

# Habitat specialisation and overlap in a guild of coral reef cardinalfishes (Apogonidae)

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**ABSTRACT:** The nocturnally foraging cardinalfishes are known to exhibit a high degree of fidelity to their daytime resting sites. However, the microhabitats 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 impact the diversity and abundance of apogonid assemblages. Here, microhabitat 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 cardinalfishes were associated with a single coral species (*Porites cylindrica*), although the degree of specialisation varied among species. *Apogon leptacanthus* and *Sphaeramia nematoptera* were almost always only found on *P. cylindrica*, while *Apogon bandanensis*, *Apogon compressus*, *Apogon fragilis*, *Archamia fucata*, *Archamia zosterophora*, *Cheilodipterus artus* and *C. 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 9 coral-dwelling apogonids exhibited a high degree of overlap in depth range and in the use of coral microhabitats. 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.

**KEY WORDS:** Abundance · Aggregation · Apogonidae · Community structure · Coral reef · Habitat specialisation · Resource overlap · Resting site

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## 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 & 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 & Morrow 1981, Futuyama & 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

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become specialised on different habitats (MacArthur 1958, Hardin 1960, Schluter & 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 microhabitat specialisation, the degree to which the available microhabitats 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 & Syms 1998, Munday & Jones 1998). Within any one family, reef fish species clearly vary both in the degree of microhabitat 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 & Lassig 1980, Hourigan 1989, Fowler 1990, Clarke 1994, Green 1996, Öhman et al. 1998). If specialisation and overlap are linked, 3 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 microhabitats (as predicted from competition theory). Finally, communities may be composed primarily of specialists on the same microhabitat, 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 microhabitat 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 microhabitats 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 2004). 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 microhabitats that are under threat. Communities composed of species with a high degree of microhabitat partitioning may be resistant to habitat degradation, provided that not all habitats are adversely affected. Conversely, if all species are specialised on the same microhabitat undergoing degradation, the whole community will be threatened (Mc-

Kinney 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 declining coral could affect a greater range of reef fish species than previously thought because of an underestimate 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 cardinalfishes (Family Apogonidae) are one of the most abundant and diverse fish families on Indo-Pacific reefs (Munday & 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 & Jones 1998, Marnane & 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 cardinalfishes 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 & 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 we examine the degree of apparent microhabitat 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, we collected species-specific information on the types and range of coral species used as resting sites. Based on the literature, we 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 microhabitat use, (3) species would show a high level of partitioning of microhabitat resources, and (4) the degree of microhabitat 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.

## MATERIALS AND METHODS

**Study site and species.** The field study was conducted at Kimbe Bay, West New Britain Province, Papua New Guinea ( $5^{\circ}30'S$ ,  $150^{\circ}05'E$ ) in September 2003 (Fig. 1a). Kimbe Bay is a large, sheltered bay with little change in water temperature throughout the year ( $31 \pm 1^{\circ}C$ ). 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 Research and Conservation Centre and 7 near Schumann Island (Fig. 1b). The Family Apogonidae is the fifth most speciose reef fish family in the bay, with 36 species recently documented (Allen & Munday 1994).

**Apogonid surveys.** Microhabitat use by species was determined from surveys of back- and forereef 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 20 m 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 17:00 h 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 nearest 0.5 m) and microhabitat 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 microhabitat used by individual cardinalfish was defined at 2 levels. The 1st 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 1). Where live, hard coral was utilised, a 2nd level of classification was applied, based on a combination of the coral genera and growth form (Table 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 10 coarse microhabitat and 15 live, hard coral categories were distinguished (Table 1).

