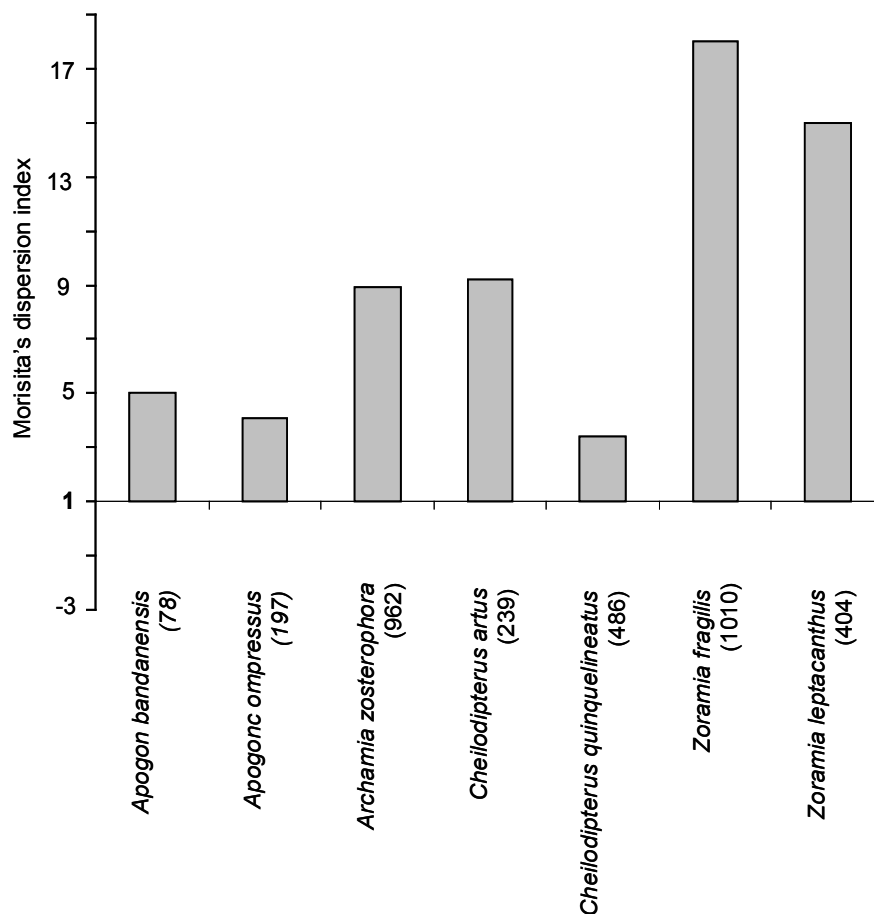
Figure 3.4 Morisita's dispersion index of cardinalfish distribution among 56 *Porites cylindrica* coral colonies. Index values > 1 indicate clumped distribution, equal to 0 indicate random dispersion and < 1 indicate even distributions. Values in brackets indicate total estimated species abundance.

3.4.2. Distribution within *P. cylindrica* coral colonies

3.4.2.1. Specialisation on refuge areas within coral colonies

As predicted, cardinalfish species varied in their degree of specialisation on refuge areas within coral colonies (Fig. 3.5). Three species were narrowly distributed and four were widely distributed. *Z. leptacanthus* was the most specialised, only resting at the colony surface amongst branch tips. *A. bandanensis* was similarly specialist and predominantly rested deep within coral colonies (in > 90% of cases). Distribution of the third specialist species *Z. fragilis* was relatively even among two refuge areas, individuals either hovering above coral colonies or among branch tips. The remaining four cardinalfish species had more generalist distributions, each utilising four to five of the six arbitrary refuge positions. *A. zosterophora* occupied five areas but was predominantly observed at the colony surface, among branch tips (75% of cases). Similarly, the distribution of *A. compressus* groups among five refuge positions was skewed towards just two; the branch tips and vertical edges of corals. *C. quinquelineatus* and *C. artus* were the most generalist users of refuge areas within coral colonies. Each used four areas and was spread evenly among the vertical and horizontal edges of coral colonies. Notably, unlike the five other species, no *C. quinquelineatus* and *C. artus* groups appeared to occupy highly cryptic positions deep within *P. cylindrica* colonies.
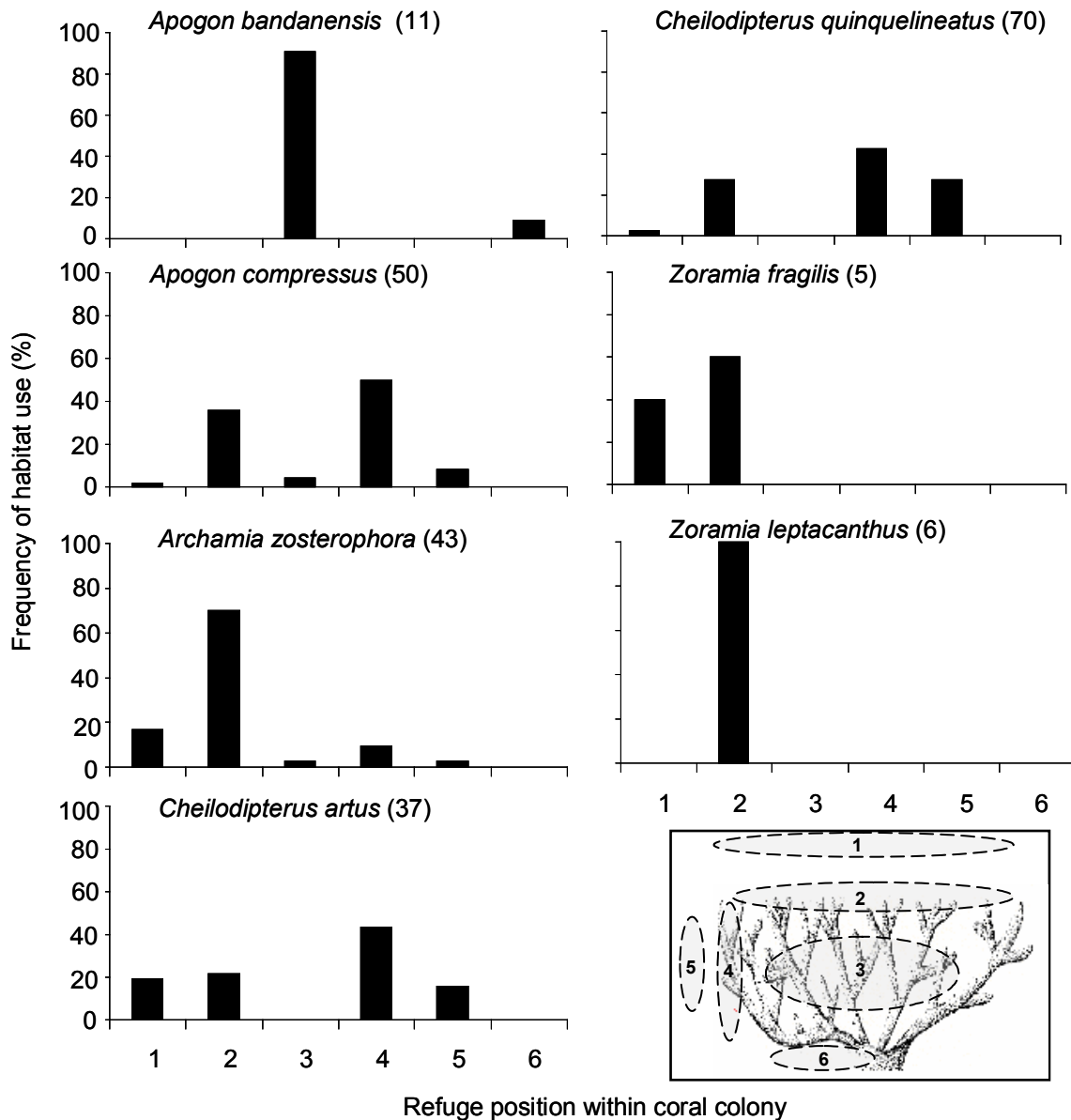
Figure 3.5 Distribution of seven cardinalfish species across six refuge positions within *Porites cylindrica* coral colonies. Positions 1-6 refer to refuge spaces within coral (shown). Values in brackets indicate number of colonies used per species. 99 colonies were surveyed.

3.4.2.2. Partitioning of refuge areas within coral colonies

I hypothesised that cardinalfish species would partition their use of refuge space within coral colonies and that partitioning would be higher among specialist species. On the whole, partitioning of refuge space within colonies was high, with pair-wise similarities in spatial distribution averaging 38% (± 6.4% s.e.; Table 3.3). As predicted, the degree of overlap among species varied in relation to their degree of specialisation on the arbitrary refuge positions (Fig. 3.5). Spatial partitioning was consistently highest between the specialist *A. bandanensis* and other species, with overlap averaging 1.5%. The weakest spatial partitioning consistently

occurred between the three most generalist species, C. q*uinquelineatus, C. artus* and *A. compressus,* with > 74% interspecific overlap in refuge use. In contrast to predictions of spatial partitioning among specialist species, two species with restricted use of refugia areas within colonies, *Z. leptacanthus* and *Z. fragilis*, had their highest overlap with each other and with *A. zosterophora* (60-76%).

Table 3.3 Percent niche overlap of seven cardinalfish species on positions within *Porites cylindrica* coral colonies. Bold and underlined values indicate highest and lowest heterospecific overlap respectively. The average interspecific overlap per species is shown and N indicates total number of colonies on which species occurred. 99 cardinalfish aggregations were surveyed. Percentage similarity measure follows Krebs (1999).

Cardinalfish species	*Ac*	*Az*	*Ca*	*Cq*	*Zf*	*Zl*	Mean	N
Apogon bandanensis (Ab)	4.0	2.3	<u>0.0</u>	2.9	<u>0.0</u>	<u>0.0</u>	1.53	11
A. compressus (Ac)		53.6	**74.9**	**80.9**	42.0	42.0	49.6	50
Archamia zosterophora (Az)			51.9	41.6	**76.3**	69.8	49.3	43
Cheilodipterus artus (Ca)				**83.9**	40.5	21.6	36.8	37
C. quinquelineatus (Cq)					30.0	27.1	45.5	70
Zoramia fragilis (Zf)						60.0	41.5	5
Z. leptacanthus (Zl)							36.8	6

For the three species with the highest degree of refuge space partitioning, *C. quinquelineatus, C. artus* and *A. compressus*, overlap on positions within coral colonies did not depend on the presence or absence of other species (Table 3.4). Each of these species did not use different refuge areas when other generalists were absent.

Table 3.4. Comparison of three cardinalfish species' positions within colonies in the presence/absence of confamilial species. Frequency distributions among six arbitrary coral positions for three 'primary' species were compared to distributions recalculated when the 'secondary' species was absent using χ^2 goodness of fit analyses. Degrees of freedom (d.f.) varied according to number of utilised colony positions per species.

Primary species	Secondary species	χ^2 statistic	d.f.	*p* - value	# of shared colonies	# of colonies not shared
Cheilodipterus quinquelineatus	*C. artus*	3.07	3	> 0.05	27	43
	A. compressus	0.82	3	> 0.05	32	38
C. artus	*C. quinquelineatus*	3.39	2	> 0.05	27	10
	A. compressus	6.73	3	> 0.05	20	17
Apogon compressus	*C. quinquelineatus*	2.09	2	> 0.05	32	18
	C. artus	3.06	4	> 0.05	20	30

3.5. Discussion

This study has revealed some of the finest-scale patterns of habitat specialisation and partitioning known for coral reef fishes. While previous work has established the overall importance of a single coral species for this guild of cardinalfishes, this study has disclosed considerable fine-scale specialisation and partitioning within this single preferred coral taxon. All species appear to preferentially occupy large coral colonies and there is very little partitioning of species among these colonies. Partitioning is limited by strong intra- and inter-specific aggregation which skews the guild's distribution towards particular large colonies. Habitat partitioning and variation in the guild's degree of specialisation is only evident at a finer scale within coral colonies. Several species predominantly inhabit narrow refuge areas within colonies while other species occur throughout the colony. Partitioning of refuge areas within corals is positively related to each species' degree of within-colony specialisation, except for two specialist species which share both coral colonies and refuge areas within these.

High species diversity in tropical systems like coral reefs leads to very fine levels of niche differentiation among sympatric species (Colwell, 1973a, Stevens, 1989, Rosenzweig, 1992). My study shows that such differentiation extends to areas within single coral taxa and raises questions as to the mechanisms of species coexistence in reef fish communities. Specialisation and partitioning of refuge spaces within colonies by cardinalfish may arise due to competition for limited habitat space. Following the principles of competitive exclusion and space resource sharing theories, spatial competition among cardinalfish could lead to the observed variation in the degree of specialisation upon refuge space within colonies (Hutchinson, 1959, Smith and Tyler, 1972, 1973, Schoener, 1974). It could also lead to the overlap in refuge space use among the three generalist species and between the specialist and generalist species. Greater performances of habitat specialist species balances moderate performances of generalist species from multiple habitats to maintain coexistence of species in habitat limited communities (Schluter and Ricklefs, 1993, Kassen, 2002). However, these theories also predict that highly specialist species should not use the same refuge spaces as occurred for two species here. Dale's 'money in the bank' hypothesis suggests overlap of multiple species in one habitat type may arise because each species' performs better on other habitats and seed populations on the shared habitat (Dale, 1978). Spatial partitioning of cardinalfish species during nocturnal foraging periods may be enough to differentiate the highly specialist species (Marnane and Bellwood, 2002). However, the diurnal habitat use of the diverse Indo-Pacific guild studied here is not partitioned along any habitat axis (i.e., reef zones, depths, substrate type, coral species or even geographic range: Marnane 2001; Chapter 2) apart from that within coral colonies. It seems more likely that Indo-pacific cardinalfish communities are structured by an interaction between

competitive exclusion processes operating across diurnal and nocturnal distributions and benefits that might be obtained from resting in heterospecific aggregations.

Physical characteristics of habitats are always important in determining animal spatial distributions. Cardinalfish may prefer larger colonies because they provide more space and host a greater diversity of internal refuge structures than small colonies. Larger and more complex coral colonies or habitat patches can benefit reef fish survivorship, reproduction and growth (Munday, 2001, Wong et al., 2005, Lecchini et al., 2007, Schiemer et al., 2008). Cardinalfish may also prefer larger colonies because they host more abundant and diverse invertebrate communities (Austin et al., 1980, Edwards and Emberton, 1980), thereby providing more diurnal feeding opportunities. In this study, there was no clear relationship between cardinalfish colony associations, coral isolation, branch complexity and colony health. A lack of isolation effect is not that surprising as this study was conducted on contiguous reef slopes where colonies are relatively well connected to other reef substrata. The nocturnal vagility of cardinalfish would also minimize the effects of habitat patch isolation seen in other fish communities (Ault and Johnson, 1998, Holbrook et al., 2002). Complexity and coral health are both important in determining spatial distributions of other coral reef fish (Beukers and Jones, 1997, Almany, 2004, Feary et al., 2007a, Feary et al., 2007b, Lecchini et al., 2007), but this study's assessment of their importance to cardinalfish was hindered by limited sampling. Branching complexity was only measured on large coral colonies and whether small *P. cylindrica* coral colonies are not used due to lower structural complexity remains to be tested. A broad range of *P. cylindrica* colonies in various states of tissue health was not available on Kimbe Bay reefs. However, in other studies, at least one species of cardinalfish appears to rely more on the structure of *P. cylindrica* coral colonies than on live tissue (Chapter 4). If structure is more important for cardinalfish habitat use than live coral tissue the family may be more resilient than other coral dwelling species to short term declines in live coral tissue. To address the hypotheses listed here regarding habitat preferences, future research should test differences in cardinalfish survivorship and growth among *Porites* and alternate branching coral species, among different coral colony sizes, and among states of coral tissue health.

Differential use of refuge areas within coral colonies by cardinalfish may result from species specific differences in predator avoidance strategies, resting energy requirements, access to diurnal prey and/or differences in species' body dimensions. For example, *A. bandanensis* may be the most cryptic in order to avoid high predator selectivity. *Cheilodipterus* species inhabiting positions on vertical edges of corals may prefer these due to easier access to occasional diurnal prey (Marnane and Bellwood, 2002). Vertical edges may increase their vulnerability to

predation (Holbrook and Schmitt, 2002, Limbourn et al., 2007) but *Cheilodipterus* species could minimize vulnerability by attaining larger body sizes (Allen, 2002). Lastly, *Zoramia* species that occupied positions above coral branches may prefer these areas due to the space afforded for shoaling and the enhanced visual field to see approaching predators (e.g., Rilov et al., 2007). Predation vulnerability in other small reef fish use is known to result from greater use of edge positions within coral colonies (Holbrook and Schmitt, 2002).

Strong aggregative behaviour by cardinalfish enhances the guilds degree of micro-habitat specialisation on large coral colonies. Attraction towards conspecific and/or heterospecific aggregations appears to increase the bias towards particular colonies and restricts a broader dispersion of individuals among available colonies. Gregarious behaviour also appears to weaken the degree of heterospecific partitioning within coral colonies. Overlap in use of colony refuge areas by two specialist species, *Z. fragilis* and *Z. leptacanthus*, may result from heterospecific attraction. The two species have very similar shoaling behaviour and similar body colorations that may enhance their ability to formed mixed species aggregations and benefit from these by means of increased survivorship (e.g. Seppänen and Forsman, 2007). However, strong oddity effects do operate in other aggregating coral reef fish (Almany et al., 2007b), such that the potential benefits of hetero-specific aggregations needs to be investigated further. I also found no evidence that negative interspecific interactions between three common generalist species restricted them from inhabiting particular refuge areas. Whether highly specialist but rarer species prevent other species from utilising 'prime' colony areas needs to be experimentally tested.

Results presented here show some evidence that partitioning of reef fish species is positively related to the degree of resource specialisation. However this was only evident at a very fine scale of habitat use - within host coral colonies. Partitioning of cardinalfish species among and within colonies was probably limited by the availability of large coral colonies. Small *P. cylindrica* colonies are abundant and occasionally used by cardinalfish, but the limited space within these would appear to restrict species' ability to partition refuge areas. Interestingly, the degree of micro-habitat specialisation by each cardinalfish species was consistent at both scales, among colonies and within colonies. Species widely distributed among colonies, such as *C. quinquelineatus,* were also widely distributed within corals. In contrast, the more gregarious and narrowly dispersed *Zoramia* species were narrowly distributed in their use of refuge areas within colonies. Patterns of resource similarity have also been shown between cardinalfish species' dietary breadth and foraging ground distributions (Marnane and Bellwood, 2002).

Differential loss of large corals from reef environments will cause considerable decline in the biodiversity and abundance of multiple reef communities including reef fish. In disturbed reef environments, colony size distributions shift towards smaller sizes (Hughes, 1984, Madin et al., 2008, McClanahan et al., 2008). If recovery of large colonies following a disturbance is actually possible the timeframe will be considerable. Species like cardinalfish that also specialise on branching morphologies face a double disturbance risk as these corals are rapidly impacted by natural and anthropogenic disturbances (Gleason, 1993, Harmelin-Vivien, 1994, Loya et al., 2001, McClanahan et al., 2001, Jones et al., 2004, McClanahan et al., 2008). For cardinalfish communities, differential loss of coral colonies that host large aggregations is also likely to affect recruitment and population connectivity due to the loss of socially attractive settlement sites.

Biodiversity of coral reef dwelling cardinalfish is clearly vulnerable to loss of large colonies. Multiple cardinalfish species specialise on these larger colonies while aggregative behaviour limits the number of larger colonies they will occupy. This study highlights the importance of large coral colonies to diversity of coral reef fish assemblages. It follows that coral colony distributions strongly affect fish distributions and need to be included in reef surveys to accurately assess assemblage health and ecosystem resilience to habitat disturbances. This work demonstrates that focusing reef conservation priorities on protection of reefs with large coral colonies will assist in maintaining diverse fish assemblages.

CHAPTER 4: Synergistic effects of habitat preference and gregarious behaviour on habitat use in coral reef cardinalfish

4.1. Abstract

Spatial distributions of coral reef fish species are potentially determined by habitat preferences and behavioural interactions. However, the relative importance of these factors and whether or not behavioural interactions reinforce or disrupt habitat associations are poorly understood. This paper explores the degree to which habitat and social preferences explain the association that three common coral reef cardinalfish species (*Zoramia leptacanthus, Archamia zosterophora* and *Cheilodipterus quinquelineatus*; family Apogonidae) have with coral substrata at Lizard Island, Great Barrier Reef. At diurnal resting sites, species were strongly associated with branching corals, with 80-90% of each species inhabiting one branching coral species, *Porites cylindrica*. Species were also highly gregarious, forming large conspecific and heterospecific aggregations in coral heads, potentially reinforcing habitat associations. Three-way choice experiments were conducted to test fishes habitat preferences for living coral over dead substrata, for particular coral species and the influence of gregarious behaviour on these habitat choices. The strength of habitat preferences differed among species, with *Z. leptacanthus* preferring live coral and *P. cylindrica*; *A. zosterophora* preferring *P. cylindrica*, whether live or dead; and *C. quinquelineatus* exhibiting no preferences. All species were attracted to conspecifics and for *C. quinquelineatus* and *A. zosterophora*, conspecific attraction resulted in stronger preferences for live corals. Gregarious behaviour also increased *C. quinquelineatus* associations with *P. cylindrica*. The relative strength of social attraction versus habitat preferences was investigated by comparing fish habitat preferences in the presence and/or absence of conspecifics. The presence of conspecifics on non-preferred rubble habitat reduced each species association with live coral. This study's results indicate that, in the field, habitat preferences and conspecific attraction combine to reinforce the association between cardinalfishes and a narrow range of coral substrata.

4.2. Introduction

Coral reef fishes are strongly dependent on the underlying reef habitat for food, shelter and other resources (Roberts and Ormond, 1987, Jones and Syms, 1998, Wilson et al., 2006). At a reef-wide scale, most species are restricted to particular reef zones, exposures, water depths and/or reef profiles (e.g., Choat and Bellwood, 1985, Williams, 1991, Nanami et al., 2005, Arias-González et al., 2006). Within these preferred habitats, the degree to which they are specialised on particular coral reef substrata and the ecological consequences of habitat specialisation have received increasing attention (Booth and Wellington, 1998, Caley and Munday, 2003, Munday, 2004b, Dirnwöeber and Herler, 2007, Feary, 2007, Wilson et al., 2008). Many reef fish appear to be associated with a narrow range of coral species, using them as either shelter (Kuwamura et al., 1994, Munday et al., 1997) or as food (Pratchett, 2005, Cole et al., 2008). Although fishes vary in the extent of habitat specialisation, the species composition of the reef habitat can be a primary determinant of the structure of reef fish communities (Wilson et al., 2006). Determining the nature and strength of apparent habitat preferences for coral species is an important step in understanding how reef fish communities will respond to dynamic or degrading coral reef environments (Jones et al., 2004, Munday, 2004b, Graham et al., 2006).