The microhabitats used were recorded as those within which individuals were first seen. Apogonids are relatively immobile on approach, making classifi-

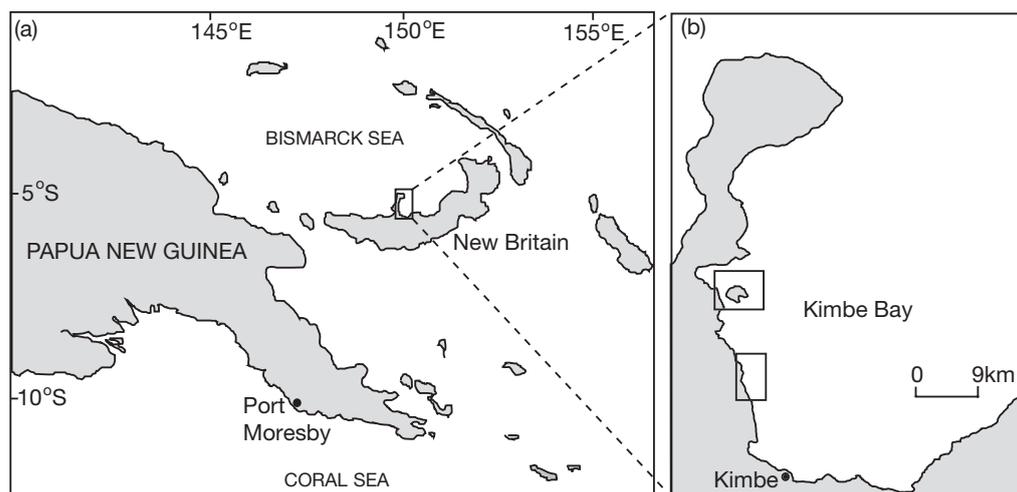


Fig. 1. (a) Location of Kimbe Bay, New Britain Province, Papua New Guinea and (b) the 2 inshore areas where reefs were surveyed

Table 1. Microhabitat categories used in this study

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

<sup>a</sup>Coral genera and morphology identifiable  
<sup>b</sup>Dead coral unidentifiable to taxonomic or morphological level

cation of microhabitats straightforward. Individuals and aggregations were occasionally seen between or within 2 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 (e.g. of sand, rubble or encrusting organisms) since the former clearly offered the dominant habitat structure.

**Microhabitat availability.** Line transects were conducted at each site to assess the availability of each microhabitat. Four 50 m transects were laid randomly across the reef slope at depths of 0, 2, 6 and 10 m. This depth range was sufficient as the majority of cardinalfishes (97.6% of individuals) were observed at or above 10 m. Each tape was marked with 100 randomly allocated points and the substratum directly beneath each point recorded. Substrata were recorded as coarse microhabitat and live, hard coral categories as per fish censuses (Table 1).

**Microhabitat specialisation.** The relative specialisation of each cardinalfish species was assessed by comparing the absolute number of substrata used, both in terms of coarse microhabitat categories and of live, hard coral substrata. Only species for which >50 individuals and >10 groups were recorded were used for comparisons of microhabitat associations. Proportional use of microhabitat 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 microhabitat 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 5 and all were above 1 (Zar 1999). Frequencies of cave use were not included because availability of this coarse microhabitat substrate could not be measured. Chi-square goodness of fit statistics require that each individual's resource use be independent of other animals. Because apogonids aggregate, we 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 microhabitats. 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 microhabitat  $i$  or coral  $i$  used and  $\pi_i$  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:

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

where  $Z_{a/2k}$  is the critical value of the standard normal distribution corresponding to an upper tail area of  $a/2k$ ,  $a = 0.05$ ,  $k =$  number of habitats used, and  $U_+$  is the estimated number of groups (per species) observed using that habitat type. Selection indices ( $\pm 95\%$  CI) above the value of 1 indicate significantly positive habitat use, while those below 1 indicate negatively significant use and those encompassing 1 show that habitat use is in proportion to habitat availability (not significant).

**Niche overlap.** The horizontal distribution of cardinalfish species was 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 microhabitats was also calculated using the percentage similarity measure. The percentage of overlap on microhabitats is calculated by:

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

where  $P_{jk}$  is the percentage overlap between species  $j$  and species  $k$ ,  $p_{ij}$  is the proportion microhabitat  $i$  is of the total microhabitats used by species  $j$ ,  $p_{ik}$  is the pro-

portion microhabitat  $i$  is of the total microhabitats used by species  $k$ , and  $n$  is the total number of microhabitat 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 a priori as groups with >10 individuals occupying the same coral head.

**Specialisation: abundance relationship.** Linear regression was applied to test the relationship between microhabitat specialisation and local abundance. The relative degrees of specialisation on both coarse microhabitats and live coral substrata were compared using the number of microhabitats 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.

## RESULTS

### General patterns

A total of 25 species, 5 genera and ca. 12 500 individual cardinalfish were observed on Kimbe Bay coral reefs (Table 2). The community was clearly dependent on live, hard coral as the primary resting habitat. Only 3 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). We observed 10 species from 4 genera with sufficient individual (>50) and group (>10) abundance to carry out detailed analyses of habitat associations (Table 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*).

### Degree of specialisation on coarse microhabitats

Species varied in the number of coarse microhabitats occupied (Fig. 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 microhabitats were utilised in less than 18% of observations (Fig. 2). Live coral cover made up less than 25% of the substrata (Fig. 3a). No species was distributed according to availability of coarse microhabitats (Chi-square goodness-of-fit test:  $\chi^2 > 5.5$ ,  $df = 8$ ,  $p < 0.05$ ). Apart from *A. nigrofasciatus*, all species occupied live hard coral more frequently than expected from substrata availability (Table 3a). This substratum was the only habitat ever utilised significantly more than availability predicted (Table 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*, *Apogon leptacanthus* and *Sphaeramia nematoptera* exhibited the highest degree of specialisation at the level of coarse microhabitats, occupying 1 to 2 substrata each (Fig. 2). When 2 substrata were used, one was always live, hard coral and the other an adjacent microhabitat. *Apogon bandanensis* and *Apogon fragilis* both utilised 4 categories (Fig. 2). Dead coral, rubble and gorgonians (*A. fragilis* only) were occupied in proportion to their availability (Table 3a). *Apogon compressus*, *Cheilodipterus artus* and *C. quinquelineatus* were the less specialised species of the group. Other than live coral use, *A. compressus* and *C. artus* utilised 2 to 3 other habitats in accordance with availability and 1 less frequently than expected (Table 3a). *C. quinquelineatus* occupied 7 coarse

Table 2. Observed apogonid species and relative abundance. \*: 10 species used in microhabitat analyses

Apogonid species	No.		% Live coral use (individuals)
	individuals	groups	
<i>Apogon fragilis</i> *	2721	23	94.5
<i>Cheilodipterus quinquelineatus</i> *	2614	311	81.5
<i>Archamia zosterophora</i> *	2415	60	100.0
<i>Apogon leptacanthus</i> *	1609	19	100.0
<i>Apogon compressus</i> *	840	111	96.7
<i>Cheilodipterus artus</i> *	800	65	81.9
<i>Apogon cyanosoma</i>	408	7	2.0
<i>Apogon nigrofasciatus</i> *	383	124	6.3
<i>Apogon bandanensis</i> *	154	22	96.1
<i>Archamia fucata</i> *	140	11	100.0
<i>Sphaeramia nematoptera</i> *	59	14	100.0
<i>Apogon fraenatus</i>	38	11	26.3
<i>Apogon novemfasciatus</i>	35	10	62.9
<i>Apogon moluccensis</i>	30	1	100.0
<i>Apogon ventrifasciatus</i>	30	1	100.0
<i>Apogon multilineatus</i>	26	20	15.4
<i>Archamia biguttata</i>	20	4	100.0
<i>Archamia macroptera</i>	20	1	100.0
<i>Apogon taeniophorus</i>	19	15	0.0
<i>Apogon kallopterus</i>	10	7	30.0
<i>Cheilodipterus alleni</i>	4	3	0.0
<i>Apogon fuscus</i>	4	2	100.0
<i>Apogon trimaculatus</i>	3	3	66.7
<i>Foa brachygamma</i>	2	3	0.0
<i>Cheilodipterus macrodon</i>	1	1	100.0