Apparent habitat specialisation or the observed association between fishes and particular substrata can be influenced by three potentially important factors. Firstly, species may exhibit distinct micro-habitat preferences and when they have the choice, will invariably associate with preferred substrata (Danilowicz, 1996, Öhman and Rajasuriya, 1998, Munday, 2001, Nakamura et al., 2007, Pratchett et al., 2008a). Secondly, if coral species vary in abundance and the fish species' preferred coral substrata are rare, observed patterns of distribution may reflect habitat availability rather than preference hierarchies. For example, in the Red Sea, *Gobiodon histrio* preferentially occupies *Acropora acuminata* and *A. digitifera* coral species. However, at sites where these coral species are in short supply, *G. histrio* is distributed proportionally amongst other *Acropora* species (Dirnwöeber and Herler, 2007). The third factor affecting the strength of fish-habitat associations is the potential for behavioural interactions within and among fish species (Jones, 1991, Bay et al., 2001, Eagle et al., 2001). Many apparent coral specialists are highly territorial and dominant competitors may restrict other individuals to less preferred substrata (Robertson and Gaines, 1986, Clarke, 1992, Robertson, 1996, Munday, 2001, Munday et al., 2001). Other coral specialists are social animals, living in conspecific and/or heterospecific groups (Sweatman, 1983, Booth, 1992, Lecchini et al., 2007). In these species social behaviour can potentially override habitat preferences, as individuals may prefer to join groups in marginal habitat, rather than live alone on preferred coral substrata.

While micro-habitat preferences, micro-habitat availability and behavioural interactions can operate together to determine coral reef fish habitat distributions their relative importance is poorly understood. Patterns of distribution and micro-habitat use in the field are often attributed to preferences, but recent work suggests patterns of habitat use may reflect micro-habitat availability (e.g., Srinivasan et al., 1999, Hattori, 2002, Srinivasan, 2003) or interactions within or among fish species (e.g., Robertson, 1996, Bay et al., 2001, Almany, 2004, Hobbs and Munday, 2004). For most reef fish families, the degree to which active choice determines the distributions of individuals has not been examined. To distinguish active choice or micro-habitat preference from other factors, manipulative experimental studies in which individuals are given equal access to a range of substratum types must be conducted (Bay et al., 2001, Feary et al., 2007b, Pratchett et al., 2008a). In addition, if habitat choice is modified by the presence of other individuals, the relative strength of preferences for substrata with and without other individuals needs to be quantified (e.g., Booth, 1992, Öhman et al., 1998, Schofield, 2003, Lecchini et al., 2007).

The overall aim of this study was to experimentally assess whether the apparent degree of habitat specialisation and spatial overlap in coral reef-dwelling cardinalfish (Family Apogonidae) is explained by habitat preferences, gregarious behaviour, or a synergistic interaction between both factors. By day, cardinalfish typically shelter within branching corals and caves (Greenfield and Johnson, 1990, Allen, 2002, Marnane and Bellwood, 2002). In the Indo-Pacific, their strongest habitat association is with a single branching coral species - *Porites cylindrica* (Chapter 2). Many species form large aggregations upon *P. cylindrica* colonies and individuals show high site fidelity to particular colonies (Marnane, 2000, Chapter 2). This concentrated distribution of cardinalfish may result from combined habitat preferences of individuals or from an interaction between social and habitat preferences. An interaction of specialist habitat preferences and positive social behaviour would increase the guild's dependence on the dynamics of just one particular coral species.

This study takes a combined observational and experimental approach to assess the degree to which cardinalfish micro-habitat and social associations are explained by micro-habitat and group living preferences and the degree to which habitat preferences are reinforced or disrupted by interactions among individuals. First, micro-habitat use and the density of resting groups were quantified to assess patterns of apparent habitat specialisation and conspecific niche overlap for three common species (*Zoramia leptacanthus, Archamia zosterophora and Cheilodipterus quinquelineatus*) on the northern Great Barrier Reef. A series of preference experiments were then carried out to test the following specific hypotheses: (1) Apparent

habitat specialisation on live branching corals and the strong association with one species (*Porites cylindrica*) is a result of habitat preferences; (2) Non-random dispersion of individuals among habitat patches can be caused by strong conspecific attraction; (3) Gregarious behaviour has a synergistic effect that reinforces the association with preferred coral substrata; and (4) the strength of habitat associations is affected by the prior presence and/or absence of conspecifics on habitat patches.

4.3. Methods

4.3.1. Study site and species

This study was conducted over several months at Lizard Island on the northern Great Barrier Reef, Australia (14º40'S, 145º28'E) during 2006 and 2009. Lizard Island lagoon is a typical patch reef, sandy lagoon. Shallow reef areas (0-4m depth) are dominated by mounds, soft corals, corymbose coral heads and large stands of branching coral habitat are scattered through deeper areas (5-15m). Three species of common coral reef dwelling cardinalfish (*Z. leptacanthus, A. zosterophora* and *C. quinquelineatus)* were selected for field observations and aquaria experiments. Populations of each species show strong patterns of habitat specialisation on *P. cylindrica* coral at this and other Indo-Pacific locations (Chapter 2). Differences in aggregation tendencies are also apparent between the species with *C. quinquelineatus* individuals typically solitary, while *A. zosterophora* and *Z. leptacanthus* are often resting in large groups of more than 50 individuals.

4.3.2. Fish habitat-use surveys

Field surveys were conducted to determine patterns of micro-habitat use by the locally present cardinalfish species. Divers surveyed 13 reef areas (3-9m depth) within Lizard Island lagoon, estimating abundance, diversity and micro-habitat use of adult cardinalfish. Density was measured as the total number of discrete aggregations ($\geq$ 1 fish) and the approximate number of individuals within each aggregation (log 2 scale). Distinction was made between live coral, dead coral, rubble, soft coral and crevice habitats. Live coral use was further categorized amongst available branching coral species and their architectural forms (following Veron, 1993). These divisions were *P. cylindrica* (finger branching coral, tightly branched); small arborescent *Acropora* spp.; large arborescent *Acropora* spp.; bushy *Acropora* spp.; corymbose *Acropora* spp.; branching *Millepora* spp.; branching *Hydnophora* spp.; and branching *Echinopora* spp. 13-30 groups of cardinalfish were observed per site, with overall totals of 31 *Z. leptacanthus* groups (approximately 3050 individuals); 18 *A. zosterophora* groups

(approximately 350 individuals); and 162 groups of *C. quinquelineatus* (approximately 2250 individuals). Sites across the breadth of the lagoon were chosen in order to give a thorough representation of cardinalfish habitat use.

4.3.3. Experimental evaluation of habitat preferences

Habitat and social preferences of adult cardinalfish were tested with multiple habitat choice experiments in large, outdoor, flow-through aquaria. Five different experiments were conducted for each species, varying in the type of habitat provided and number of individuals released per aquaria.

4.3.3.1. Experiment 1: Preference for living corals

The first two experiments tested the hypothesis that the degree of apparent habitat specialisation observed in the field is due to habitat preferences. Experiment 1 tested preferences for live coral over non-living substrata. Individual *Z. leptacanthus*, *A. zosterophora* and *C. quinquelineatus* fish were given a choice between using live *P. cylindrica*, rubble, or dead coral habitat patches. Dead coral constituted dead *P. cylindrica* in order to examine whether cardinalfish would choose live coral or simply a substratum of certain complexity.

4.3.3.2. Experiment 2: Preference for coral species

The second experiment tested whether cardinalfish exhibit a preference for *P. cylindrica* over other available branching coral species and/or growth forms. Individuals of each cardinalfish species were presented with three habitat patches of live *P. cylindrica*, *Acropora yongei* and *Acropora nobilis*. Each of these corals are abundant in Lizard Island lagoon and occupied by various cardinalfish species. In this lagoonal habitat *A. nobilis* is a small arborescent coral with wide inter-branch spaces, *A. yongei* is a bushy branching coral with narrower inter-branch spaces and *P. cylindrica* is the most tightly branched of the three corals.

4.3.3.3. Experiment 3: Preference for conspecifics

The hypothesis that the observed insitu dispersion of cardinalfish among *P. cylindrica* coral colonies is due to active conspecific attraction was tested by assessing the dispersion of a group of cardinalfish amongst several empty coral colonies. Three conspecific individuals were released in aquaria containing three equally sized patches of *P. cylindrica*. Individuals could thereby choose (1) to all use the same coral colony (nil dispersion), (2) all use separate colonies

(complete dispersion), or (3) display partial dispersion with two individuals sharing one colony and the third using a separate colony. It was predicted that each species' strength of conspecific attraction would contribute to any differences seen amongst species' group sizes in field surveys.

4.3.3.4. Experiment 4: Synergistic effect of aggregation upon habitat preferences

If gregarious behaviour positively affects a species' habitat association then, in the presence of conspecifics, it would be expected that individuals in groups would exhibit stronger associations with preferred habitat types, compared with solitary individuals. In order to test the effect of cardinalfish aggregation on habitat preferences for live coral and for *P. cylindrica*, Experiment 1 and 2 were repeated with three conspecifics released into aquaria. One of the three fish was designated as the focal individual. The habitat choices of focal fishes were subsequently compared to those of individual fish amongst the same substrata (i.e., results of experiment 1 and 2).

4.3.3.5. Experiment 5: Do social interactions reinforce and/or disrupt habitat preferences?

The relative strength of social attraction on cardinalfish habitat preferences was investigated by measuring the strength of habitat preferences for corals with and without conspecifics already present. The hypothesis that the strength of the choice for particular habitat would be modified by the presence of conspecifics was tested by examining the strength of habitat choice with prior residents present on either the preferred or less preferred habitats. If gregarious behaviour positively affects habitat associations then associations with a preferred substratum should be greater in the presence of conspecifics than in their absence. If social attraction is stronger than habitat preference, the presence of conspecifics on non-preferred habitat should shift the preference to the less preferred habitat type. These hypotheses were tested by recording the association of an individual fish with either live *P. cylindrica* coral or with rubble in the presence and/or absence of conspecifics held in cages on the habitat patches. The frequency of habitat choice was compared for three treatments: (1) Conspecifics absent from both coral and rubble habitat; (2) Conspecifics present on coral but not rubble; and (3) Conspecifics present on rubble but not coral.

4.3.4. Apparatus and experimental protocols

Cardinalfish were collected between 08:00 and 17:00h from lagoonal patch reefs using clove oil (1:10 clove oil/ethanol dilution) and small hand nets. Fish were held in aquaria a maximum of

48 hours prior to experiments. Individual fish were only used once in experiments. Fish of similar body lengths were used to avoid size effects during conspecific trials. Typical standard lengths were: *Z. leptacanthus* 4.5-5cm; *A. zosterophora* 6cm; and *C. quinquelineatus* 8-10.5cm. Live coral and rubble patches were collected from Lizard Island lagoon. Dead *P. cylindrica* coral patches were made from dried coral branches. Habitat patches of equal size were placed equidistantly around aquaria upon approximately 2cm of sand (Fig. 4.1). Between trials habitat patches were rotated and sand stirred to prevent anoxia. Water was replaced every second day in experiments 1-4 and between trials for experiment 5.

Experiments 1-4 were performed in large circular aquaria (300L capacity) with eight overnight trials conducted per treatment and species. Fish were released at night (after 1900hrs) into aquaria via clear, tall Perspex cylinders positioned at the tank centre (Fig. 4.1a). Fishes were given a 30 minute acclimation period before cylinders were slowly removed, leaving them in the centre of aquaria. Habitat choice of all individuals was scored the subsequent morning at four intervals; 6:00 (dawn), 7:00, 8:00 and 10:00h. Habitat choice was defined as the habitat type in which individuals were located. Fish observed swimming around tanks or not in obvious proximity to habitats were recorded as not having chosen a habitat. In all but four of 136 trials, habitat and/or social choices were consistent in the last two observation periods such that the 10:00h record was used in all preference analyses. In conspecific habitat choice trials (Experiment 4), a focal individual was randomly chosen and subcutaneously tagged with fluorescent elastomer (North-West Marine Technologies). Tagging took place at least two hours prior to experimental release and is known to have minimal behavioural effects on cardinalfish (Beukers et al., 1995, Marnane, 2000).
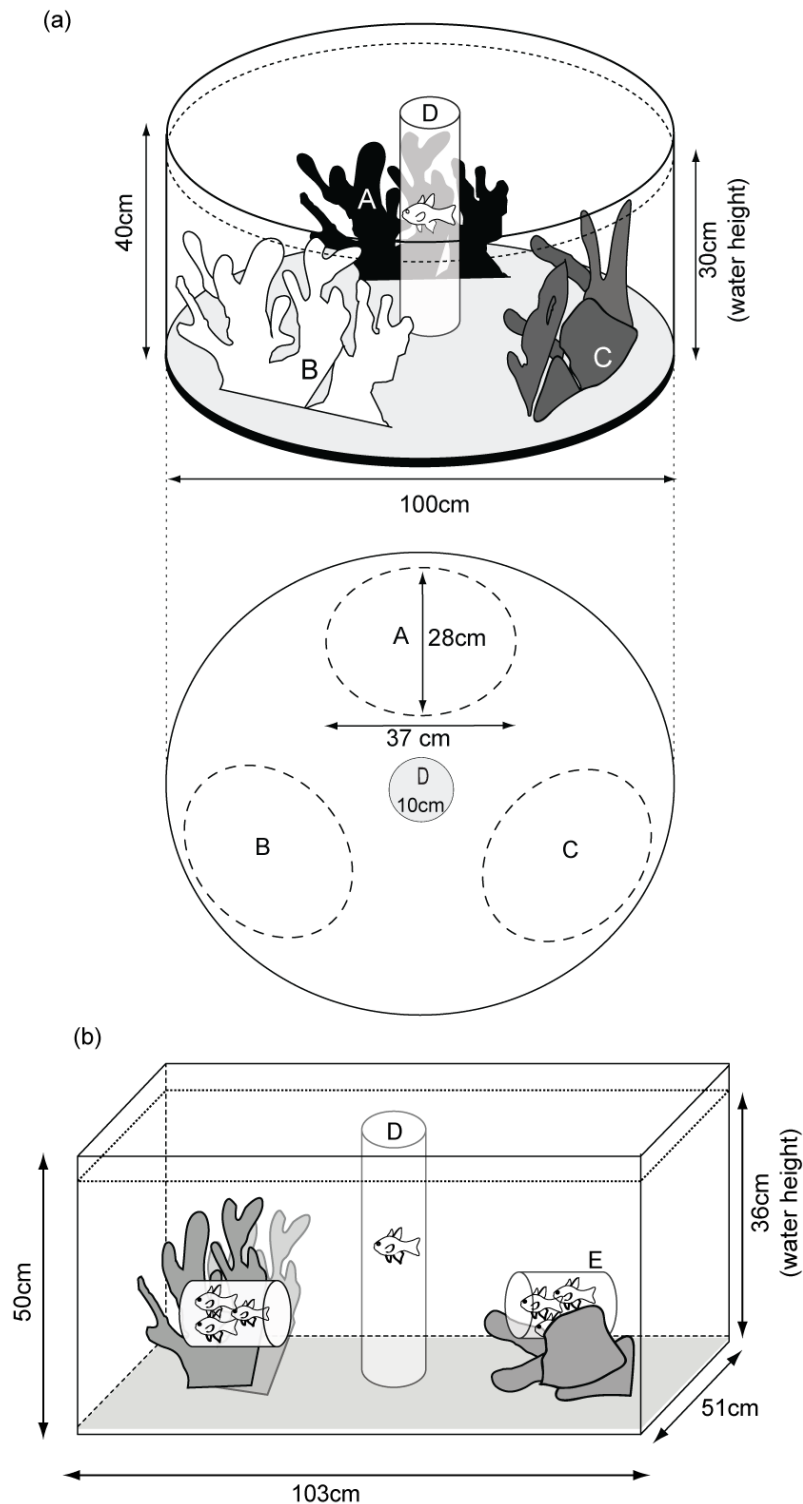
Figure 4.1 Aquarium design used in cardinalfish preference experiments. (a) Circular tank setup used in experiments 1-4; A - C indicate the position of three habitat patches placed equidistantly around tank. Habitat type varied according to requirements of each experiment. Test fish were acclimatised for 30 minutes in a clear Perspex cylinder (D), then slowly released. (b) Rectangular aquaria setup used in Experiment 5 to test the effect of conspecific presence on habitat preferences. Two habitat patches were placed on opposite sides of the tank from live *Porites cylindrica* coral and rubble. A clear cylinder with mesh ends (E, 'model cage') was positioned within each habitat patch. Model cages held either 3 conspecific fish or 0 fish, as per treatment requirements (cage dimensions = 3.5cm radius, 16 cm length). Test fish were held for

20 minutes in acclimation cylinder D, then slowly released. Aquaria floors were covered with approximately 2cm of coarse beach sand and habitat patch heights were approximately 22cm.

Experiment 5 was carried out in rectangular aquaria (250L) in which one coral and one rubble patch of similar breadth (31cm) were positioned at opposite ends of aquaria, approximately 30cm apart. Within each habitat patch a small, clear Perspex cage (600ml volume) with mesh ends was positioned (Fig. 4.1b). Three conspecific fish were placed in the cages on patches designated as 'habitats with conspecifics' while cages in 'habitats without conspecifics' remained empty. One test fish individual was placed into a centrally positioned acclimation cylinder and released after 20 minutes. The test fish's habitat choice was then recorded every 15 minutes for two hours. Pilot studies indicated a longer time frame did not alter habitat choice responses. The position of the test fish after two hours was used in analyses as the habitat choice. Approximately 20 replicates of each treatment (three treatments) were conducted per species. Replicates were repeated on new individuals if test fish exhibited any fright response in their behaviour (e.g., rapid movement into habitat due to observer presence).

4.3.5. Statistical analyses

For experiments 1 to 4, the binomial distribution was used to compare the frequency of success for particular habitat and social preferences against randomly expected probabilities. Where an individual's choice of habitat type was assessed (Experiment 1, 2 & 4) individuals had an equal probability of selecting one of three available habitats. The dispersion of individuals in conspecific preferences (Experiment 3) had 10 possible outcomes such that the randomly expected probability of three fish using the same habitat patch is 0.3, two habitat patches is 0.6 and dispersed amongst all three habitat patches is 0.1. Deviations less than 5% from the expected binomial probability were interpreted as statistically significant habitat preferences. Pearson Chi-squared tests of independence were used to evaluate the effect of group behaviour on individual habitat preferences. This involved comparison of individual habitat choice distributions (Experiment 1) to that of the focal individual (Experiment 4) for each species and habitat category (living corals and coral species). Due to the limited number of trials (n = 8) exact p-values were obtained.

For experiment 5, the null hypothesis that coral habitat choice is independent of the presence/absence of conspecifics on either coral or rubble habitat was tested. Independence of habitat choice amongst the three treatments was calculated using Pearson Chi-squared tests of independence on 2×3 contingency tables (2 habitats $\times$ 3 treatments). Odds ratios with 95% confidence intervals were calculated to assess lack of independence between any two treatments

and the relative effect each pair-wise combination had on the overall Chi-squared analysis (as per Quinn and Keough, 2002). Independence amongst two treatments was rejected (at $a = 0.05$) if 95% confidence intervals for the odds ratio did not include one. Odds ratios were calculated on the probability of choosing the coral habitat.

4.4. Results

4.4.1. Patterns of micro-habitat use

Within Lizard Island lagoon, the test cardinalfish species *Z. leptacanthus*, *A. zosterophora* and *C. quinquelineatus* occupied live coral and particularly *P. cylindrica* corals almost exclusively (Fig. 4.2). All *Z. leptacanthus* and *A. zosterophora* groups used live coral habitats and 90% of these were associated with *P. cylindrica* (Fig. 4.2a,b,d,e) This coral species was also occupied by 75% of *C. quinquelineatus* and only 19 of the 162 *C. quinquelineatus* aggregations were not in live corals (Fig. 4.2c). *C. quinquelineatus* was found in a greater range of branching coral forms than *Z. leptacanthus* and *A. zosterophora* (Fig. 4.2f). The latter two species occupied three types of branching corals, while *C. quinquelineatus* occupied seven categories.
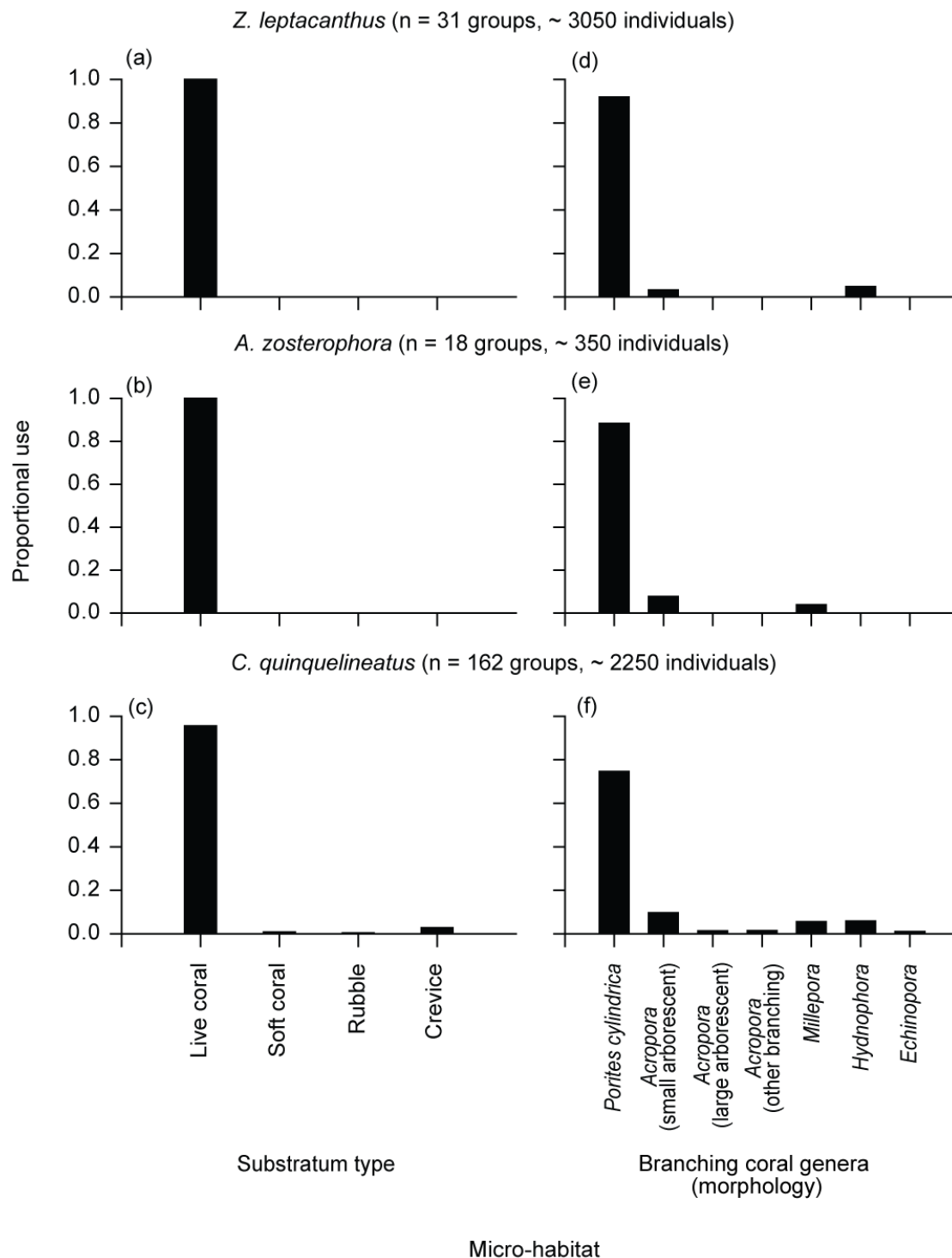
Figure 4.2 Micro-habitat use by groups of cardinalfish species *Zoramia leptacanthus, Archamia zosterophora* and *Cheilodipterus quinquelineatus* within Lizard Island lagoon, northern Great Barrier Reef. Charts (a), (c) and (e) indicate distribution of groups amongst live & non-living substratum. Charts (b), (d) and (f) show the distribution of groups amongst live branching corals. 'n' refers to the number of discrete groups (≥ 1 fish) observed per species and the approximate total number of individuals seen.