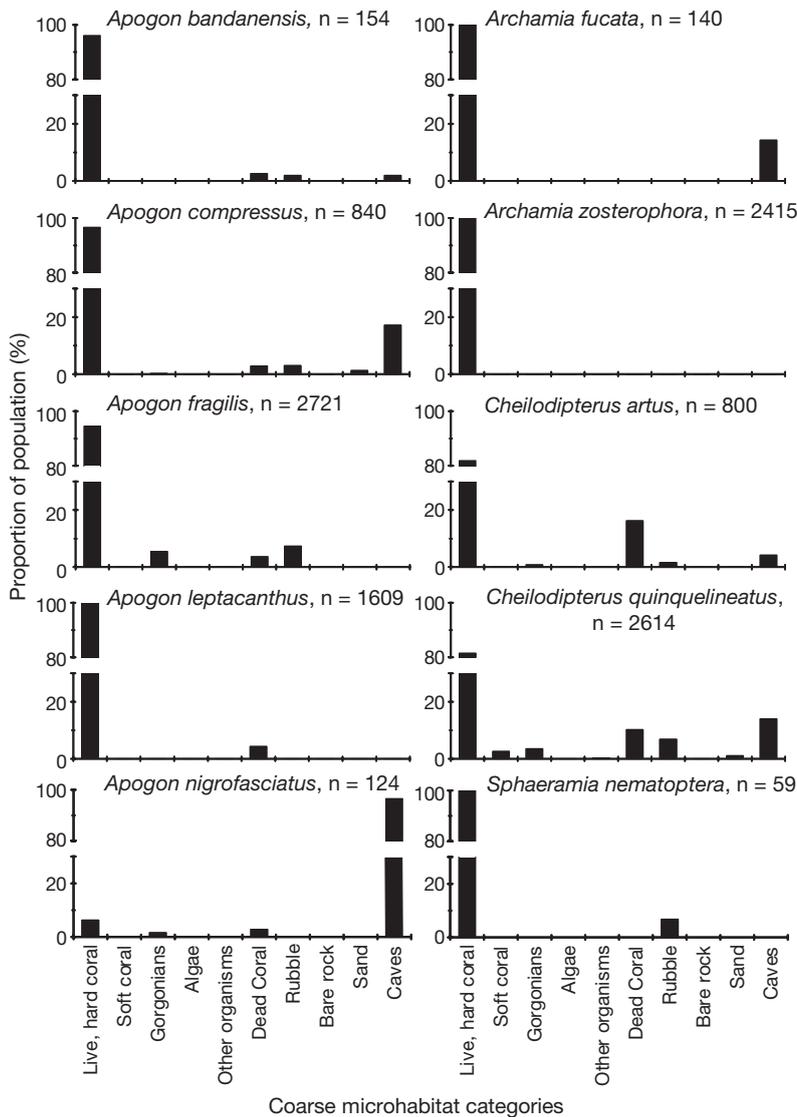


Fig. 2. Relative proportions of populations of 10 common apogonid species associated with the different coarse microhabitats, including living and non-living substrata (n = estimated no. of individuals sampled per species)

substrata categories. It occupied most non-living coral substrata in proportion to their availabilities (Table 3a). The remaining species *Apogon nigrofasciatus* predominantly used cave habitats (Fig. 2). Unlike other common species, it occupied live, hard coral less frequently than expected on the basis of availability (Table 3). Gorgonians were the only coarse microhabitat it used in proportion to its availability.

#### Degree of specialisation on live coral substrata

The 9 cardinalfish species associated with live coral exhibited an apparent selection for *Porites*

*cylindrica* outcrops (Figs. 3 & 4). The proportion of individuals associated with this single coral species ranged from 24% in *Cheilodipterus quinquelineatus* to 94% in *Apogon leptacanthus*. Branching corals accounted for less than 21% of the available live coral cover, and *P. cylindrica* accounted for less than 5% (Fig. 3). Although all fish species varied in the range of live, hard corals occupied, none of these 9 species was distributed according to the availability of coral substrata (Chi-square goodness-of-fit test:  $\chi^2 > 15.5$ , df = 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 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. *Apogon leptacanthus* and *Sphaeramia nematoptera* exhibited the highest degree of apparent specialisation on live, coral taxa, utilising 2 and 3 categories respectively (Fig. 4). Over 90% of individuals in these species used *Porites cylindrica*. *Acropora* and *Anacropora* (*S. nematoptera* only) branching corals were occupied in proportion to their availability (Table 3b). *Apogon fragilis* was found in 4 branching coral categories, but only *P. cylindrica* was used more frequently than expected (Fig. 4, Table 3b). *Archamia fucata*, *Archamia zosterophora*, *Apogon bandanensis*, *Apogon compressus* and *Cheilodipterus artus* utilised a wider range of

coral categories. However, 39 to 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 3b). *C. quinquelineatus* was clearly the least specialised apogonid species, using all 15 live, hard corals (Fig. 4). Like other species, it occupied *P. cylindrica* more than any of the other corals. Of the 9 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 3b).

**Niche overlap**

The 10 common cardinalfish species exhibited very high levels of overlap in their use of habitats with respect to zonation, depth and microhabitat use. The communities of cardinalfish species observed within

backreef, forereef and lagoons were highly similar with pair-wise percentage similarities each greater than 66% (Forereef: Backreef: 89.76%, Forereef: Lagoon 66.14%, Backreef: Lagoon 71.41%). There was a significant difference in observed mean depths ( $F = 2.60, p < 0.01$ ); however, the depth range of species

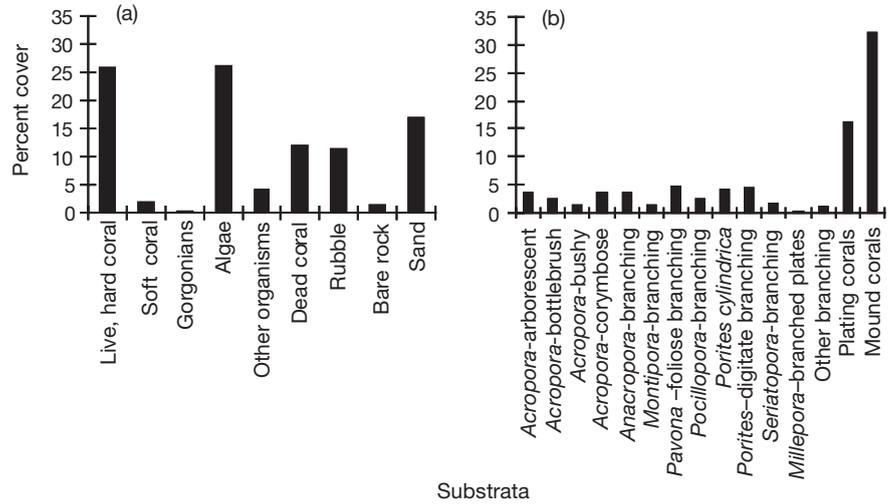


Fig. 3. Relative cover of different microhabitat types based on field estimates of (a) coarse microhabitat categories, including living and non-living substrata, and (b) live coral substrata

Table 3. Significance of habitat use by 10 common Apogonid species in Kimbe Bay using resource selection ratios and Bonferroni Z-corrected 95% confidence intervals (Manly et al. 2002). (a) Use of coarse microhabitat 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

	<i>Apogon bandanensis</i>	<i>Apogon compressus</i>	<i>Apogon fragilis</i>	<i>Apogon leptacanthus</i>	<i>Apogon nigrofasciatus</i>	<i>Archamia fucata</i>	<i>Archamia zosterophora</i>	<i>Cheilodipterus artus</i>	<i>Cheilodipterus quinquelineatus</i>	<i>Sphaeramia nematoptera</i>
<b>(a)</b>										
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>(b)</b>										
<i>Acropora</i> - arborescent	=	=	=	=		U	U	=	+	U
<i>Acropora</i> - other branching	U	=	U	U		=	U	=	=	=
<i>Anacropora</i> - branching	=	+	=	U		U	+	=	+	=
<i>Pavona</i> - foliose branching	=	=	U	U		=	=	=	=	U
<i>Porites cylindrica</i>	+	+	+	+		+	+	+	+	+
<i>Porites</i> - digitate branching	=	+	U	U		U	=	=	=	U
Other branching <sup>a</sup>	=	=	=	U		U	=	=	=	U
Plating	U	-	U	U		=	-	U	-	U
Mounds, encrusting and other	-	-	U	U		-	U	=	-	U