4.4.2. Size of aggregations

Cardinalfish were typically found in aggregations yet the size of groups varied amongst the three species (Fig. 4.3). The average group size for *Z. leptacanthus* was 98 individuals ($\pm$ 27 s.e.). More than 70% of *Z. leptacanthus* groups contained between 15 and 125 individuals. This species' largest conspecific group held approximately 700 individuals and only two groups with less than six individuals were found. *A. zosterophora* was relatively rare in Lizard Island lagoon with only 18 groups observed that contained a total of approximately 350 individuals. Groups were smaller in size than *Z. leptacanthus*, averaging 20 individuals per group ($\pm$ 5 s.e.). Three observations of paired or solitary *A. zosterophora* individuals were made and the largest group size was 80 individuals. *C. quinquelineatus* formed the smallest groups with aggregation density averaging 13 individuals ($\pm$ 1 s.e.). Nearly half the observed *C. quinquelineatus* were in small groups of 1-6 individuals (73 counts). The largest adult *C. quinquelineatus* aggregation contained 84 individuals.

4.4.3. Experiment 1: Preference for living corals

In habitat choice experiments, cardinalfish species differed in their choice of micro-habitat types (Fig. 4.4a-c) and in the degree to which these choices mirrored field distribution patterns (cf. Fig. 4.2). Solitary *Z. leptacanthus* individuals showed strong and statistically significant preferences for live coral over dead coral or rubble habitats (Binomial probability: $p = 0.002$). Individuals occupied the live coral patch throughout the observation period in all but one of the eight trials and consequently the species only used two of the three available habitats (Fig. 4.4a). This pattern mirrored that seen in field surveys of habitat use (Fig. 4.2a). *A. zosterophora* habitat choices did not match apparent field preferences for live coral. Instead two thirds of aquaria tested individuals occupied dead coral (Fig. 4.4b). Rubble habitat was avoided. *C. quinquelineatus* habitat choices also contrasted the apparent live coral specialisation seen in field surveys. Individuals showed no clear habitat preferences with all three available habitat types used in equal proportions (Fig. 4.4c).
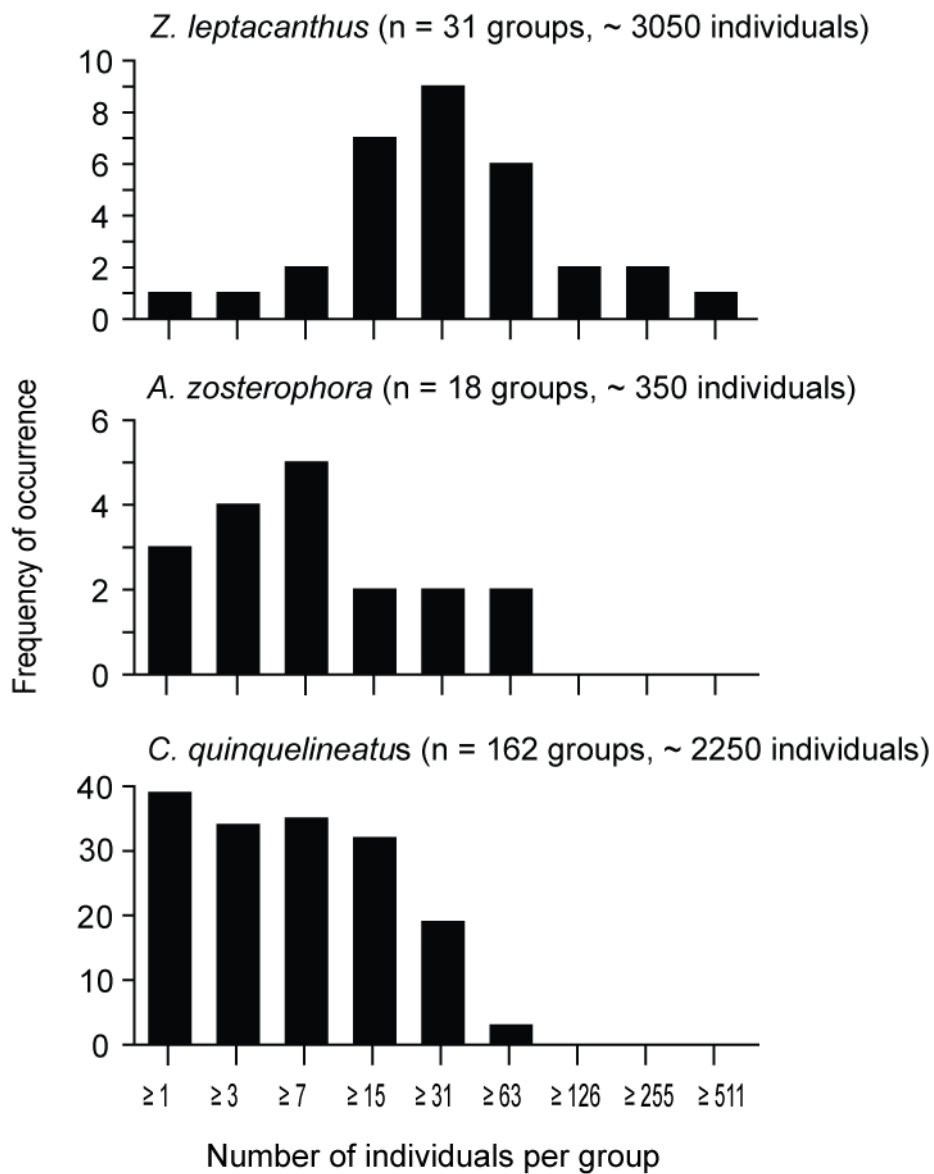
Figure 4.3 Frequency distribution of aggregation density in cardinalfish species *Zoramia leptacanthus*, *Archamia zosterophora* and *Cheilodipterus quinquelineatus*. Data were pooled from 13 survey sites within Lizard Island lagoon, northern Great Barrier Reef. The estimated number of individuals in each group is categorised on a Log 2 scale. 'n' refers to the number of discrete groups observed in live coral and the approximate total number of individuals.
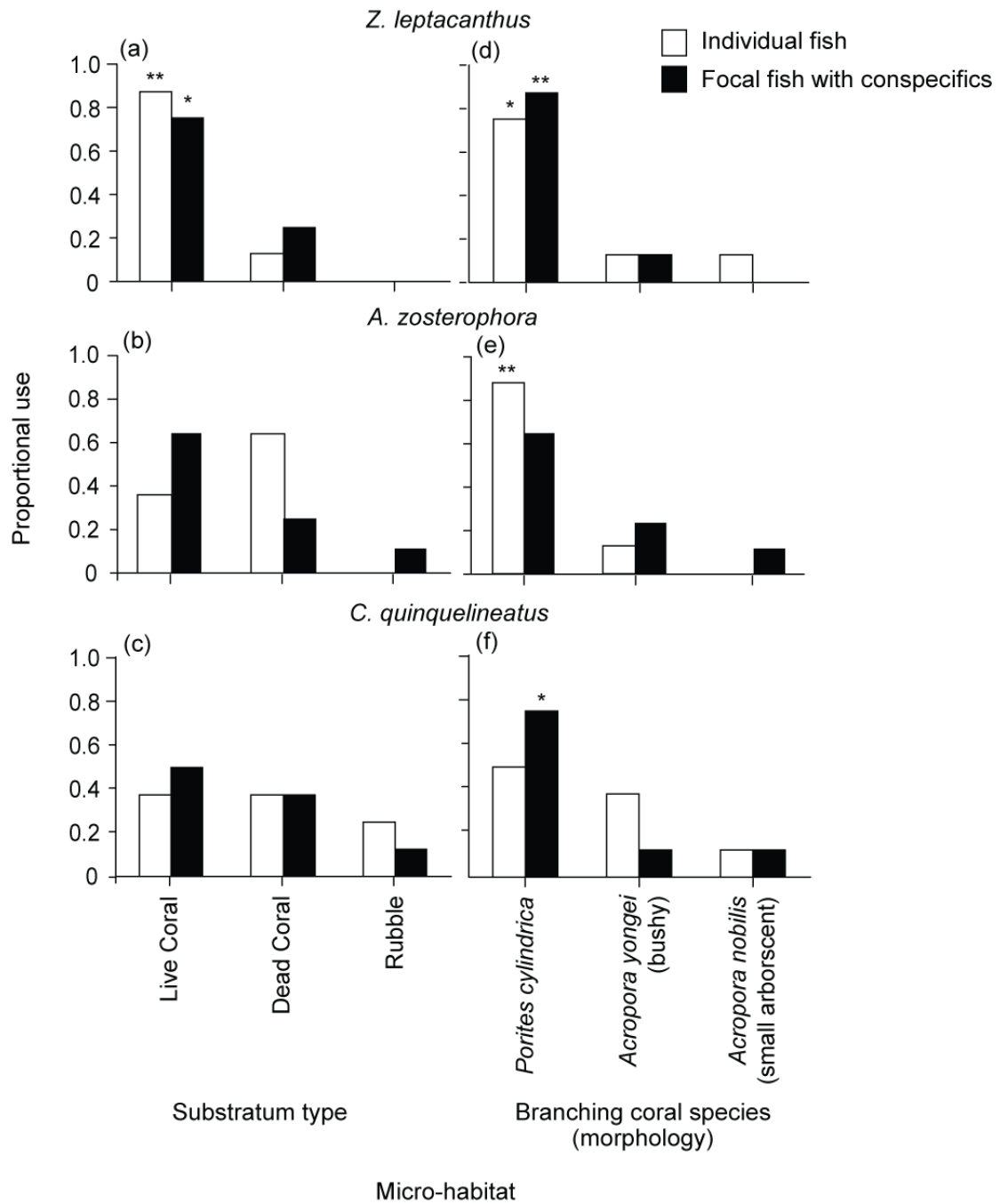
Figure 4.4 Micro-habitat preferences of *Zoramia leptacanthus, Archamia zosterophora* and *Cheilodipterus quinquelineatus* amongst living and non-living substrata (a-c) and amongst three common branching coral species (d-f). White bars indicate preferences of solitary individuals (Experiment 1 and 2), black bars indicate preferences of focal individuals released simultaneously with 2 conspecifics (Experiment 4). Eight trials per species and treatment were conducted. The binomial probability of habitat preference was not significant except where indicated by * $p < 0.05$ and ** $p < 0.01$.

4.4.4. Experiment 2: Preference for coral species

As predicted, all three cardinalfish species chose *P. cylindrica* more often than the two *Acropora* corals (Fig. 4.4d-f). Significant preferences for *P. cylindrica* by *Z. leptacanthus* and *A. zosterophora* predict the strong insitu patterns of habitat specialisation (Fig. 4.2d,e). 75% of solitary *Z. leptacanthus* and 87% of *A. zosterophora* individuals chose *P. cylindrica* (Binomial probability: *p* = 0.017 and 0.003 respectively), avoiding other branching coral species. The distribution of *C. quinquelineatus* individuals was more equally spread between *P. cylindrica* (50%) and *Acropora yongei* (37.5%) the latter coral having slightly wider branch spacing. This weaker *P. cylindrica* preference is in contrast to the strength of habitat specialisation that field surveys results depict (Fig. 4.2f).

4.4.5. Experiment 3: Preference for conspecifics

Two of the three cardinalfish species exhibited strong conspecific preferences (Fig. 4.5). There were no trials in which individuals were dispersed among all three available habitat patches. *Z. leptacanthus* had the strongest aggregation preferences with individuals always grouping together in one patch (Binomial probability: *p* < 0.001). Similarly, *A. zosterophora* grouped into one patch in six of eight trials, significantly more than randomly expected (Binomial probability: *p* < 0.001). This strong conspecific preference meant that the two trials with *A. zosterophora* dispersed amongst two patches were less than the expected 60%. *C. quinquelineatus* trials resulted in individuals predominantly split amongst two of the three available patches, as per random expectations (Binomial probability: *p* = 0.27). This indicates a lower strength of social preference for conspecifics than the previous two cardinalfish species had. The strength of social attraction gives a relatively good prediction of each species tendency to form aggregations, as observed in field surveys (Fig. 4.3).
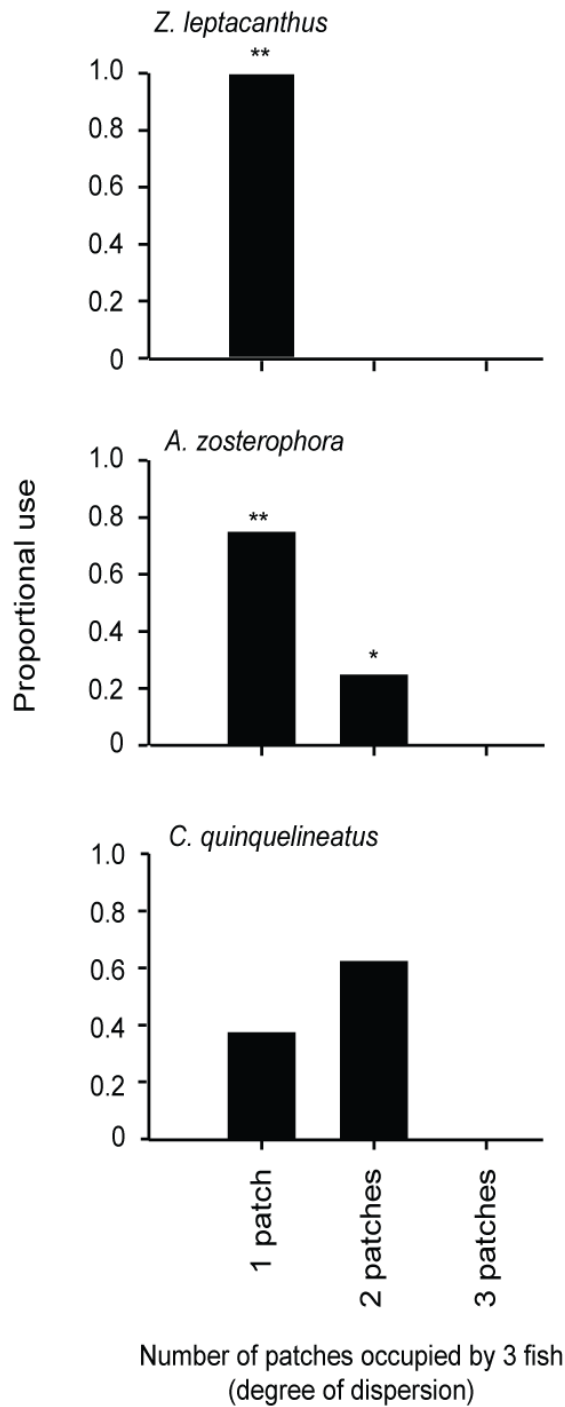
Figure 4.5 Conspecific preferences of *Zoramia leptacanthus*, *Archamia zosterophora* and *Cheilodipterus quinquelineatus* as indicated by the dispersion of three conspecific individuals amongst three coral patches. The use of one patch by all three fish indicates nil dispersion (strong conspecific preference); two patches indicates partial dispersion; and three patches indicates complete dispersion (no conspecific preference). Eight trials per species were conducted. The binomial probability of conspecific preference was not significant except where indicated by * $p < 0.05$ and ** $p < 0.01$.

4.4.6. Experiment 4: Synergistic effects of aggregation upon habitat preferences

Gregarious behaviour had a positive effect on the strength of each species' apparent preference for particular habitat types, including live over dead coral and for *P. cylindrica* over other branching corals (Fig. 4.4). When in groups, focal individual preferences of *Z. leptacanthus* for live coral and for *P. cylindrica* were strong at 75 and 87% respectively ($p < 0.05$, Fig. 4.4a,d). Individual habitat preferences for these substrata were already strong (Experiment 1 and 2) hence no significant increase in distribution occurred (live coral choice; $\chi^2 = 0.41$, df = 1, exact *p*-value > 0.05. *P. cylindrica* choice; $\chi^2 = 1.08$, df = 2, exact *p*-value > 0.05).

Gregarious behaviour increased the preference for live corals in *A. zosterophora* and *C. quinquelineatus* and the preference for *P. cylindrica* in *C. quinquelinearus*. For *A. zosterophora,* the use of live coral over dead coral and rubble doubled in the presence of conspecifics compared with solitary individuals (Fig. 4.4b). Similarly, *C. quinquelineatus* increased its choice for live coral by 12.5% (Fig. 4.4c). When given the choice of three branching coral species, individuals of *A. zosterophora* in groups selected *P. cylindrica* in similar proportions to solitary individuals (Fig. 4.4e). However, *C. quinquelineatus* in groups exhibited a 25% higher preference for *P. cylindrica* than solitary individuals. Focal fish in groups significantly preferred this coral, while solitary individuals did not (Fig. 4.4f; Binomial probability of focal fish habitat preference: $p = 0.002$). Apparent shifts in habitat associations by focal *A. zosterophora* and *C. quinquelineatus* were not statistically significant (*A. zosterophora* live coral choice: $\chi^2 = 2.29$, df = 1, exact *p*-value > 0.05. *P. cylindrica* choice: $\chi^2 = 1.67$, df = 2, exact *p*-value > 0.05. *C. quinquelineatus* live coral choice: $\chi^2 = 1.03$, df = 2, $p > 0.05$. *P. cylindrica* choice: $\chi^2 = 1.44$, df = 2, $p > 0.05$). Consistent with conspecific preferences (Experiment 3), strong social behaviour occurred for all three cardinalfish species. The three individuals grouped together in 15 of 16 *Z. leptacanthus* trials; 14 of 16 *A. zosterophora* trials; and in 10 of 16 *C. quinquelineatus* trials.

4.4.7. Experiment 5: Do social interactions reinforce and/or disrupt habitat preferences?

The presence of prior residents on preferred corals in habitat choice experiments did not appear to reinforce habitat preferences, but prior residents on less preferred habitat altered habitat preferences. Habitat choice for live *P. cylindrica* coral over rubble patches was not independent of the presence and position of conspecifics (Fig. 4.6). The prior residence of conspecifics on rubble reduced the preference for coral by up to 40%, equating to relatively equal use of both

coral and rubble habitats. Choices by *A. zosterophora* and *C. quinquelineatus* were statistically dependent on the presence and position of prior residents (Table 4.1). For these species, the odds of choosing coral were greater when conspecifics were present on coral rather than rubble (Treatment 2 vs. 3). *Z. leptacanthus* coral preferences were not statistically different among treatments however 25% more fish chose rubble over coral when residents were present on the rubble habitat (Treatment 2 vs 3; Fig. 4.6, Table 4.1).

In contrast to predictions, gregarious behaviour did not significantly increase the strength of association with the preferred coral habitat, as each species chose live coral over rubble with more than 62% frequency in both Treatment 1 (no conspecifics present) and Treatment 2 (conspecifics present on coral only; Fig. 4.6). Odds ratios comparing the outcomes of these two treatments showed no evidence that the presence of conspecifics on live coral influenced habitat choice (Table 4.1).
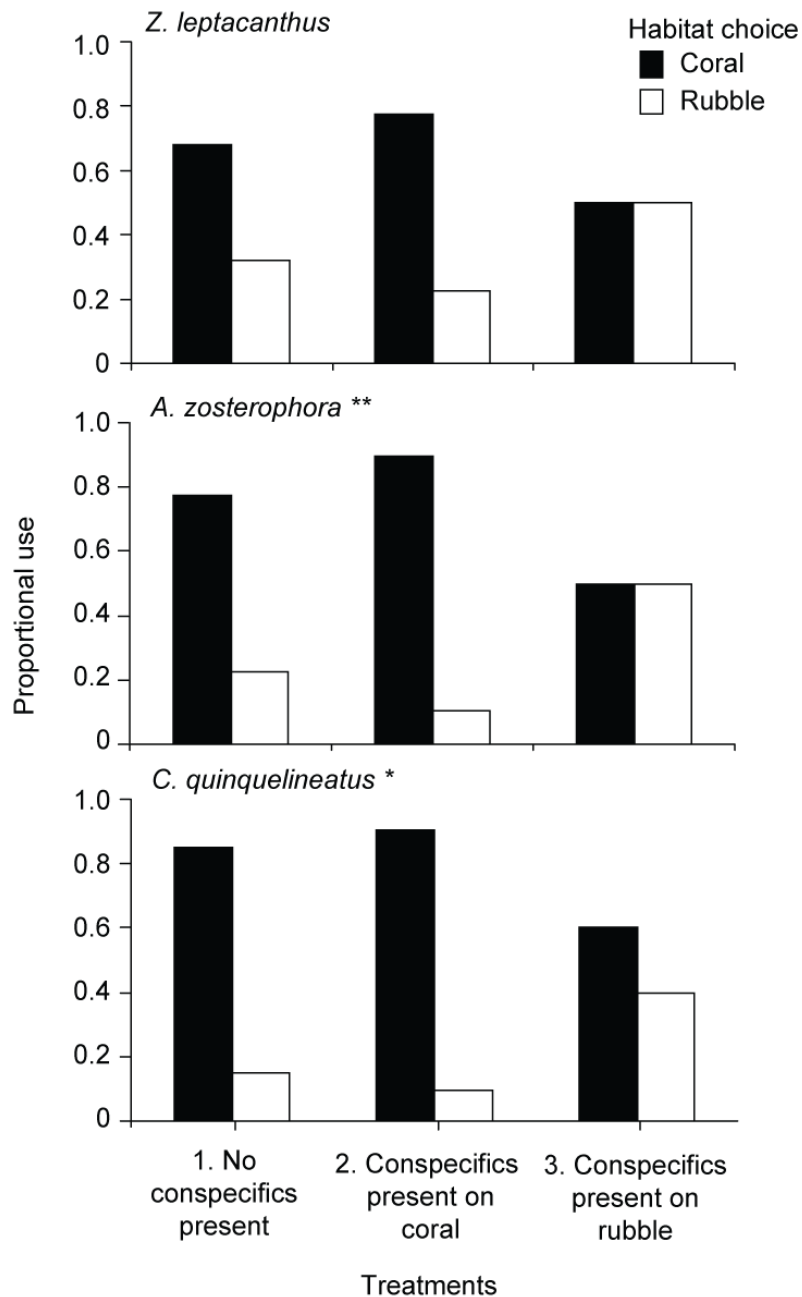
Figure 4.6 The effect of conspecifics on habitat preferences for three cardinalfish species; *Zoramia leptacanthus, Archamia zosterophora* and *Cheilodipterus quinquelineatus*. Habitat choices for either coral (*Porites cylindrica*) or rubble were recorded in the presence and absence of conspecifics (Treatments 1-3). Conspecifics were absent from both habitats in Treatment 1, held only on *P. cylindrica* coral in Treatment 2 and held only on rubble in Treatment 3. Habitat choice was significantly different amongst treatments at * $p < 0.05$ and ** $p < 0.01$. Sample size and significance tests are shown in Table 4.1.