<sup>a</sup>Includes *Millepora*, *Montipora*, *Pocillopora*, *Seriatopora* and other branching corals

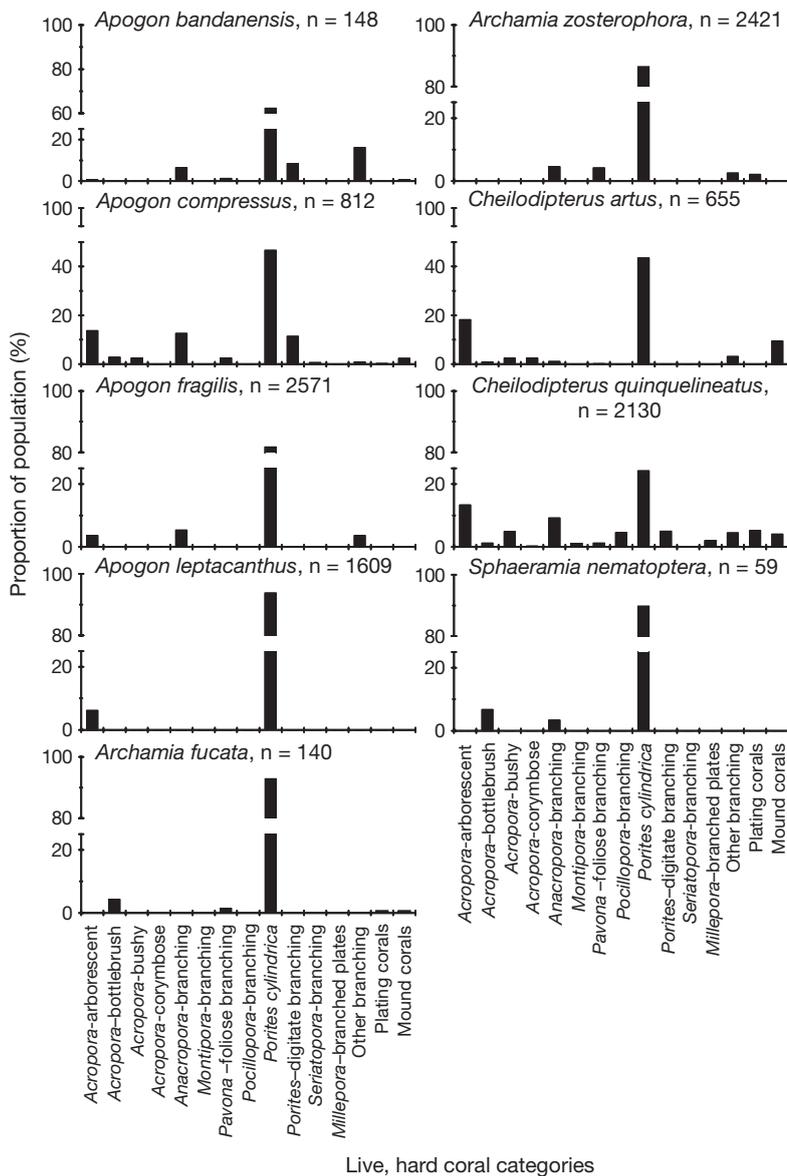


Fig. 4. Relative proportions of populations of 9 common apogonid species associated with different live coral substrata (n = estimated no. of individuals sampled per species)

broadly overlapped in shallow water (Fig. 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.