Table 4.1 The effect of conspecifics on habitat preferences of three cardinalfish species; *Zoramia leptacanthus, Archamia zosterophora* and *Cheilodipterus quinquelineatus*. Habitat choices for either coral (*Porites cylindrica*) or rubble were recorded in the presence and absence of conspecifics (Treatments 1-3).

| Habitat choice [a] | Treatment | | | | Relative contribution to independence of treatments | | |
	(1) No conspecifics	(2) Conspecifics on coral	(3) Conspecifics on rubble	Total	Treatments compared	Odds ratio	95% confidence interval
Z. leptacanthus							
P. cylindrica coral	15	17	11	43	(1) v (2)	0.63	0.17 to 2.41
Rubble	7	5	11	23	(1) v (3)	2.14	0.63 to 0.73*
Total	22	22	22	66	(2) v (3)	3.40	0.93 to 12.49
X^2 = 3.74, *p* = 0.155							
A. zosterophora							
P. cylindrica coral	17	17	10	44	(1) v (2)	0.40	0.07 to 2.35
Rubble	5	2	10	17	(1) v (3)	3.40	0.90 to 12.83
Total	22	19	20	61	(2) v (3)	8.50	1.54 to 46.87*
X^2 = 9.62, *p* = 0.008							
C. quinquelineatus							
P. cylindrica coral	17	19	12	48	(1) v (2)	0.60	0.09 to 4.01
Rubble	3	2	8	13	(1) v (3)	3.78	0.83 to 17.25
Total	20	21	20	61	(2) v (3)	6.33	1.15 to 35.01*
X^2 = 6.11, *p* = 0.047							

[a] Data for each species were analysed separately using the Chi-squared test of independence amongst treatments for a 2x3 contingency table. The contribution of differences to independence among treatments was calculated using log odds ratio with 95% confidence intervals, on the probability of choosing coral (see Quinn & Keough 2002).

* Comparison represents a significant contribution to statistical independence of treatments

4.5. Discussion

This study is one of the first to document synergistic effects of social attraction and habitat preferences on the dispersion of coral reef fishes. The strong association between cardinalfish species and particular micro-habitats and the high level of conspecific niche overlap observed elsewhere (Chapter 2) appear to be explained by these behavioural choices. The experiments establish that when given a choice, individuals of several species exhibit clear habitat preferences, but the strength of preference can be modified by the presence of conspecifics. A synergistic interaction between intrinsic habitat preferences and conspecific attraction appeared to increase the observed association with live corals and with particular coral species. In situ patterns of grouping were well explained by each species' positive social preferences. In fact, social attraction in all test species was strong enough to disrupt habitat preferences. That is, many individuals chose less preferred habitats with conspecifics present over preferred habitats without conspecifics. Overall, diurnal habitat distributions of cardinalfish on coral reefs appear to be explained by a synergistic interaction between intrinsic habitat preferences and conspecific attraction.

Cardinalfish habitat preferences for living substratum and for a particular coral species (*P. cylindrica*) were only consistent with the apparent levels of habitat specialisation (observed in field surveys) for one of the three test species, *Z. leptacanthus*. Neither of the other two study species, A. *zosterophora* and *C. quinquelineatus,* chose live coral as a preferred substratum. Instead *A. zosterophora* individuals frequently chose dead coral over live coral and *C. quinquelineatus* had strong habitat generalist tendencies. When preferences among branching coral types were examined the preference of *C. quinquelineatus* for *P. cylindrica* was also weaker than predicted by patterns of in-situ habitat use. The addition of conspecifics to preference experiments resulted in an increase of both *A. zosterophora* and *C. quinquelineatus* preferences for live *P. cylindrica* coral. Gregarious behaviour thereby increased habitat preferences to explain the patterns of habitat specialisation seen in field surveys for these species.

This study is one of the first to show a positive effect of social preferences on habitat specialisation and particularly within coral reef fish communities. Interactive effects of social attraction and resource preferences are evident in a number of other animal systems (e.g., Birds: Muller et al., 1997; Insects: Kent et al., 2003; Molluscs: Jeanson and Deneubourg, 2007; and Mammals: Ersts and Rosenbaum, 2003; Campomizzi et al., 2008). Conspecific attraction in several bird species drives new individuals to choose occupied habitat sites rather than equally suitable but empty sites (Muller et al., 1997, Ahlering et al., 2006). This has the effect of

increasing habitat specificity towards particular locations. A similar drive in cardinalfish communities would explain their use of only a small proportion of the available *P. cylindrica* coral colonies (Chapter 2). The disruption of habitat preferences by conspecific attraction indicates the strength social behaviour has on animal habitat distributions. Such an effect has been shown in juvenile lobsters and cockroaches (Eggleston and Lipcius, 1992, Jeanson and Deneubourg, 2007). Whether aggregation preferences can increase coral reef fish species' discrimination of different habitat types and enhance specialisation is not known. Given the strong influence of social cues on habitat selection by naïve individuals, it is a likely outcome (Sweatman, 1985, 1988, Booth, 1992).

A synergistic interaction of cardinalfish social and habitat preferences is likely driven by survivorship and reproductive benefits. Cardinalfish are heavily preyed upon and have high rates of population turnover (Kingsford, 1992, Marnane, 2001, Beukers-Stewart and Jones, 2004). Aggregative behaviour in other teleosts benefits individuals by diluting predation risk, increasing predator vigilance and increasing mating opportunities (Krause and Ruxton, 2002). Micro-habitat preferences in reef fish typically reflect greater rates of survival and growth (Jones, 1987, Nemeth, 1998, Öhman et al., 1998). In resting individuals these habitat and social benefits would also assist in minimizing energy output (Kerth et al., 2001).

The habitat and social preferences observed in this study were relatively species specific. Each species' strength of preference will depend on the particular strategies it uses to maximise survivorship, reproduction, growth and other fitness parameters. *Z. leptacanthus* was the most specialist in habitat choices and the most gregarious in both insitu and aquarium environments. Of the three test species, *Z. leptacanthus* was the smallest in body size of the three test species and maybe more susceptible to predation. Stronger shoaling behaviour and high habitat specificity could be its primary strategy for reducing predation losses. In contrast *C. quinquelineatus* may use larger body size as the main predator refuge mechanism. This species had generalist habitat preferences and the lowest aggregation tendency. Disentangling species specific behaviours within cardinalfish communities will require manipulations of predation rates, group sizes and variation of refuge structures (i.e., coral branch spacings).

A. zosterophora exhibited intermediate habitat specialisation and aggregating behaviour. Aquarium choices indicate a preference for the structure of *P. cylindrica* coral rather than a live coral tissue preference. This association with dead coral over live coral is not observed in field studies due to the rarity of dead *P. cylindrica* corals which degrade quickly. The species' minimal discrimination between live and dead corals may increase the species short-term resilience to disturbance events, particularly where coral reef structures remain intact.

Synergistic interactions between social attraction and habitat preferences could make either positive or negative contributions to a species' resilience to changes in habitat distributions. Where social attraction increases habitat specificity the negative result will be greater reliance on fewer coral species. Conversely where social attraction broadens the range of habitat use, aggregations could be established on less-disturbed substratum. For example, if several individuals are 'forced' to move into marginal habitats, positive social behaviour could attract more individuals and shift the population's habitat association towards that marginal habitat. The current study shows preliminary support for this theory as social behaviour increased the use of non-preferred rubble habitat. Future experiments will establish the effect that social attraction and use of marginal habitats have on cardinalfish growth and survival and thus the capacity for long-term shifts of habitat associations.

This study highlights the importance that species distributions of corals can have on the dynamics and distribution of reef fish communities. Habitat preference and co-occurrence in cardinalfish communities interact to generate high degrees of habitat specialisation on *P. cylindrica* and the apparent reliance on this coral species. The flexibility of such preferences, particularly for the single substratum species will be a key factor determining the resilience of cardinalfish to future stresses on their habitat.

CHAPTER 5: Extreme site fidelity and homing behaviour in coral reef cardinalfishes

5.1. Abstract

Site fidelity and homing behaviour can benefit animals whose survival and/or reproduction is enhanced by familiarity with the local habitat. However, under conditions of widespread habitat loss, strong bonds with home sites may restrict population connectivity and limit resilience to habitat change. The response of coral reef fish to habitat loss may be exacerbated by site fidelity and homing, but relatively little is known of these phenomena. This study explores the extent of site fidelity and homing behaviour in coral reef cardinalfishes (Family Apogonidae) in Kimbe Bay, Papua New Guinea. It focuses on four species that are typically restricted to resting in large colonies of a preferred coral species after nocturnal foraging migrations. High fidelity to resting sites was observed for two study species, *Archamia zosterophora* and *Cheilodipterus quinquelineatus*, with individuals staying faithful to their original coral colonies and to specific areas within these colonies. In contrast, individuals of two other species, *Zoramia fragilis* and *Cheilodipterus artus*, either moved amongst nearby coral colonies or disappeared. Homing behaviour of cardinalfish displaced short distances (< 500m) across both continuous reef areas and deep open-water channels was strong and fast. Remarkable homing behaviour over long distances (2 and 5 km) was observed for one species. Extreme site fidelity and homing behaviours in some cardinalfish may act in concert to restrict the capacity of individuals to relocate when home sites are destroyed. It is predicted that this type of behaviour will exacerbate the susceptibility of coral reef fishes to habitat loss and fragmentation.

5.2. Introduction

In many animal species, individuals spend much of their time living at particular home sites (Switzer, 1993, Schmidt, 2004). Home site fidelity refers to an individual's continued use of a previously occupied location, rather than other available and suitable sites (Gerking, 1959, Switzer, 1993). Fidelity to home sites may arise because familiarity with particular areas improves access to resources such as food, nest sites or shelter from predators (Switzer, 1993, Lewis, 1995, Yoder et al., 2004, McDougall and Kramer, 2007). While some animals remain associated with small home ranges throughout their lives (Burt, 1943, McNab, 1963), other more mobile animals may exhibit homing behaviour, returning to home sites after substantial

daily or seasonal migrations (Papi, 1992, Dingle, 1996, Quinn et al., 2006). Homing behaviour involves directed movement to return to a home site (Papi, 1992), which in extreme cases, may involve migrations over 1000's of kilometers.

Strong site fidelity and homing behaviour have important ecological implications. Homing animals tend to exhibit discrete populations with more limited connectivity than may be expected given the scale of movements (Bowen and Karl, 2007, Rooker et al., 2008). Also, a strong reliance of particular places increases a species vulnerability to habitat change, as species may not be able to relocate to undisturbed habitats (McKinney, 1997, Webb and Shine, 1997, Laidre and Heide-Jorgensen, 2005). These factors combine to increase local extinction risks and limit the potential for recovery. However, the extent of site fidelity and the ability to home are not always known.

Some coral reef fishes are known to exhibit extreme site fidelity, with individuals of many small species confined to single coral colonies or anemones (Sale, 1971, Fautin and Allen, 1997). Home ranges may be an order of magnitude smaller than terrestrial animals of equivalent body size (Sale 1978b). More mobile fishes undertake migrations or forays within the broader reef area, with distances varying from 0.4-4.6 km (Sale, 1978b, Kramer and Chapman, 1999, Chapman and Kramer, 2000). Increasing evidence indicates high fidelity and strong homing behaviour may be the norm. Experimental displacement of individuals outside of their familiar home ranges has found high rates of return to capture sites (Ogden and Buckman, 1973, Ogden and Ehrlich, 1977, Buchheim and Hixon, 1992, Beets and Hixon, 1994, Marnane, 2000, Kolm et al., 2005, Wall and Herler, 2009). Homing has been observed over distances of up to 3km (Ogden and Ehrlich 1977). However, for most reef fishes the extent of site fidelity and homing behaviour is poorly understood. Whether or not homing behaviour contributes to population subdivision and the scale over which this occurs are generally unknown. Also, whether or not site fidelity is so strong that individuals cannot relocate in response to local disturbances has received limited attention. Given the global degradation of coral reef habitats (Hoegh-Guldberg, 2004, Wilkinson, 2004, Graham et al., 2006), knowledge of the extent of site fidelity and homing behaviour is necessary to assess the resilience of coral reef fish populations.

The extent of site fidelity and homing in reef fishes is particularly uncertain because of the mosaic structure of coral reef environments. Coral reef habitats can be separated by considerable distances, but the extent to which site fidelity and homing maintain isolated populations is unknown. Most coral reef fishes have a pelagic larval phase which may connect spatially discrete populations (Sale, 1980, Doherty et al., 1995). However, recent studies suggest many larvae settle on home reefs (Jones et al., 1999, Swearer et al., 1999, Taylor and

Hellberg, 2003, Jones et al., 2005, Almany et al., 2007a, Froukh and Kochzius, 2007, Gerlach et al., 2007). In addition, while many adult fishes may regularly migrate among adjacent reefs (Reese, 1989, Chapman and Kramer, 2000, Kaunda-Arara and Rose, 2004, Meyer and Holland, 2005, Starr et al., 2007), the integrity of populations may be maintained if they return to home reefs on a routine basis. The ability to home may depend on whether fish need to follow paths within reefs or can return home though open water environments. Homing may increase the effectiveness of local management practices such as no-take marine protected areas. On the other hand, increased fragmentation due to habitat disturbances such as climate induced coral bleaching (Hoegh-Guldberg, 1999, Sheppard, 2003, Donner et al., 2005) may impact on the ability of migratory fishes to find home sites.

The aim of my study was to document the extent of site fidelity and homing ability in a guild of coral-dwelling cardinalfishes (Family: Apogonidae). Many apogonids species migrate between nocturnal feeding grounds and diurnal refuge sites (Greenfield and Johnson, 1990, Marnane and Bellwood, 2002). Single- and multi-species groups persist on individual coral colonies, while other similar corals can remain vacant. Fidelity and homing behaviour of several species to specific refuge sites have been demonstrated within a large lagoonal area on the Great Barrier Reef using displacement experiments (Marnane 2000). However, in mosaic reef environments, the relative ability of apogonids to home within and among isolated reef habitats has not been investigated. Common Indo-Pacific cardinalfish species show strong reliance on one branching coral species as refuge habitat (Chapter 2). While the biodiversity of reef fishes is declining due to degradation of such habitats (Jones et al., 2004, Wilson et al., 2006, Munday et al., 2008, Pratchett et al., 2008b), here I assess whether or not site fidelity and homing may contribute to the vulnerability to habitat loss. In the first part of the study, site fidelity is examined by tagging individuals at diurnal resting sites and recording the movement of individuals amongst adjacent resting sites. This is followed by displacement experiments that investigate: (1) the relative abilities of different species to home over similar distances within and among isolated reef platforms and (2) the distances over which homing can occur.

5.3. Methods

5.3.1. Study site and species

This study was conducted on fringing and inshore platform reef slopes in eastern Kimbe Bay, PNG (5°30′S; 150°05′ E; Fig 5.1), near the Mahonia Na Dari Research and Conservation Centre. Reefs in this area are separated by 0.2-1km of open water with slopes rising steeply from depths of 30 to 60m (Jones et al., 2004, Srinivasan and Jones, 2006). Cardinalfish numbers are most abundant in patchy coral reef habitats on the leeward slopes, where coral bommies are interspersed with areas of rubble and sand. Site fidelity and homing studies were conducted in 3 to 15m depth, below which the study species and branching coral habitats were rarely found.

Four species of cardinalfish common in the shallow reef areas were chosen for tagging observations and displacement experiments: *Archamia zosterophora, Zoramia fragilis, Cheilodipterus artus* and *C. quinquelineatus*. Of the more than 36 species known from this location, these four were the most abundant and most widely distributed among individual reefs. Each species exhibits a strong diurnal habitat preference for the branching coral species *Porites cylindrica* (Chapters 2 and 4), itself relatively abundant on leeward slopes. Fish used were 30 to 60mm in standard length. Fish were captured using clove oil based anesthetic (Munday and Wilson, 1997), small hand nets and/or a Bincke net (Anderson and Carr, 1998). Fish were tagged using various colour combinations of fluorescent elastomere (VIE-NorthWest Marine Technology) inserted into dorsal and/or caudal musculature.
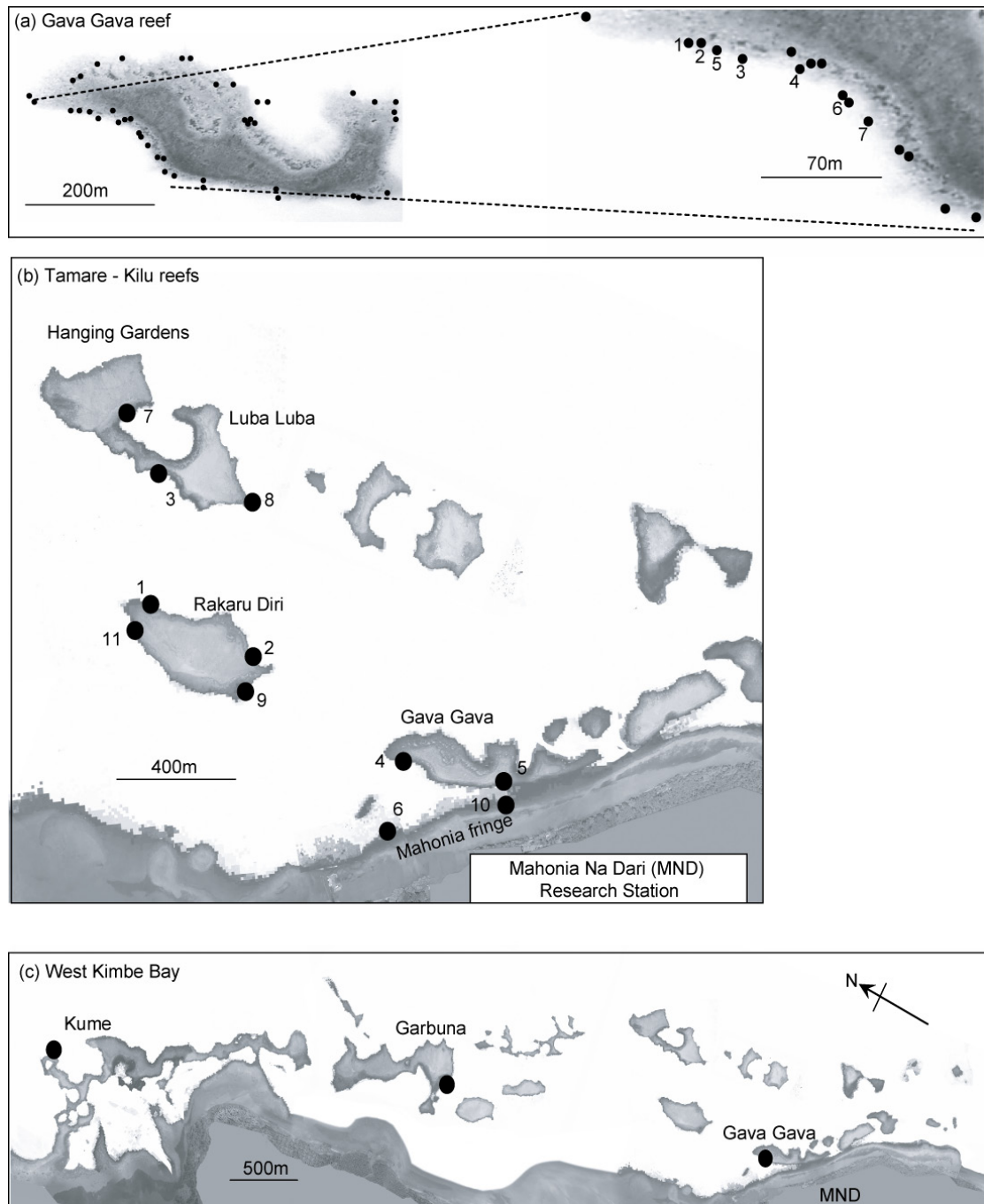
Figure 5.1

The inshore reef areas used to study cardinalfish site fidelity and homing behaviour within Kimbe Bay, Papua New Guinea. Particular reef areas were used to assess (a) fidelity to coral bommies, (b) homing behaviour amongst and within reefs and (c) long distance homing behaviour. (a) Closed circles indicate coral colonies used as diurnal refuge sites by cardinalfish. Numbers 1-7 indicate 'home' coral colonies of tagged individuals (3-4 home sites were used per species; some sites contained more than one species). Rope grids were placed above corals 1-4 to measure fidelity to refuge areas within colonies. (b) Numbers indicate 3 replicate control (C) sites for four species and corresponding within-reef (WR) and inter-reef (IR) displacement locations. *Archamia zosterophora* & *Zoramia fragilis*; C = 1-4-7, WR = 2-5-8, IR = 3-6-1. *Cheilodipterus artus*; C = 9-4-7, WR = 1-5-8, IR = 3-6-1. *C. quinquelineatus*; C = 5-10-11, WR = 4-6-2, IR = 6-4-3. (c) Three reef locations indicate home site (Gava Gava) of tagged *A. zosterophora* individuals and displacement locations 2km (Garbuna) and 5km (Kume) away.

5.3.2. Site fidelity: tagging observations

5.3.2.1. Fidelity to coral bommies

I investigated 'natural' patterns of fidelity to particular coral colonies and/or movement among adjacent corals using a mark-resight study. Individuals of the four cardinalfish species were tagged in November 2007 on the back reef slope at Gava Gava reef (Fig. 5.1a). Comprehensive visual surveys of all coral bommies identified all diurnal refuge sites of cardinalfish. The majority were located at the north-western end of the reef in a slope area extending about 200m in width and 3 to 15m in depth. Four sites with aggregations of *A. zosterophora* and *Z. fragilis* and three sites with *C. artus* and *C. quinquelineatus* aggregations were selected and 10 to 16 individuals per site and species were tagged. Only three aggregations of adult *C. quinquelineatus* and *C. artus* existed in this study area. Fish were uniquely tagged using a combination of five tag colours and five body positions. All fish were given a minimum 30 minute recovery period prior to release at capture sites.

Daily surveys of focal aggregations were carried out over a 10 day period and all resightings of tagged individuals were recorded. An additional survey was carried out three months later to examine longer-term site fidelity. These surveys included all known refuge sites of the focal cardinalfish and other suitable refugia (branching corals and large crevices) within the fore-mentioned 200m strip of reef slope. Alternative suitable refugia on Gava Gava reef were considerable distances (> 100m) from this area. Reef-wide surveys were carried out at the end of the initial monitoring period and repeated three months later, in order to find fish moving longer distances. To check for possible inter-reef movement, a 400m wide area of the fringing reef adjacent to Gava Gava was monitored (Fig. 5.1a).

Each survey recorded individual tagged fish as (1) at home, (2) relocated - in a neighboring colony or (3) missing - not found in the reef area. Species were not always surveyed on the same days, hence time was categorised into day 1, day 2, days 4-6, days 7-9 and 3 months. For each response category (home, relocated or missing) the proportional response of species across time was compared with a two-way fixed factor ANOVA. Proportional data was arcsine transformed to improve normality and heterogeneity of variances, as assessed with residual plots and Cochran's C test. Site data were pooled to compare each species' frequency of movement between coral colonies and range of distances moved.

5.3.2.2. Fidelity to positions within coral bommies

I hypothesised that species with high fidelity to specific coral colonies may also show fidelity to positions within the refuge. In order to investigate this four coral colonies with large cardinalfish aggregations (particularly of *A. zosterophora*) were selected as study sites (Fig. 5.1a). Rope grids with 20 × 20cm squares were constructed approximately 50cm above each of the four coral colonies and positions of resident tagged fish grid referenced. Rope grids (3mm rope diameter) did not appear to constrict movement of fish within and around the coral colonies. Tagging and monitoring of individuals took place in association with the previous site fidelity study, using the same 10 to 16 tagged individuals. Fish positions were recorded six times over a period of ten days. Within coral positions were only assessed for individuals seen in 'home' coral colonies four or more times and that had not been sighted in neighboring corals.

For each resident individual (i), I calculated the total grid area used over ten days (q), site specific coral surface area (r = maximum width × perpendicular length), and converted this to the proportional surface area used (p), where:

$$p_i = q \, / \, r$$

Only one species (*A. zosterophora*) had sufficient abundance of resident individuals for among site comparisons of colony area used. Differences in the mean proportional area used amongst sites were checked for *A. zosterophora* with one-way ANOVA. Area was arcsine transformed to meet normality & heterogeneity assumptions. Results for other species were pooled across sites.

The amount of colony surface area utilised by 40 tagged *A. zosterophora* individuals was compared to a random expectation of area used. Random grid coordinates for 1000 fish with five repeat sightings each were created for each of the four coral colonies. Minimum convex polygons (MCPs) of utilised grid areas were then constructed for each actual and hypothesised individual. Observed and expected MCP areas were statistically compared for each colony using a two-sided t-test with separate variances. MCP area was log transformed to meet homogeneity of variance assumptions. MCPs were constructed using ArcGIS 9.3 and Hawth's tools for animal movement (Beyer, 2004).

5.3.3. Homing behaviour

Displacement experiments were conducted at two spatial scales, <500 m and 2-5 km, to assess the ability of cardinalfish to home within and among reefs and to home over different distances.

5.3.3.1. Experiment 1: Within versus among reefs

Here I tested the hypothesis that cardinalfish homing behaviour will be more successful for individuals traversing continuous reef than those returning from neighboring reefs across deep open-water channels. Visual surveys of reef slope areas identified three suitable diurnal refuge sites per species which were used for homing behaviour experiments (Fig. 5.1b). These, termed 'home' sites, consisted of one to three *P. cylindrica* coral colonies in close proximity with high conspecific abundance (> 100 fish). Independence of replicates was maintained by using home sites either on different reefs or more than 250m apart on continuous reefs. For each home site, two displacement locations approximately 400m away were designated as (1) the 'within reef' (WR) and (2) 'inter-reef' (IR) displacement sites. These locations differed in the type of environment homing fish would need to traverse, being either over continuous reef habitat (WR) or across open water (IR). Displacement sites were also chosen so as to vary the direction of displacement among replicates.

At each of the species' three replicate home sites approximately 60 conspecific adults were caught, tagged and displaced. Individuals were randomly assigned to one of three groups; (1) control, (2) within reef displacement or (3) inter-reef displacement. Each group had approximately 20 individuals. Groups were identified using unique tag color combinations. Fish were transported by boat to displacement locations. Fish were captured, tagged and transported by day (08:00-17:00) and released from temporary holding containers after dusk (18:30-20:00). Control groups underwent the same transport and holding conditions but were released at the capture site. Pre-release mortalities due to tagging and transport conditions were minimal and excluded from analyses. The number of tagged fish found at home sites was recorded for seven days post-displacement. Pilot studies indicated decrease rather than increase in tagged fish counts after this period (see also Marnane 2000). Monitoring included visual surveys of reef area within 100 m of each home site. In addition, the displacement site and surrounding reef area (to within 100 m) were surveyed the morning after displacement. The mean proportion of tagged fish 'homing' to capture sites was compared amongst species and displacement locations using a two-way fixed factor ANOVA. Normality and homogeneity of variances were verified using Levene's test and residual plots. Post-hoc comparisons were conducted with Tukeys Honestly Significant Difference (HSD) tests.

5.3.3.2. Experiment 2: Long distance homing

Long distance homing capacity of a single species *A. zosterophora* was assessed by a 2km displacement and a 5km displacement from one home site (Fig. 5.1b). 30 fish per distance were captured, tagged and displaced following the above methods and released at displacement

locations immediately. The presence of returning fish at home coral colonies was monitored for the next 26 days. Given the distance and open-water crossings required, no returns were expected.

5.4. Results

5.4.1. Site fidelity

5.4.1.1. Home coral bommies

The four different cardinalfish species differed in their fidelity to particular coral colonies over the ten days of observation (Fig. 5.2). *A. zosterophora* and *C. quinquelineatus* displayed strong fidelity to specific home coral colonies, with 50 to 75% of individuals on average remaining in capture sites (Fig. 5.2a). In contrast, *Z. fragilis* and *C. artus* displayed relatively low fidelity to capture positions. On average less than 35% of individuals stayed in the 'home' coral colony (Fig. 5.2a). Fidelity was statistically higher in *A. zosterophora* and *C. quinquelineatus* than in *Z. fragilis* and *C. artus* (Table 5.1a). The mean proportion of individuals sighted in home coral colonies did not differ during the first ten days of observation. There was however a significant decline after three months (Fig. 5.2a, Table 5.1a). Of all four species *C. quinquelineatus* individuals showed the highest long term persistence with up to 55% of individuals resighted in their original coral colony after three months.
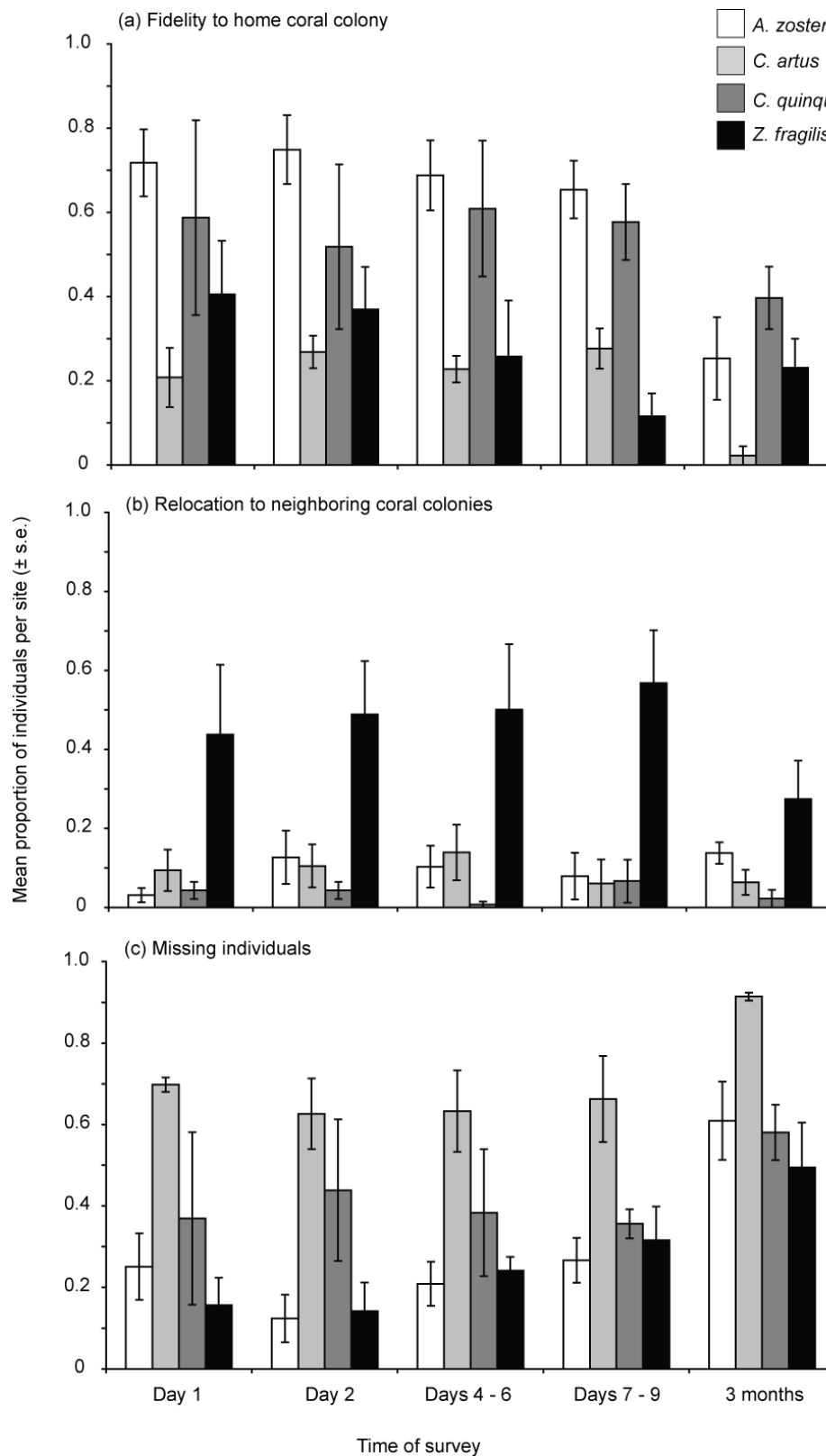
Figure 5.2

Patterns of natural fidelity and movement of four cardinalfish species amongst diurnal refuge sites (coral bommies). Observations were taken on consecutive days over a 10 day period and repeated three months later. Columns indicate the mean proportion (± s.e.) of tagged individuals sighted (a) within initial capture sites, (b) on nearby coral colonies and (c) not sighted. 10-16 individuals per species were tagged on 3-4 refuge sites per species.

Table 5.1 Statistical comparison of four cardinalfish species' fidelity and movement amongst diurnal refuge sites over a 10 day and three month period. Two-way fixed factor ANOVA results compare (a) the proportion of tagged individuals located in home coral colonies, (b) proportion of individuals located in neighbouring coral colonies, (c) proportion of missing individuals. 3-4 sites per species were included with 10-16 individuals tagged at each site. Proportional data was arcsine transformed. TUKEYS HSD post-hoc comparisons amongst species and time show statistically independent groups (A and B) for significant variables

| | Source of variation | df | MS | F | p | TUKEYS Homogenous groups | |
						A	B
(a)	Species	3	0.95	14.69	***	*A. zosterophora & C. quinquelineatus*	*C. artus & Z. fragilis*
	Time	4	0.28	4.33	**	Days 1, 2, 4-6 & 7-9	Days 7-9 & 3 months
	Species × Time	12	0.06	0.96	0.49		
	Error	48	0.07				
(b)	Species	3	1.18	19.12	***	*Z. fragilis*	*A. zosterophora, C. artus & C. quinquelineatus*
	Time	4	0.02	0.30	0.88		
	Species × Time	12	0.04	0.57	0.86		
	Error	48	0.06				
(c)	Species	3	0.86	17.51	***	*C. artus*	*A. zosterophora, C. quinquelineatus & Z. fragilis*
	Time	4	0.34	6.87	***	Days 1, 2, 4-6 & 7-9	3 months
	Species × Time	12	0.02	0.47	0.92		
	Error	48	0.05				

** $p < 0.01$, ** $p < 0.001$

The species with the highest degree of movement amongst adjacent coral colonies was *Z. fragilis*. Over the ten day period, approximately 40% of *Z. fragilis* individuals switched between colonies that hosted conspecific aggregations, four times that of other species (Fig. 5.2b, Table 5.1b). The degree of movement was quite constant within the initial monitoring period, but declined after three months as more individuals went missing from the surveyed areas.

For each species, individuals that moved amongst coral colonies predominantly only changed refuge sites once and most relocated to colonies less than 15m away (Table 5.2). In terms of the maximum distance moved on a daily basis, *A. zosterophora* and *Z. fragilis* were both found on corals up to 100m away. This was despite clear differences in their strength of fidelity to the capture location. Reef wide surveys of cardinalfish aggregations, conducted after the ten day monitoring period, found only one tagged fish (*A. zosterophora*) outside of the study area, 157m from its capture site. No tagged individuals were located on the neighboring fringing reef, despite the presence of conspecific aggregations.

Table 5.2 The distance and frequency of inter-bommie movement by cardinalfish that used different diurnal refugia (neighbouring coral colonies). N is the total number of individuals that moved from their original colony between monitoring periods. The frequency of inter-bommie movement refers to the proportion of individuals switching between diurnal refuges either once, twice or three times over a 10 day period.

		Distances moved		Frequency (%) of Inter-bommie movements		
Species	N	Range	Mode	1	2	3
Z. fragilis	24	13-102m	13m	67	17	17
A. zosterophora	11	3-102m	7.6m	82	18	0
C. artus	9	4-72m	12m	44	44	11
C. quinquelineatus	2	6-8m	7m	0	100	0

The proportion of missing fish also differed amongst species. The difference was driven by 55-80% disappearance of *C. artus* individuals over the initial ten days (Fig. 5.2c, Table 5.1c). After three months the few *C. artus* individuals that had initially stayed at their capture locations were also missing, raising the species disappearance level to 95%. The proportion of missing individuals for other cardinalfish species was relatively steady over the initial ten days (~ 30%) but increased to approximately 50% after three months (Fig. 5.2c).

5.4.1.2. Positions within corals

In addition to high fidelity to home coral colonies, *A. zosterophora* also showed fidelity to narrow areas within colonies. In total 39 *A. zosterophora* individuals were repeatedly observed (four to seven times) in their 'home' coral colonies. Of these, 72% remained within in a 60 × 40cm grid area, equivalent to using less than 8% of the available coral surface area (Table 5.3). Three individuals remained in a single grid area (0.04m^2) over the ten day study period. Three months later, five remaining resident individuals were still within 40 to 60cm of previous positions. On average only 10% of the colony area was used by *A. zosterophora* individuals. The proportional area occupied did not differ amongst the four coral colonies (1-way ANOVA; F_3 = 1.58, p = 0.22).

This small proportion of colony surface area used by *A. zosterophora* individuals was significantly narrower than that expected from random use of available colony positions (t = - 18.45, d.f. = 38.5, p < 0.001). The average MCP area of observed individuals was 10 to 20 times smaller than that of random expectations.

C. quinquelineatus individuals displayed a similar level of fidelity to positions within coral colonies. In total 17 individuals were determined to be 'residents' in three of the four gridded coral colonies. Of these 52% were consistently sighted within 40 to 60cm of original positions and three remained within 20 to 40cm (Table 5.3). On average *C. quinquelineatus* individuals used 7% of the available colony surface area. Only six *Z. fragilis* and seven *C. artus* individuals remained consistently in the gridded coral sites. This low sample number excluded a statistical comparison of positional fidelity amongst all four cardinalfish species. However, resident *C. artus* individuals do appear to move within their coral colonies at least twice as much as other species. The resident *C. artus* individuals used 24.5% of the colony surface area whilst other species used less than 10%, on average (Table 5.3).

Table 5.3 Fidelity of tagged cardinalfish individuals to positions within coral colonies. High fidelity is indicated when species only use a small proportion of the available colony surface area. 'N resident fish' refers to the number of individuals repeatedly sighted in the home coral colony at least 3 times over a 10 day period and were not seen in alternate refugia. Coral colony ID refers to colonies identified in Fig. 5.1(a).

Species	Coral Colony	Colony surface area (m^2)	N resident fish	Frequency of surface area (m^2) used (number of individuals)					Mean % surface area utilised (± s.e.)
				0.04	0.16	0.32	0.64	>0.64	
A. zosterophora	1	6.480	8	0	3	1	0	4	9.5 (3.1)
	2	3.895	10	2	3	2	0	3	8.0 (2.5)
	3	2.512	12	1	9	1	0	1	8.7 (2.6)
	4	2.497	9	0	4	2	2	1	13.7 (3.4)
	Total		*39*	*3*	*19*	*6*	*2*	*9*	*9.9 (1.5)*
C. quinquelineatus	1	6.480	4	0	1	2	1	0	4.6 (1.4)
	2	3.895	9	0	5	1	3	0	7.5 (2.1)
	3	2.512	4	0	0	0	0	4	7.16 (1.5)
	Total		*17*	*0*	*6*	*3*	*4*	*4*	*6.8 (1.2)*
C. artus	*Total*		*8*	*0*	*0*	*1*	*2*	*5*	*24.5 (4.4)*
Z. fragilis	*Total*		*7*	*0*	*3*	*1*	*1*	*2*	*6.2 (1.7)*

5.4.2. Displacement experiments

5.4.2.1. Within and among adjacent reefs (< 500 m)

All five cardinalfish species displayed homing ability across both continuous reef and open-water environments (Fig 5.3a). On average 20 to 80% of displaced individuals returned to 'home' coral colonies, with up to 100% in several replicates. Homing behaviour occurred quickly. For most species two thirds of the individuals that returned from inter-reef displacements did so in the first evening. Homing success did not differ significantly between the two displacement locations, but control numbers were consistently higher than inter-reef returns (Table 5.4).

Inter-specific differences in homing strength occurred independently of displacement locations (Table 5.4a). *A. zosterophora* displayed the strongest homing success with more than 75% of individuals returning to capture sites. The proportion homing was approximately 30% greater than that of *C. quinquelineatus* (Table 5.4b). *C. quinquelineatus* had the weakest homing performance with only a 20% average return rate for groups displaced across open water environments and 45% for those displaced along the continuous reef (Fig. 5.3a).

The majority of displaced *C quinquelineatus* individuals that did not return home set up residence in the area they were displaced to. Post displacement surveys located 20 to 50% of tagged *C. quinquelineatus* individuals near displacement sites, the morning after relocation (Fig. 5.3b). In contrast, relocation of other species in displacement sites was rare and correlates to their higher return rates (Fig. 5.3a). Displaced individuals were typically found scattered amongst conspecific aggregations in branching corals. Ad-hoc surveys of inter-reef displacement locations (two to eight days later) found that 60 to 80% of the initially relocated *C. quinquelineatus* individuals had persisted in their new refuge positions.
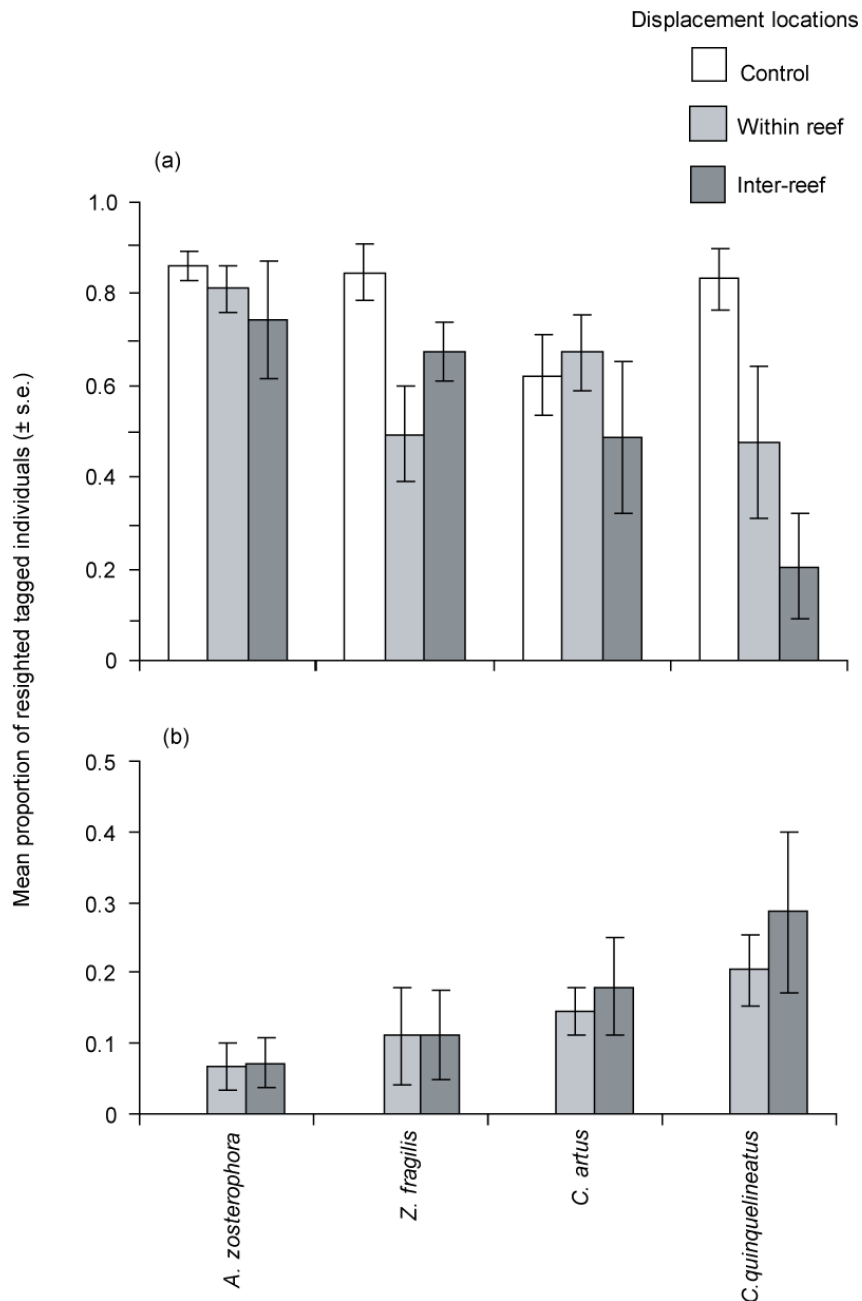
Figure 5.3
Strength of homing behaviour by four cardinalfish species displaced approximately 400m within and between reefs (inter-reef displacement). (a) The mean proportion of tagged individuals that returned to capture locations within seven days. Approximately 20 fish per treatment group and species were tagged and released. (b) The mean proportion of tagged fish resighted at displacement locations the morning after release.

Table 5.4 Statistical comparison of homing success amongst four cardinalfish species and 3 displacement locations (control, within reef and inter-reef). Results are shown for (a) Two-way fixed factor ANOVA testing differences in the proportion of tagged fish returning home and (b) Tukey's HSD post-hoc comparison amongst species and locations. Post-hoc comparisons amongst species pairs are only shown where significant.

(a)	Source of variation	*df*	MS	F	*p*	
	Species	3	0.147	4.631	*	
	Displacement location	2	0.217	6.845	**	
	Species × displacement	6	0.069	2.209	0.077	
	Error	24	0.032			

(b)	Source of Variation	Paired comparisons		mean difference	*p*
	Species	*C. quinquelineatus*	*A. zosterophora*	- 0.301	**
	Displacement location	Control	Within-reef	0.177	0.056
			Inter-reef	0.264	**
		Within-reef	Inter-reef	-0.086	0.473

* *p* < 0.05, ** *p* < 0.01

5.4.2.2. Among distant reefs (2 and 5km)

Archamia zosterophora demonstrated the capacity to 'home' to specific coral refugia from displacements 2 and 5km away. Thirty six percent of individuals displaced 2km returned to the capture site within 11 days. One individual returned in the first evening and five more in the second evening. One individual from the 5km displacement returned home sometime between 8 and 11 days. No further returns from this distance were observed.

5.5. Discussion

This study found for the first time that cardinalfish show strong site fidelity and they are capable of homing over long distances across open water habitats. Despite a seeming plethora of vacant refuge sites, approximately two thirds of aggregating *A. zosterophora* and *C. quinquelineatus* individuals return daily to their 'home' *Porites cylindrica* resting site, demonstrating strong site fidelity. In addition, the majority of individuals of *A. zosterophora* return to the same resting positions within home coral colonies. The degree of fidelity varies among species. A third cardinalfish species, *Z. fragilis,* appears to regularly alternate between adjacent coral colonies. When experimentally displaced, cardinalfish return overnight to capture sites, homing along both continuous reef areas and deep open water channels. One species is capable of homing across multiple reef-scapes from both two and five km away. Hence, despite

nocturnal foraging migrations, site fidelity and homing are likely to contribute to sustaining the integrity of populations on different reefs and in specific refuge areas within these reefs. The homing tendency may increase susceptibility to local disturbances and constrain the ability of individuals to emigrate to intact habitats.

The results of my study corroborate similar work on cardinalfish from higher latitude populations (Marnane 2000). Most striking is the similarity in the speed and strength of homing capacity with both studies recording overnight returns from displacements up to 2km away. For the species common to both studies, *C. quinquelineatus* and *C. artus,* the return rates for fish homing over shallow continuous reef environments (lagoon and reef slope) were quite similar averaging 50-65% and 60-80% for *C. quinquelineatus* and *C. artus* respectively. The success of homing behaviour across deep open water channels, shown here for multiple species, illustrates the capacity of cardinalfish to navigate through a mosaic of reef environments from both short (500m) and long (2-5km) distances and within a few days.

Marnane (2000) reported high fidelity of three cardinalfish species to initial resting locations on the southern Great Barrier Reef (GBR), Australia. I expand on this information to demonstrate that the degree of fidelity is species-specific. Two of this study's species showed very strong fidelity to refuge sites, even to positions within coral colonies, while a third moved between resting sites. For the cardinalfish species common to both studies, several patterns are apparent. Firstly, *C. quinquelineatus* has high short term (9 to 10 days) fidelity to diurnal resting locations. However, long term fidelity results differ. In Kimbe Bay, the persistence of tagged individuals at resting sites after 3 months (40% of individuals) is two times lower than those on the southern GBR (75% of individuals after four months; Marnane 2000). This contrast probably reflects natural survivorship and/or life-history differences between locations rather than fidelity or movement. In Kimbe Bay only the proportion of *C. quinquelineatus* individuals missing from the study area increased with time and not the rate of relocation to adjacent colonies. For *C. artus*, short term site fidelity appears to differ between Kimbe Bay and southern GBR locations. In Kimbe Bay, few individuals returned to their original resting places while southern GBR individuals have high fidelity. Results for *C. artus* in Kimbe Bay are probably affected by high mortality of tagged individuals rather than high natural movement. Mortality of *C. artus* individuals in the homing experiment was quite high (averaging 30% for control groups) suggesting the species was susceptible to handling. The strength of homing behaviour for *C. artus* individuals in Kimbe Bay suggests they do have strong site fidelity, similar to that observed on the GBR.

Strong site fidelity was demonstrated, not only to home reefs, but to specific coral colonies within reefs and for some species to positions within these corals. The benefits of such strong site specificity include familiarity with both the spatial environment and with neighboring individuals. In high predation environments, occupying sites where escape routes are familiar can dramatically improve survivorship (Lopez et al., 2000, Yoder et al., 2004). This could be a key strategy for small coral reef fish whose distribution and abundance is strongly affected by predation (Hixon, 1991). However, the degree of site fidelity individuals have is typically strongly affected by their reproductive history at that location (Switzer, 1993). Given the apparent equality of 'nesting' habitats in this study (i.e., *P. cylindrica* coral colonies), the use of particular sites may be driven by the predictability of relocating mates. Mate reunion may have been the motivation for the individual that homed five kilometers in this study, which was seen in a strong pair association for at least 16 days afterward. Site fidelity benefits to reproductive output will be particularly important for short-lived species like cardinalfish (Marnane, 2001). Investigating the links between predation and reproductive output will be key to understanding the mechanisms and benefits of site fidelity in small reef fish species.

The sensory mechanisms used by cardinalfish to find home sites are not known. Three possible information sources direct animal homing; sensory, memory-based and genetic (Jander, 1975, Papi, 1990). Sensory and memory-based cues are learned or imprinted preferences while genetic sources are innate. The contribution of these cues in maintaining site fidelity and directing homing of small reef fish is predominantly unknown. Use of olfaction by larvae and adults in discrimination between reefs and suitable micro-habitat types and locations has been demonstrated in several reef fish groups, including cardinalfish (Sweatman, 1988, Arvedlund et al., 1999, Atema et al., 2002, Lecchini, 2004, Døving et al., 2006, Gerlach et al., 2007, Dixson et al., 2008). Spatial memory is important in directing migrations of larger reef fish (Helfman et al., 1982, Reese, 1989, Mazeroll and Montgomery, 1998) and may assist smaller species moving between neighboring coral colonies. Both olfaction and spatial memory cues are of likely importance in discrimination amongst coral colonies or home range territories within narrow reef areas (e.g., the 200m wide reef slope area studied here). However, the passage of site-specific signals or knowledge of routes to reefs greater than 2km away, across multiple reef areas seems unlikely. Directional information at this level may be contributed to by magnetic cues as known in several other marine species (Klimley, 1993, Walker et al., 1997, Lohmann et al., 2008).

Site fidelity and homing behaviour of cardinalfish has direct implications for the guild's vulnerability to habitat loss. Fragmentation of reef habitats is predicted to increase, with some reef areas, coral species and colonies likely to suffer greater disturbance than others (Jones and

Syms, 1998, Loya et al., 2001, Graham et al., 2006, Madin et al., 2008). Coral reef fish species with strong fidelity to particular coral colonies (e.g., *A. zosterophora*) will be more vulnerable to loss of these home sites than species that already move between adjacent colonies (e.g., *Z. fragilis*). With a greater flexibility in site use the latter species are theoretically better adapted to any increased fragmentation of refuge sites. The anomaly to this pattern, as observed in the current study, is species like that of *C. quinquelineatus*, with strong site fidelity but weaker homing behaviour. The degree of fidelity predicts a vulnerability to the loss of home sites. However, the persistence of tagged individuals in displacement locations indicates that *C. quinquelineatus* may have an adaptive capacity to set up residence in a new refuge area should it be forced to relocate. Testing a species' degree of vulnerability to habitat loss and fragmentation will require experimental disturbance of home sites and tracking of the displaced fish.

The extreme degree of site specificity and homing behaviour demonstrated here by coral reef fish has important implications for local level management of coral reef systems. The constrained movement of individuals among neighboring habitat patches, despite their physical capacity to move long distances, serves to concentrate populations in specific locations. Determining the degree of site fidelity and homing in other common reef fish groups will help identify the key species and locations most vulnerable to habitat loss. Future research should focus on the behavioural response of these reef fish to degradation of home locations, exploring behavioural adaptations to habitat loss. Populations of coral reef fish with reliance on specific locations and habitat types are of particular concern.

CHAPTER 6: Can strongly site-attached coral reef fish relocate in response to habitat loss? An experimental analysis.

6.1. Abstract

The strength of site fidelity will determine many species response to habitat disturbance, particularly the loss of 'home' sites. Many coral reef fishes migrate between specific foraging, resting and spawning locations, but the degree to which they rely on these sites is unknown. This chapter investigates the extent to which two homing coral reef cardinalfish species are reliant on home resting sites or have the ability to relocate following a local disturbance. Home coral heads were experimentally disturbed by draping them in netting to exclude cardinalfish access for 10 days. Patterns of site fidelity and relocation of tagged individuals was compared with controls, before and after the disturbance. Most individuals remained faithful to home sites prior to the manipulation and on control sites throughout the experiment. However, when access to home sites was blocked, individuals either died (40%) or emigrated to nearby aggregation sites (50%). Most individuals resisted moving from the home site for more than 4 days, before emigrating. Many of these individuals subsequently remained faithful to a new site (56%), but a quarter returned to the home location after access was restored. Results suggest association with home sites is based on a strong tradition and while some can relocate to new homes, increased mortality may result. If traditional aggregation sites are permanently lost, long-term population decline is predicted.

6.2. Introduction

Many mobile animals exhibit strong site fidelity or a prolonged association with particular locations (Switzer, 1993, Dingle, 1996, Mettke-Hofmann and Gwinner, 2003). These may function as resting or roosting sites (Lewis, 1995, Grether and Switzer, 2000), foraging areas (Irons, 1998, Buzby and Deegan, 2000, Mettke-Hofmann and Gwinner, 2003), mating or nesting sites (Greenwood and Harvey, 1982, Thorrold et al., 2001, Matthiopoulos et al., 2005), refuges from competitors or predators (Yoder et al., 2004, McDougall and Kramer, 2007) or a combination of these factors. Given that different sites vary in the quality of the resources they provide, site fidelity may reflect local habitat selection by individuals for the best quality sites (van Bergen et al., 2004, Mabry and Stamps, 2008). In social animals, group site fidelity may arise as a result of copying behaviour and result in traditional site use (Stamps, 1987). In

general the relative importance of habitat and tradition in explaining long-term site fidelity in social animals is not well understood. Traditional mechanisms of site use may be favoured in stable environments but could be disadvantageous in disturbed or fluctuating environments (Switzer, 1993, Galef and Laland, 2005). The best individual strategy may be for individuals to be flexible and maintain the ability to use a combination of habitat or social cues and to be able to abandon traditional sites when they are no longer suitable (Laland, 2004, Galef and Laland, 2005).

Many aggregating coral reef fish species exhibit daily migrations between resting, foraging and spawning sites and despite an apparent abundance of potential sites, individuals exhibit strong fidelity to particular locations (Sale, 1971, Ogden and Buckman, 1973, Beets and Hixon, 1994, Chapman and Kramer, 2000, Marnane, 2000, Wall and Herler, 2009). Numerous studies have shown that reef fish can make preferences based on a range of features of the habitat (Roberts and Ormond, 1987, Jones, 1988, Tolimieri, 1995, Steele, 1999, Gladstone, 2007, Kane et al., 2009), competitors or predators (Öhman et al., 1998, Schofield, 2003, Dixson et al., 2010) and mate characteristics (Itzkowitz et al., 1998, Warner and Dill, 2000, Haley et al., 2004). However, it is not known whether these factors explain persistent aggregations of fish at particular resting, foraging or spawning locations. To date, only two studies have investigated the potential for traditional behaviour to explain site choices in reef fish. Helfman and Shultz (1984) found that naïve French grunt individuals (*Haemulon flavolineatum*) learn migration routes and aggregation sites from other individuals. Warner (1987, 1988, 1990a, b) showed that spawning sites chosen by female *Thalassoma bifasciatium* on particular reefs were traditional sites. When he replaced the entire female population, new traditional sites were established that persisted over time. Despite the prevalence of species exhibiting site fidelity, little work has been done investigating the relative importance of different underlying mechanisms and implications of this behaviour.

Given the increasing degradation and fragmentation of coral reef habitats, understanding the basis and implications of site fidelity in coral reef fishes is of particular importance (Pandolfi et al., 2003, Hoegh-Guldberg, 2004, Graham et al., 2006, Wilson et al., 2006). The response of aggregating reef fish to habitat loss will be affected by the flexibility of their site fidelity. At one extreme, individuals may have an essentially obligate association with home sites, as a result of an entrenched reliance on a single shelter site and they may not be able to relocate. Alternatively, they may readily move to alternate sites and new traditional sites may be established as a result of copying behaviour (Stamps, 1987, 1988, Laland and Williams, 1997). The use of both habitat and social cues is not mutually exclusive in these alternate scenarios.

However, the strength of site fidelity or the ability to relocate is critical to understanding the impact of habitat change.

Recent progress has been made towards understanding site fidelity in the common coral reef fish family - the cardinalfish (family Apogonidae). These are nocturnal planktivores that migrate daily between foraging areas and diurnal resting sites (Hobson, 1965, Marnane and Bellwood, 2002). On Indo-pacific coral reefs, cardinalfish are abundant on inshore and sheltered reef areas (Marnane and Bellwood, 2002) where they are most often found resting in large groups on colonies of one branching coral species *Porites cylindrica* (Chapters 2 and 3). However, only a small proportion of *P. cylindrica* coral heads are occupied by cardinalfish and many apparently suitable resting sites are left unused (Chapter 3). After foraging at night, most individuals home to specific resting sites and they can return to these sites when displaced considerable distances (Chapter 5, Marnane, 2000). Clearly, there is the potential for both social traditions and habitat cues to explain the persistent use of particular resting sites (Chapter 4). However, whether cardinalfish have an obligate dependence on particular sites or whether they can shift their allegiance to new sites in a changing environment have not been tested.

This study tests the mechanisms and implications of site fidelity for two homing cardinalfish species, *Archamia zosterophora* and *Zoramia fragilis*. I employed a small-scale habitat disturbance experiment to assess the strength of species' site fidelity with particular resting sites. That is, to determine whether they have obligate associations with particular home sites, or the ability to relocate and establish new home sites. Obligate associations may arise as a result of strong preferences for a habitat site, whereas successful relocation may rely on using social cues from nearby conspecifics. However, it was recognised that choices based on habitat or social cues are not mutually exclusive and a range of outcomes were possible: (a) all individuals would remain at the disturbed home site until they eventually disappear; (b) all individuals could immediately relocate to nearby alternate refugia; or (c) relocation may occur gradually, with some individuals successfully re-establishing and others not. To determine if copying behaviour is important in locating and establishing a new home, I investigated whether relocation was related to the number or proximity of nearby conspecific aggregations or the physical attributes of the corals.

6.3. Methods

6.3.1. Study site and species

Experimental work was carried out on shallow near-shore reef slopes of Kimbe Bay, Papua New Guinea in February - July 2007 (Fig. 6.1a). Preliminary surveys identified locations of cardinalfish aggregations on reefs near Mahonia Na Dari Research Station. Based on patterns of local abundance, the two most common cardinalfish species on these reefs were selected as study species: *Archamia zosterophora* and *Zoramia fragilis*. Cardinalfish aggregations on these reefs were primarily found on branching *Porites cylindrica* coral colonies, larger than 1m^2 in surface area (Chapter 3). Ten *P. cylindrica* colonies hosting > 100 *A. zosterophora* and *Z. fragilis* individuals were selected as study sites and henceforth termed 'home' sites (Fig. 6.1b). *A. zosterophora* and *Z. fragilis* co-occurred in large numbers on coral colonies, such that the same home sites were used. The ten sites were located either on separate reefs, or separated by more than 150m of sand and rubble dominated slopes. Five sites were haphazardly designated as treatment sites and five as control sites. Based on earlier monitoring of cardinalfish movement patterns (Chapter 5), fish movement between study sites was considered highly improbable.

6.3.2. Experimental design and analyses

An experiment was designed to test whether disturbing a home site would result in an increased frequency of relocation to other nearby resting sites, compared with the movement of individuals away from undisturbed resting sites. The disturbance involved covering coral colonies with nets for 10 days which prevented fish using their normal refuge spaces. The presence of tagged fish at and around each home site was monitored 10 days before the disturbance and during the disturbance period. At the end of the disturbance period access to the original home sites was restored to test whether individuals would return to the home coral colony or remain in the coral colony into which they had moved during the disturbance period. Fish were deemed to have relocated or changed home sites when they were sighted using an alternate resting location at least once and did not return to the home site during that monitoring period.

Prior to the experiment, at each site, 50-80 individuals per species were captured using clove oil (Munday and Wilson, 1997), hand nets and a Bincke net (Anderson and Carr, 1998). Only adult fish, with standard lengths of 25-60mm were used. Each individual received a unique identification mark based on the body position and colour of two elastomere tags. Monitoring of tagged fish began at least 48 hours after tagging to minimise the influence of handling and

tagging-induced mortality on final results. Only fish that were observed at least twice during the 30 day survey period were included in analyses. This resulted in 30 – 70 tagged fish per species and site being used for comparative analyses of disturbance effects.
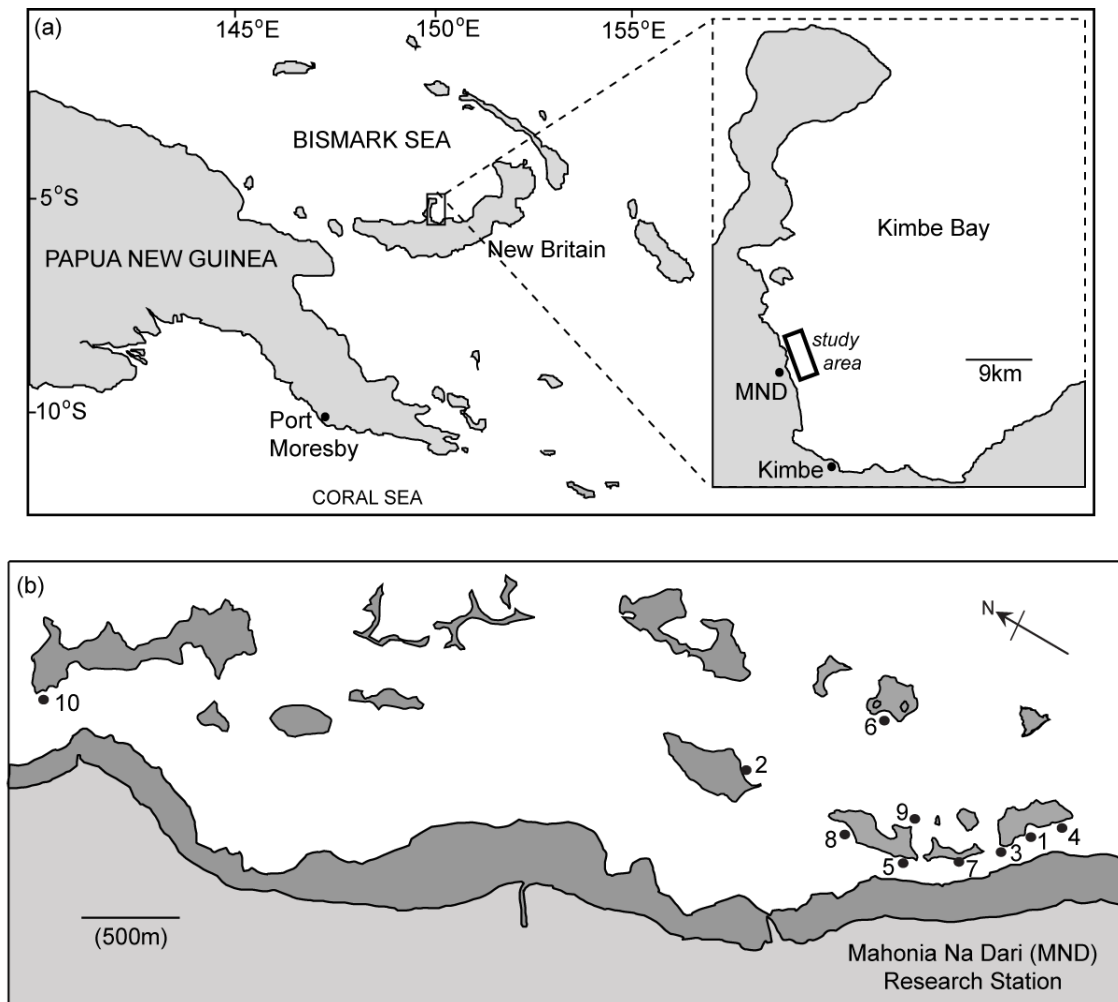
Figure 6.1. (a) Location of study area on inshore reefs near Mahonia Na Dari Conservation and Research Centre (MND), Kimbe Bay, Papua New Guinea. (b) Positions of cardinalfish 'home' aggregation sites on sheltered reef slopes. Sites 1-5 were controls and 6-10 were treatments.

Monitoring involved divers finding and counting tagged individuals in the original coral colonies (home sites) or in the surrounding reef slope areas (within 80m). Comprehensive surveys of these areas were conducted on each day of monitoring. The position of all tagged fish was recorded as (1) home, (2) relocated, or (3) missing. 'Relocated' fish were individuals seen resting in non-home branching coral colonies (typically *P. cylindrica*). Fish not seen in a survey were categorised as missing. The monitoring schedule was as follows: 10 days preceding disturbance - each control and treatment site was surveyed 3-6 times; 10 days of disturbance - control sites were surveyed 2-3 times and treatment sites were surveyed on the first and second day of disturbance and a further 2-3 times. At the end of the experiment, 2-4 more surveys per

control and treatment site were conducted, the first taking place the day after disturbance ceased. In total, study areas were surveyed over a period of 30 days.

Home site disturbance involved preventing cardinalfish accessing home coral colonies. At the end of the pre-disturbance period, in the evening, the five treatment coral colonies were covered with small 'mosquito' netting. This effectively restricted cardinalfish from sheltering within their home coral colony. Nets were placed after dusk, between 19:00 and 20:00h, when all cardinalfish had left colonies for nightly foraging. Visual checks were made to ensure no cardinalfish remained within colonies before net placement. Stakes and ropes were used to hold the netting above and around coral colonies minimising abrasion of coral tissue. Nets were removed from treatment sites after ten days.

Comparison of counts from each survey day within the pre-disturbance period typically showed minimal variation (~10%) in the numbers of fish seen at each home site (see Fig. 6.3). Records from the final day of each period were therefore deemed appropriate for comparative analyses of the overall disturbance affect (see 6.3.3 and 6.3.4 below). One treatment site (site 8) showed up to 25% differences between days but there was a consistent trend in fish movement responses. Counts from the last day were therefore still considered to be an appropriate record of fish responses for that site.

6.3.3. Natural fidelity to home sites vs. relocation

In order to determine how cardinalfish responded to habitat disturbances, it was necessary to first establish their strength of association with home resting sites (i.e., fidelity). Fidelity to home refugia before disturbances was determined by comparing the total number of individuals using the home site, neighbouring sites (i.e., relocated) and the number of missing individuals (i.e., mortality). The numbers recorded per category at the end of the pre-disturbance monitoring period were used. I compared the observed frequencies to a null hypothesis of high site fidelity in which the number of fish at home would be greater than those that either relocated or went missing (Ho: home 85% > relocated + missing 15%). equal distribution among the three responses (home, relocated or missing). Chi-square analysis compared the observed and expected response ratios on pooled 'before disturbance' data from the 10 sites. Longer term patterns in species' natural fidelity, relocation and mortality were examined over the 30 day monitoring period using the total number of fish observed in the control groups.

6.3.4. Disturbance response: fidelity vs. relocation

Following habitat disturbance cardinalfish were expected to either (a) all remain at the disturbed home site; (b) all immediately relocate to nearby alternate refugia; or (c) relocate gradually, with some individuals successfully re-establishing and others not. The disturbance response of cardinalfish was tested in several parts. Firstly, I determined whether fish would all stay at home sites or not. Secondly, I examined whether any relocation of fish was immediate or gradual. Thirdly, I examined the successfulness of relocation. To verify whether experimental disturbance altered refuge behaviour, ratios of proportional response were compared among control and treatment groups after disturbance. A lack of difference would indicate disturbance did not affect diurnal refuge use.

To determine whether fish moved or not, I compared the number of treatment fish that used home sites to those that relocated and those that were missing (presumed dead). Ultimately, if more fish relocated than remained faithful to the home site, then strong site preferences did not constrain cardinalfish response to habitat disturbance. If the frequency of fish missing was greater in treatment than control groups, habitat loss increased mortality rates. Observed frequencies were tested against the null hypothesis that response was independent of disturbance level (control and treatment). 2×3 contingency tables with log-likelihood statistics and Pearson residuals were evaluated, with responses per site pooled for each control and treatment group. Cells with large residuals indicated large deviations from the null hypothesis of independence and + or - signs indicated the direction of departure (Agresti, 1996). Location frequencies recorded on the last day of disturbance monitoring were used in the analyses. Differences in responses (3 categories) among sites were investigated with 3×5 contingency tables for each control and treatment group (5 sites each).

The speed of fish relocation following disturbance was assessed by comparing changes in fish fidelity to home colonies over the 10 day disturbance period. An immediate versus gradual movement of fish away from the home treatment sites (either by relocation or disappearance) was assessed on both pooled treatment site results and for individual sites.

6.3.5. Successfulness of relocation attempts

Successful relocation following disturbance depends on whether fish can establish new home sites. Relocation was deemed successful if a treatment individual was located in the same non-home coral colony during consecutive surveys, thereby demonstrating site fidelity to the new refuge site. To determine the overall relocation success of each cardinalfish species I examined the frequency of movement among non-home refuge sites during the disturbance period, for

treatment fish. Evaluation of movement patterns included: (a) the number of colonies used by fish in consecutive survey periods; (b) whether site fidelity to a new coral colony occurred; and, if so, (c) whether this coral colony was the first one selected or whether fish moved among several colonies before settling down. A species overall degree of relocation success was deemed higher when the frequency of movement among sites was low and fish predominantly settled in their first or second site selection. Relocation success was deemed lowest when fish were missing after emigrating from the home site or when fish repeatedly moved sites.

6.3.6. Characteristics of new home sites

The last aim of this study involved determining whether social cues and habitat preferences constrain the relocation of cardinalfish affected by habitat loss. To explore whether dispersal of displaced fish was affected by availability of social cues, the degree of fish relocation was compared to the number of conspecific aggregations in treatment study areas. Social and physical attributes of coral refugia used by displaced individuals were recorded to determine if particular attributes increased the frequency of site use and therefore relocation success. These were: the presence or absence of resident cardinalfish; colony size (volume and surface area); and proximity to the home colony. Colony volume and horizontal surface area were approximated using colony height, the maximum surface diameter, and a secondary diameter placed at right angles. Pearson correlations were used to assess relationships between fish movement, refugia availability and coral colony attributes.

6.4. Results

6.4.1. Natural fidelity to home sites and relocation

Both *A. zosterophora* and *Z. fragilis* demonstrated very strong natural fidelity to home coral colonies. On average, 80% of both species occupied their original coral colony before disturbance took place (Fig. 6.2a,b, Table 6.1). In this period, neither species had strong relocation tendencies (< 4%) and the number of missing individuals averaged 10% for *A. zosterophora* and 13% for *Z. fragilis*. The pooled frequency for each response was not significantly different to the null hypothesis of high fidelity among response categories (*A. zosterophora:* $\chi^2 = 3.628$, df = 1, $p > 0.05$. *Z. fragilis*: $\chi^2 = 0.489$, df = 1, $p > 0.05$).
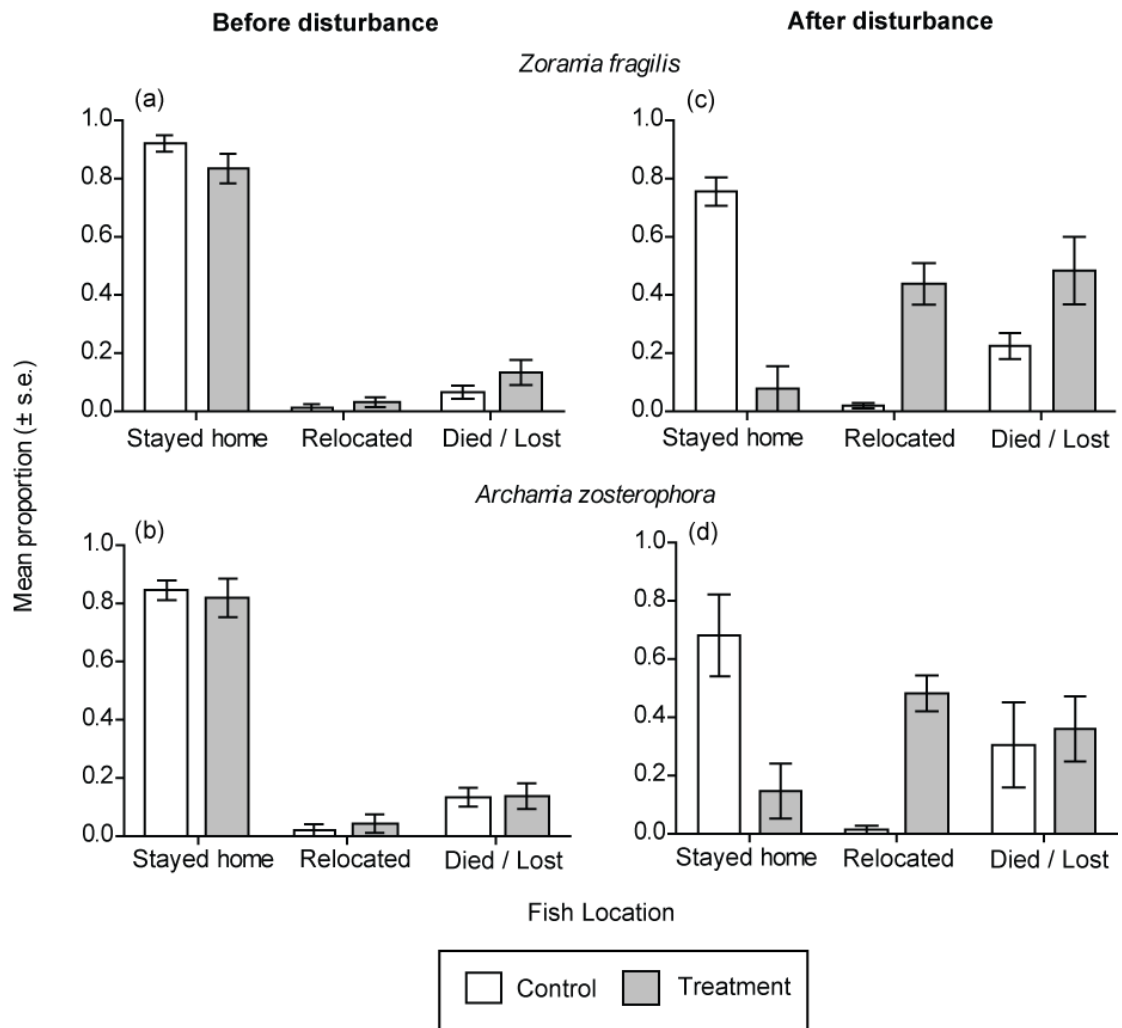
Figure 6.2. Response of cardinalfish species (*Archamia zosterophora* and *Zoramia fragilis*) to experimental disturbance of home sites. Three categorical movement responses are compared before and after disturbance for treatment and control groups.

Table 6.1. Observed response counts of tagged *Archamia zosterophora* and *Zoramia fragilis* individuals in 5 control and 5 treatment groups, before and after habitat disturbance. Records show the counts taken on the last day of the respective periods. 'Total' refers to the total sample size of tagged individuals used per site.

		Site	Total	Before disturbance			After disturbance		
				Response type			Response type		
				Home	Relocated	Missing	Home	Relocated	Missing
Archamia zosterophora	Control	1	40	37	0	3	37	0	3
		2	41	41	0	0	30	0	11
		3	47	40	3	4	30	2	15
		4	52	45	0	7	36	1	15
		5	52	50	0	2	41	2	9
	Treatment	6	36	33	2	1	14	18	4
		7	43	40	0	3	0	16	27
		8	35	23	3	9	0	11	24
		9	38	30	0	8	0	12	26
		10	58	51	1	6	0	40	18
Zoramia fragilis	Control	1	42	35	0	7	36	0	6
		2	33	32	0	1	4	0	29
		3	29	23	3	3	25	2	2
		4	58	45	0	13	45	0	13
		5	62	53	0	9	49	0	13
	Treatment	6	50	49	1	0	25	23	2
		7	36	30	0	6	2	16	18
		8	36	22	6	8	0	13	23
		9	57	47	0	10	0	35	22
		10	67	60	2	5	12	42	13

Fidelity to home coral colonies was also demonstrated over a longer 30 day period and more fish consistently used home sites than relocated or disappeared. On average, 80% of *A. zosterophora* and 73% of *Z. fragilis* individuals were always observed at control home sites. After 30 days, 70% of *A. zosterophora* and 60% of *Z. fragilis* were still using control home sites (Fig. 6.3a,b). Relocation of both species remained low over the 30 day period however, *Z. fragilis* appeared to have greater relocation tendencies than *A. zosterophora,* with 9% of *Z. fragilis* using non-home colonies after 30 days and 3% of *A. zosterophora*. Mortality of control groups steadily increased for both species, averaging $39 \pm 13\%$ (s.e.) for *Z. fragilis* and $28 \pm 4\%$ (s.e.) for *A. zosterophora* after 30 days. While response levels were relatively consistent among control sites, *Z. fragilis* had greater variability in fidelity and mortality than *A. zosterophora* (Fig. 6.4a,c,e,g).
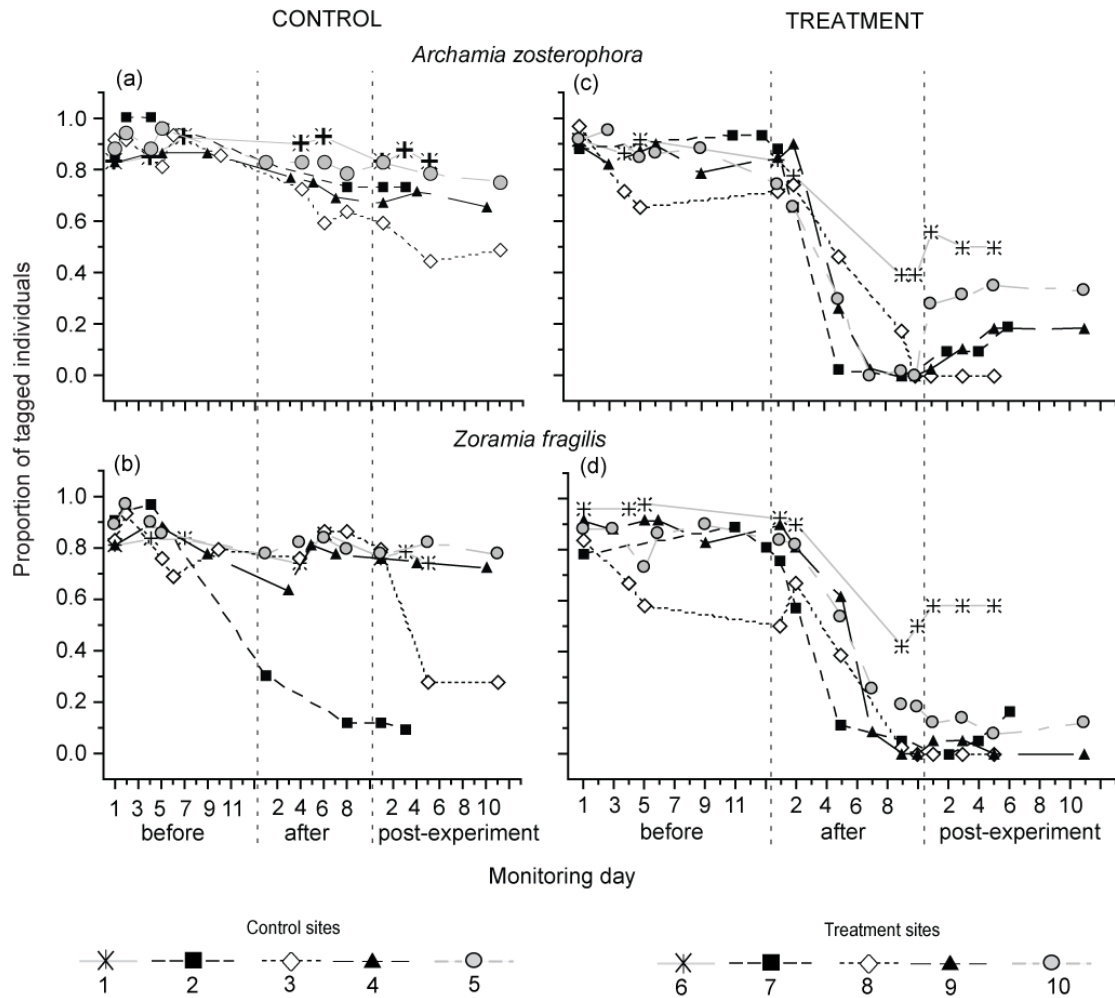
Figure 6.3. Home site fidelity of tagged *Archamia zosterophora* and *Zoramia fragilis* individuals from 5 control (a, b) and 5 treatment groups (c, d). Cardinalfish locations were monitored before disturbance, after habitat disturbance and after the experiment had ended, with each period lasting 10 days.
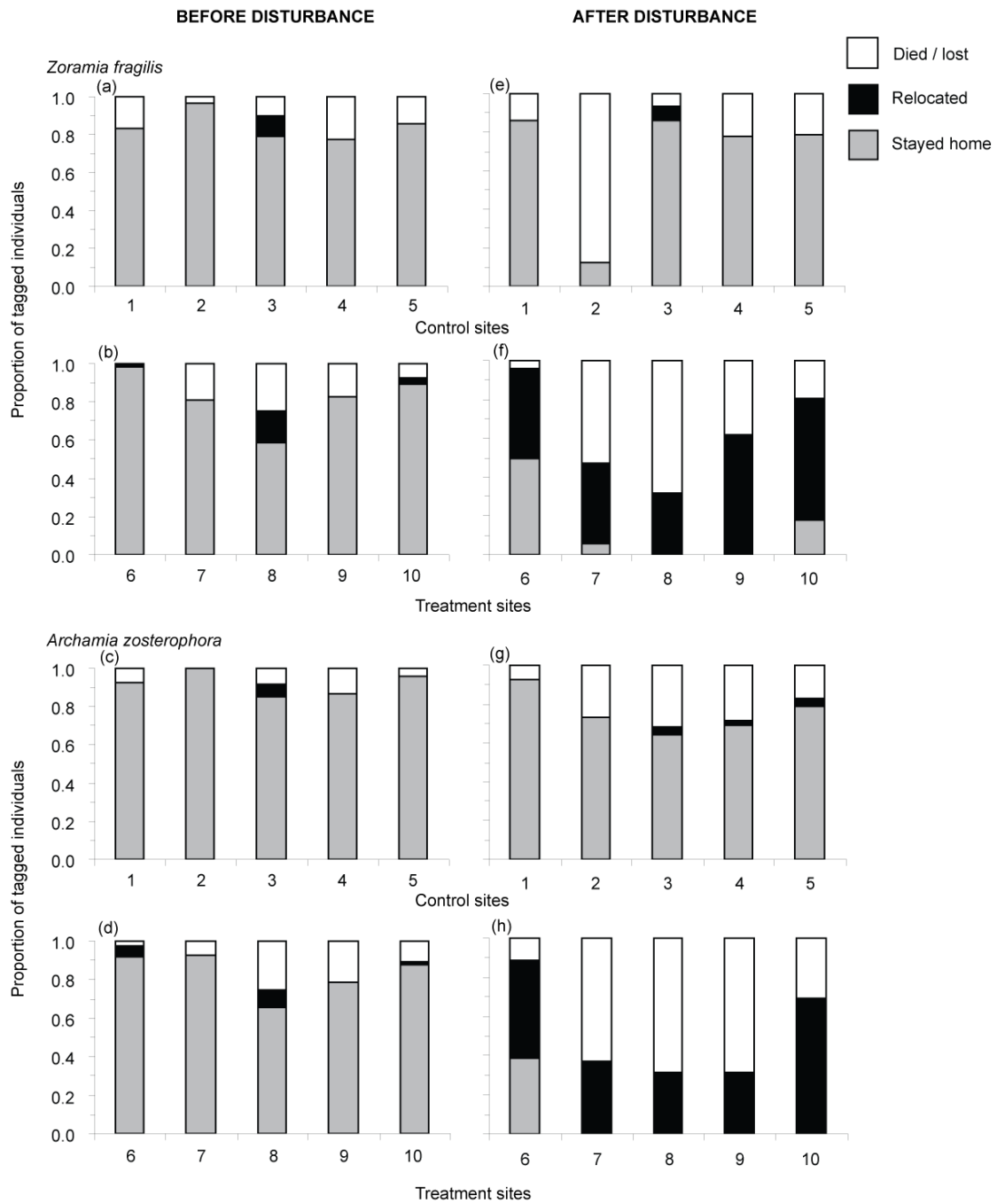
Figure 6.4. Site variation in the movement response of control and treatment groups for *Archamia zosterophora* and *Zoramia fragilis* before and after disturbance. Sites 1-5 were control groups and sites 6-10 were treatment groups.

6.4.2. Response to habitat disturbance: fidelity vs. relocation

Experimental disturbance strongly affected diurnal refuge use of treatment cardinalfish. Following disturbance, most treatment cardinalfish either moved into nearby corals or died (Fig. 6.2c,d). In total 40% of individuals died and 50% emigrated. On average only 11% of all treatment fish kept using the disturbed site, a 7-fold decline from fidelity observed in control groups and an 8-fold difference to fidelity of treatment fish before disturbance (cf. Fig. 6.2a,b). The response of each species was strongly dependent on the disturbance effect (control vs treatment; Table 6.2). Treatment fish in both species had lower fidelity to home sites and higher relocation than control fish (Table 6.2). Nearly 50% of each species relocated after the disturbance. In contrast, only a few fish moved from control colonies (Fig. 6.2c,d). Loss of tagged *A. zosterophora* fish in treatment groups was double that of control groups which indicated that habitat disturbance strongly increased mortality (Fig. 6.2c, Table 6.2). In contrast, *Z. fragilis* mortality was similar among control and treatment groups (-1 < residuals > -1. Table 6.2). Loss of this species was therefore due to natural mortality rates, not disturbance. The degree of response to habitat disturbance varied among particular treatment groups as response frequencies were significantly dependent on site effects (Fig. 6.4f,h; tests of site independence for both species' treatment groups: $G^2 > 16.35$, $df = 8$, $p < 0.05$).

Displacement responses were gradual for both species. During the first two days individuals of both species predominantly hovered around the edges of their netted home coral-colonies, with 75% of both *A. zosterophora* (± 4% s.e.) & *Z. fragilis* (± 6% s.e.) observed at home (Fig. 6.3c,d). Relocation and mortality did not outweigh fidelity until after five days. There were minor differences among treatment sites (Fig. 6.3c,d).

Table 6.2. Tests of independence on the disturbance response of cardinalfish among all treatment and control groups. G^2 represents log-likelihood test of independence on 2×3 contingency table with degrees of freedom (df) and significance (*p*-value) shown. Pearson residuals for each response and disturbance level indicate the direction and size of deviations from cell values expected under null-hypothesis of independence between treatments and response categories.

	Archamia zosterophora Response type			*Zoramia fragilis* Response type		
Disturbance	Home	Relocated	Missing (mortality)	Home	Relocated	Missing (mortality)
Control	7.582	-6.634	-2.998	5.110	-41.814	-0.668
Treatment	-7.970	6.972	3.152	-10.318	5.268	0.592
G^2, df, p	275.50, 2, <0.001			235.93, 2, <0.001		

6.4.3. Relocation success

Relocation was a successful endeavour for most displaced cardinalfish (Fig. 6.5). Of the 118 *A. zosterophora* and 148 *Z. fragilis* individuals that relocated due to disturbance, half selected one non-home colony and persisted there. A further 18% and 14% of each respective species moved from one new site to another and remained at the second. These 'successful' individuals were resighted using their new refugia in subsequent surveys and did not switch refuge choices. Relocation success did vary among the five treatment groups but was greater than 50% in all treatments. Fidelity to the first or second site occurred in 55-95% of each *A. zosterophora* treatment group and 52-87% of each *Z. fragilis* treatment. Displaced cardinalfish therefore appear capable of establishing new home sites.

A quarter of *A. zosterophora* and a third of *Z. fragilis* did not relocate successfully. Individuals were deemed unsuccessful at establishing new home sites because they either died after using another coral refugia or repeatedly switched among non-home colonies. 14% of both species disappeared after initially moving to a non-home colony. Switching behaviour was slightly more prevalent in *Z. fragilis* than *A. zosterophora*. 14 displaced *A. zosterophora* individuals (12%) and 30 *Z. fragilis* (20%) repeatedly switched between different non-home resting refugia. Overall, the relatively low frequency of switching behaviour in both species is consistent with the low relocation behaviour observed in control groups for both species (Fig. 6.2).
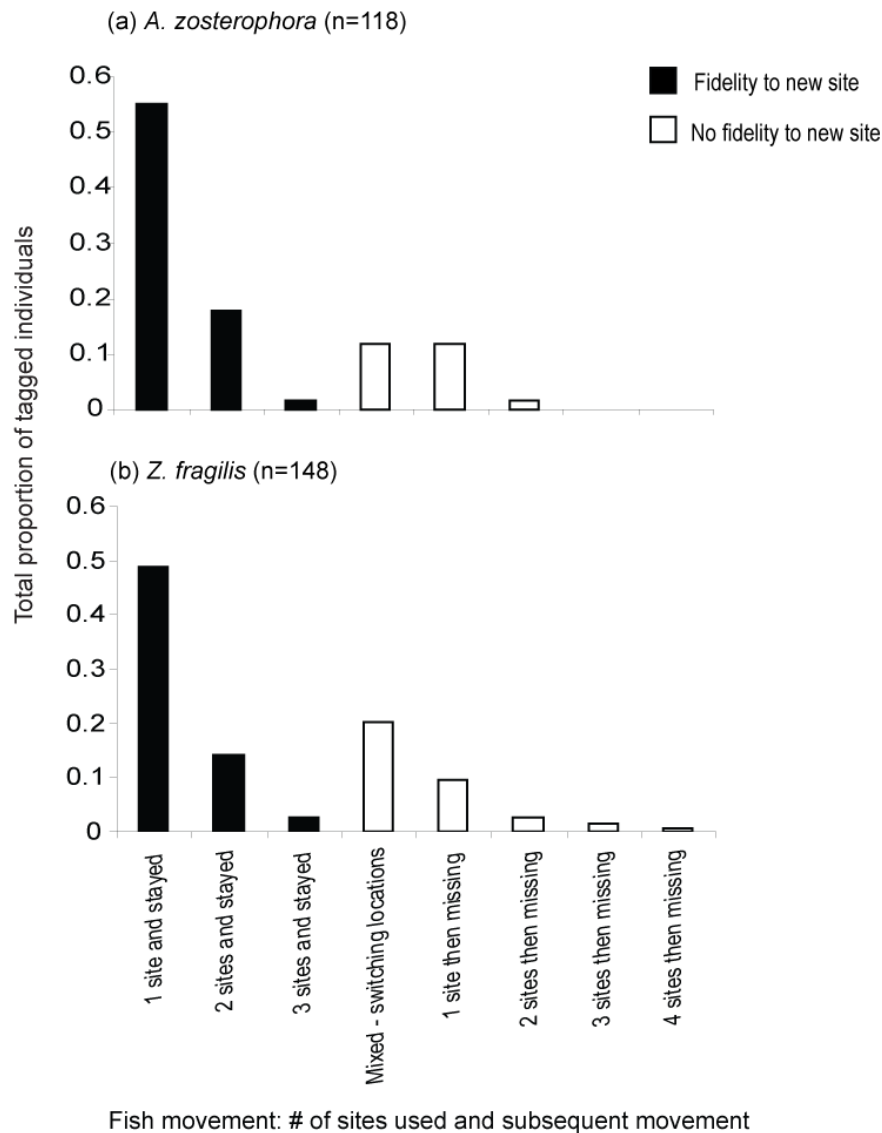
Figure 6.5. Relocation success of displaced cardinalfish into non-home coral colonies. Categorical responses indicate the frequency of movement among available resting refugia. Strong fidelity to a new site indicated successful relocation while switching among multiple sites and disappearances indicate low success in establishing new home sites. 'n' indicates the total number of individuals per species that moved due to home site disturbance.

6.4.4. Characteristics of new home sites

Relocation of cardinalfish from disturbed sites appeared limited by availability of social cues. Displaced fish only settled in existing cardinalfish aggregations. *A. zosterophora* only joined existing conspecific aggregations. *Z. fragilis* predominantly joined conspecific groups but in five instances individuals joined heterospecific aggregations that did not include *Z. fragilis*. In both species the degree of relocation was higher when there more conspecific aggregations nearby (*A. zosterophora*: r = 0.76, *p* = 0.011; *Z. fragilis*: r = 0.95, *p* <0.001). *A. zosterophora* aggregations were plentiful in the study areas, with 8-22 aggregations near home treatment

sites. In contrast *Z. fragilis* groups were fewer with only 4-5 in treatment study areas. The limited number of the latter suggests relocation of *Z. fragilis* individuals may be hampered by availability of social information, especially compared to *A. zosterophora*. 25-50% of *A. zosterophora* aggregations near treatment sites were not utilised by displaced fish. In contrast all *Z. fragilis* aggregations were joined by at least one displaced *Z. fragilis*. The ability to join heterospecific groups indicates a lack of conspecific cues does not prevent dispersal of *Z. fragilis* from disturbance.

Dispersing fish did not appear to select new coral colonies on the basis of physical attributes. Utilised colonies ranged in volume and surface area from $1.05-151m^3$ and $1.17-68.85m^2$, respectively, for both *A. zosterophora* and *Z. fragilis*. More individuals did not use bigger colonies. Similarly, selection of a new site was not based on the coral's proximity to the original home site which ranged from 0.5-80m. Closer corals were not used more frequently.

6.4.5. Effect of experimentally restoring access to original home site

Upon removal of nets, many individuals that had previously relocated, returned to their home coral colonies. 37 *A. zosterophora* individuals (31% of relocated fish, 18% of total treatment fish) and 27 *Z. fragilis* (18% of relocated fish, 11% of total treatment fish) returned to home coral colonies after nets were removed. For both species two-thirds of these returns happened immediately, the day after disturbance ceased. The remainder came back within 3-9 days and 1-2 individuals of each species returned home after 10 days.

6.5. Discussion

Few studies have established whether coral reef fishes can successfully move and survive in response to localised disturbances. This study showed that cardinalfish fidelity to particular home coral colonies is neither obligate nor completely arbitrary. When experimentally denied access to home sites, 50% of individuals departed and two thirds of these successfully became established at new home sites. However, displacement from the home site also exacted a cost, with 40% mortality over 10 days following the habitat disturbance. Relocation into alternate resting sites appeared dependent on availability of other social groups and no role of habitat quality could be detected. Displaced cardinalfish appeared to copy choices of other individuals in selecting new resting locations. The preferences for original home sites remained strong even after apparent resettlement, with 24% of individuals returning to original home sites when access was restored. Hence, while home site fidelity is extreme in these species, there is some

hidden flexibility in the reliance on particular home locations which may buffer them against small scale habitat disturbances.

Site fidelity in cardinalfish appears to be primarily the result of social copying in which site use is traditional, rather than the result of distinct habitat preferences for particular coral colonies or structural attributes of the colony. When utilised coral colonies were disturbed, individuals slowly relocated and joined alternate cardinalfish aggregations, albeit with high mortality. While a strong allegiance to the original home colony was clearly retained, this did not preclude relocation. Displaced cardinalfish did not select new sites based on structural attributes of colony size or proximity. Cardinalfish do exhibit refuge site preferences for larger coral colonies of one branching coral species (Chapters 2, 3, 4). However in reef areas with a relatively abundant supply of this habitat, structural attributes were less important than social cues in predicting relocation success. In addition, 67% of displaced cardinalfish did not appear to sample alternate refugia, but settled in their first or second position, in refugia that already hosted cardinalfish aggregations. Social cues are therefore important in enabling shifts away from disturbed locations and in establishing new traditional sites. These findings are corroborated by previous research on cardinalfish habitat use which illustrated that conspecific attraction is strong enough to override individual habitat preferences (Chapter 4) and can modify home site preferences via olfaction (Døving et al., 2006). Site fidelity may operate differently for one unique cardinalfish species, *Pterapogon kauderni*, which appears to have greater preferences for the home site rather than conspecifics (Kolm et al., 2005) Heterospecific cues may also assist individuals establish new refuge sites (Monkkonen et al., 1999, Seppänen and Forsman, 2007). This would be useful if aggregative species like *A. zosterophora* and *Z. fragilis* can copy suitable site choices from more solitary species like *Cheilodipterus quinquelineatus* and thus form new traditional sites.

Overall, both species responded similarly to disturbance, showing strong home site fidelity before disturbance, greater than 50% relocation and successful re-settlement behaviour after habitat loss. However, slight divergence in mortality and relocation behaviours reflects important differences in each species' resilience to habitat loss. Disturbance caused a greater loss of *A. zosterophora* than *Z. fragilis*. In addition, *A. zosterophora* had 10% more resettlement success than *Z. fragilis* which had greater movement among alternate sites. Thirdly, once disturbance ceased, 31% of displaced A. *zosterophora* returned to home refugia, twice as many as *Z. fragilis*. These differences are likely due to differentiation in the species' natural fidelity and movement behaviour in which A. *zosterophora* has stronger home site attachment and *Z. fragilis* has more movement amongst refugia. These natural patterns, observed in pre-disturbance monitoring and in control sites, have also been shown in previous studies on these

species (Chapter 5). Stronger site fidelity behaviour in A. *zosterophora* meant that disturbance had a greater impact on this species. In contrast, greater movement behaviour in *Z. fragilis* provides more resilience to habitat loss.

Loss of access to home refugia resulted in a very apparent mortality of treatment individuals, averaging 40% for *A. zosterophora*. In addition, disappearance rates of control individuals after 30 days approximately 25% for both species. Such mortality rates, of around 1% per day, are considered very high for adult coral reef fish and would predict very short life spans for Kimbe Bay cardinalfish. While individuals that disappeared in this study were presumed to have died, some may have simply migrated outside of the survey areas. However, the lifespan of these low latitude populations does appear to be relatively short, within 1 year. Previous tagging and monitoring studies of Cardinalfish in Kimbe Bay (Chapter 5) found very low numbers of individuals persisted in their home refugia for more than 1 year, and this was true of species that persist more than 3 years in single coral colonies in higher latitude coral reefs (Marnane, 2000). Similarly disappearance rates of tagged, non-treatment fish in Chapter 5 were of a similar order to this study, 50-60% of individuals within 3 months. The high numbers of missing individuals recorded in the current study are therefore considered to be primarily due to mortality, but with some longer distance migrations certainly possible.

The cost of home site disturbance incurred by treatment fish is expected to be lower in more natural situations of habitat degradation. The disturbance regime modelled here caused an abrupt removal of home site access to individuals and forced relatively rapid relocation attempts. This kind of rapid disturbance might normally arise due to rare and isolated reef disturbances like intense storms, anchor damage, landslides or earthquakes. Even in these situations access to refuge spaces in the coral colony would not be not completely prevented. The more typical degradation processes currently acting on inshore reef areas, such as sedimentation, cause a much slower decline in habitat quality and availability. Given the relocation success of more than half the treatment affected reef fish in this study's disturbance regime, the likelihood of most cardinalfish individuals shifting into alternate refugia, during longer term degradation processes, is quite high.

In the context of increasing disturbance and habitat loss on coral reefs, coral dwelling species with strong site attachments, like cardinalfish, appear highly vulnerable. This study shows that actual responses can be more flexible than observations on natural fidelity would predict. For cardinalfish, while higher mortality occurs, a substantial proportion of the disturbance-affected population can shift into undisturbed habitats. However, the success of this relocation behaviour appears dependent on copying behaviour and an ability to find other aggregation sites in the

near vicinity. As the scale and intensity of disturbance increases, mortality through displacement is likely to increase. Ultimately, the strong site fidelity in these species may hinder their survival in degrading coral reef environments.

CHAPTER 7: General Discussion

7.1. Key findings

Each chapter in this thesis contributed evidence of close relationships between coral reef dwelling Indo-Pacific cardinalfish species (family Apogonidae) and their diurnal coral reef resting habitats and strong behavioural associations among cardinalfish individuals and species. The combination of extreme habitat specialisation, high niche overlap and strong site fidelity resulted in a high dependence, not only on a single coral species, but on particular coral colonies. The majority of common species examined in PNG and Australia exhibited a strong association with a single coral species *Porites cylindrica* and a high level of co-occurrence on this habitat (Chapter 2). Multiple species selected the same larger coral colonies of this species, but partially differentiated their use of refuge areas within the colonies (Chapter 3). Habitat preference and conspecific choice experiments showed that micro-habitat distribution of cardinalfish is driven by an interaction of strong habitat and social preferences (Chapter 4). The strong association with particular coral colonies was demonstrated by strong site fidelity and homing behaviour, with homing detected within and among reefs, over distances up to 5km (Chapter 5). Experimental disturbance of resting refuge habitats resulted in a dramatic impact on the community because fidelity to home coral colonies constrained the ability of individuals to relocate to intact refugia (Chapter 6). Both fidelity to home sites and the refuge choices made by displaced fish appear to be facilitated by social cues (Chapter 6). I conclude that the biodiversity of the cardinalfish family in the Australia/PNG region is threatened by habitat loss or degradation. The destruction of a relatively small proportion of the larger colonies of a single species (*P. cylindrica*) is predicted to have devastating effects on many of the common reef-associated species.

7.2. Emerging hypotheses

The diurnal spatial distribution and behaviour of Indo-Pacific cardinalfish is likely to be jointly determined by predation pressure and the requirements for successful reproduction. Habitat preferences for complex branching corals can reduce the impact of predation (Beukers and Jones, 1997, Almany, 2004) and aggregative behaviour can also aid in predator avoidance (Morse, 1977, Pitcher, 1986, White and Warner, 2007) and facilitate mating (Krause and Ruxton, 2002). Micro-habitat specialisation in cardinalfish appears to be a common result of predation vulnerability, which has led to convergence on a single coral species that maximises

protection. Within coral colonies, some species may have greater specificity for a particular refuge area because resting in that position increases their survivorship. Site fidelity or prolonged use of familiar environments can enhance the survival benefits of being associated with a preferred coral species (Lopez et al., 2000, Yoder et al., 2004). The evolution of homing behaviour may be explained by the strong survival benefits of finding an appropriate and popular coral shelter site quickly as individuals return from their nocturnal foraging. Among cardinalfish there is species-specific variation in the strength of habitat specialisation, aggregative behaviour and site fidelity, suggesting that there are different ways to solve the predator avoidance problem. More aggregative species may rely on shoaling behaviour to minimise predation threats. They would therefore have less need for habitat protection and consequently lower habitat specificity, greater niche overlap and lower site fidelity.

Gregarious behaviour, site fidelity and homing are all likely to facilitate cardinalfish reproduction. Individuals could increase their chance of mating by joining larger groups. Homing may assist mate fidelity within pairs and the stability of social groups. Cardinalfish may use a variety of mating strategies to increase reproductive output including mate-switching, the formation of long-term bonds within groups and/or the formation of stable social groups with dominance hierarchies. In other aggregating animals, males in dominance hierarchies benefit reproductively by returning to traditional 'nesting' sites in which they have a history of reproductive success (Widemo, 1997). Preliminary evidence of both low site fidelity due to mate-searching and high fidelity in social groups with apparent hierarchies has been observed in cardinalfish (Okuda and Yanagisawa, 1996, Okuda, 1999, Kolm et al., 2005).

7.3. Implications for ecological theory

Controversial ecological theories regarding the structure of coral reef fish communities, like competitive exclusion (Schoener, 1974); resource overlap (Smith and Tyler, 1972, 1973, Dale, 1978, Smith, 1978); the lottery hypothesis (Sale, 1974, 1977, 1978a); and recruitment limitation (Doherty, 1982, 1983, Victor, 1983, 1986) do not satisfactorily explain the diurnal distribution of Indo-Pacific cardinalfish. Spatial competition theories predict that niche overlap on critical habitats will not occur as inter-specific competition for limited habitat drives partitioning of spatial resources (Schoener, 1974). Resource overlap theories extend the competition theme and suggest that heterospecific overlap may occur on some habitats because species do not share their most essential and productive habitat resources (Smith and Tyler, 1972, 1973, Dale, 1978, Smith, 1978). Sale's lottery hypothesis predicts that the relative abundance of species on similar habitat patches is primarily driven by random recruitment and the order of colonization (Sale, 1974, 1977, 1978a). Recruitment limitation suggests larval supply is insufficient to satiate

resource availability and that the distribution of reef fish among habitats is dependent on the number of larval arrivals (Doherty, 1982, 1983, Victor, 1983, 1986). For the cardinalfish community studied here, competition for diurnal habitat resources are not apparent, the available habitat was not saturated and instead of segregation species share living space at a variety of scales. All preferentially use shallow depths and sheltered reef zones (Chapter 2 and Marnane 2001) and aggregate on large colonies of a single coral species. Diurnal partitioning is only partially apparent at a fine scale within coral colonies. Homing behaviour and strong social attraction contrast predictions of the lottery and recruitment limitation hypotheses. These behaviours result in aggregations of individuals at particular locations that appear to persist regardless of recruitment variation or limitation. Recruitment variation will make a difference to the relative abundance of species but cardinalfish have high recruitment and the general patterns of habitat use are not likely to be affected by this variation. As discussed previously, models of predation appear to have a more determinant role in structuring cardinalfish communities.

7.4. Implications for ocean climate change

The future for cardinalfish is not promising due to the variety of anthropogenic influences on branching coral habitat. Anthropogenically induced climate change is increasing the frequency and intensity of coral reef disturbance events (Kleypas et al., 1999, Hoegh-Guldberg et al., 2007, Brierley and Kingsford, 2009). The degrading effect of coral bleaching events, increased storm activity and ocean acidification on live coral structures are of particular concern. The coastal reef areas inhabited by cardinalfish assemblages are also particularly vulnerable to increased eutrophication (Rabalais et al., 2009). In addition, branching coral habitats and particularly larger coral colonies are the most susceptible reef substrata to disturbances (Dollar and Tribble, 1993, Loya et al., 2001, Madin et al., 2008, McClanahan et al., 2008). Ocean warming will also directly affect cardinalfish survival as species appear unable to cope with the increased metabolic demands of a 3-4°C in temperature (Nilsson et al., 2009, Gardiner et al., 2010). The long-term prognosis for cardinalfish communities is therefore not good but in the immediate time frame (10-50 years) their high population numbers, high reproductive turnover and use of a coral species that is relatively resilient to bleaching and sedimentation means they are not as vulnerable as obligate *Acropora* associates and/or rarer reef fish guilds.

7.5. Future directions

Future research on Indo-Pacific cardinalfish should focus on the determinant role of predation in diurnal habitat associations and social behaviour and on the possibilities of behavioural

adaptations for living in altered reef habitats. To evaluate whether predation vulnerability affects habitat use and site fidelity, differences in survivorship should be compared among different sizes of *P. cylindrica* colonies, branching corals of different complexities and among refuge areas within colonies. The latter would involve measuring the predation rate of individuals occupying particular sections of a coral colony. If specialisation is related to predation vulnerability, habitat-specific species would have higher mortality when they are not using their preferred refugia. To test whether site familiarity increases survivorship and drives homing behaviour, experiments would compare the predator-induced mortality of individuals placed in familiar and un-familiar habitat patches. Familiar experimental habitats maybe considered as those in which individuals are given a longer acclimation period.

Exploring the role of gregarious behaviour is critical to understanding cardinalfish habitat associations and particularly their apparent lack of diurnal spatial partitioning. If gregarious behaviour decreases predation losses, larger groups are expected to have lower mortality per capita and, where habitat space allows, attract more recruits. To assess these hypotheses, the loss and recruitment of cardinalfish from small versus large aggregations should be evaluated. It appears likely that aggregating and returning to particular groups may increase reproductive success. Testing this requires long-term monitoring of group membership, pair fidelity and reproductive output. Long-term bonding between pairs in aggregations could be tested by maternity analysis of eggs brooded by males. A key feature not explored in this thesis is the social preference for heterospecifics. Evaluating whether multispecific aggregations occur due to social preferences for other cardinalfish species requires establishing the degree of attraction among heterospecific individuals given ample habitat availability. Preliminary work suggests heterospecific attraction is strong (Gardiner, unpubl. data) however the evolutionary benefit of this is not clear. Assessing whether fish choose to join heterospecifics housed on degraded habitats rather than utilising quality refugia in isolation could indicate the potential for species shifts in habitat associations.

A key result not established in this thesis is whether the apparent habitat specialisation and strong habitat preferences of coral reef cardinalfish indicates absolute dependence on just one branching coral species, on larger colonies, and on particular colonies currently hosting aggregations. The next step in testing this hypothesis is too evaluate performance costs incurred by individuals using non-preferred coral species and colonies. If fitness costs are higher on alternate refuge habitats then cardinalfish communities will indeed be negatively impacted by long-term loss of P. cylindrica habitats. Future research should therefore compare survival, growth, reproduction and movement rates of cardinalfish on different branching coral species, and colony sizes.

The aggregative nature of cardinalfish may be the community's key to surviving reef habitat changes. If multispecific preferences occur, aggregation sites could become established on degraded coral substrata, or upon artificial shelter structures, by generalist species that subsequently attract other species and conspecifics to that shelter structure. The capacity of cardinalfish to live successfully in altered habitats firstly requires determining living success on non-living coral structures and on smaller coral colonies. A critical test of this would involve seeding habitats with recruit cardinalfish and monitoring the long-term growth, survival and reproduction output of the individuals. Secondly, the degree of attraction to the seeded residents on such habitats needs to be established, both for conspecifics and heterospecifics. In particular research should address whether permanent aggregation sites on 'degraded' refuge sites can be established.

Cardinalfish species occur in a diverse array of marine and aquatic environments and micro-habitats. The family clearly has the evolutionary capacity to inhabit and thrive in an array of habitat structures. While many Indo-Pacific coral reef species are highly specialised on a single coral species and colony type, their strong social behaviour provides hope that the guild will adapt to gradual shifts in reef habitats.

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