With the exception of the cave dweller *Apogon nigrofasciatus*, niche overlap on coarse microhabitat subdivisions was always higher than 80% (Table 4a). This reflects the high level of use of live coral in 9 of the 10 most abundant species. The lowest pair-wise over-

lap generally occurred between species that contrasted in their degree of apparent specialisation (e.g. 81.5% overlap between *Archamia fucata* and *Cheilodipterus artus*, and 81.9% overlap between *Archamia zosterophora* and *C. quinquelineatus*). *A. nigrofasciatus* clearly utilised different niche space than 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 (*Porites cylindrica*) (Table 4). Generally, the more specialised on this coral type the 2 species being compared were, the higher their overlap. Similarly, the least specialised species exhibited highest overlap with each other (e.g. 71.5% between *Cheilodipterus quinquelineatus*, *C. artus* and *Apogon compressus*). The lowest niche overlap values occurred between the most and least specialised species. For example, 35.9% between *Apogon leptacanthus* and *C. quinquelineatus*, 34.6% between *Sphaeramia nematoptera* and *C. quinquelineatus*, and 33.3% between *Archamia fucata* and *C. quinquelineatus*.

Apogonids not only exhibited a high degree of overlap in habitat use, they also frequently co-occurred in the same coral. Multispecific aggregations of cardinalfishes accounted for >75% of 74 aggregations on *Porites cylindrica* of >10 individuals (Fig. 6). There were usually 1 to 4 species per aggregation (16 to 27% occurrence) with 3 the most number of species recorded (27%). The highest species richness in a single aggregation was 7 species, but this was rare (2.7% frequency).

#### Relationship between specialisation and abundance

The abundance per species was positively related to the range of coarse and live coral microhabitats used, but only when measured as the number of groups per species (Fig. 7). That is, the more specialised a species was, the rarer groups were (Fig. 7a,c). For example, only 19 *Apogon leptacanthus* groups and 14 *Sphaeramia nematoptera* groups were found compared to 311 groups of the less specialised *Cheilodipterus quin-*

*quelineatus* (Table 2). The number of individuals per species was not correlated to the number of habitats they occupied (Fig. 7b,d). There was a poor relation-

ship between the number of groups and the number of individuals ( $r = 0.36, p > 0.05$ ), which explains the lack of correspondence between the 2 levels of examining specialisation/abundance relationships.

**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 emphasised 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. Our 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 daytime 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 & Bouchon 1989) and obligate coral-dwelling gobies (Munday et al. 1997, Munday 2000).

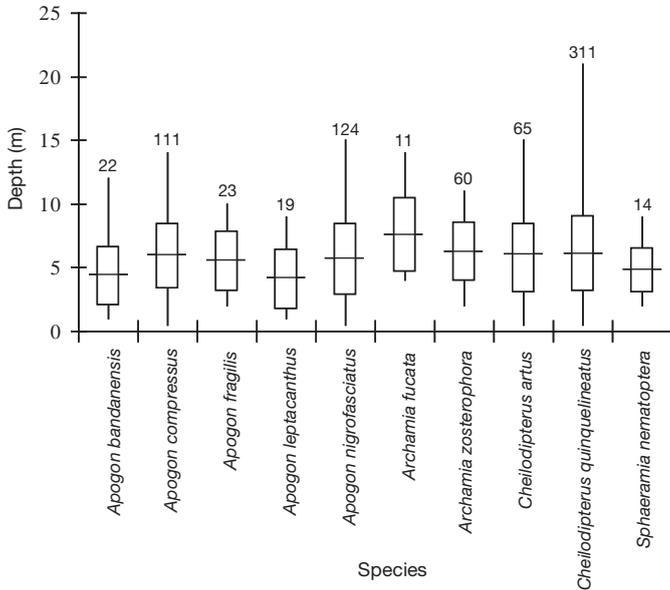


Fig. 5. Depth distributions of 10 common apogonid species, including mean depth (horizontal line), standard error (vertical rectangle), total depth range (vertical line) and no. of groups per species

Table 4. Niche overlap of 10 cardinalfish species using percentage overlap method (Krebs 1999) on (a) coarse microhabitats and (b) live coral substrata (*Apogon nigrofasciatus* excluded)

	<i>Apogon compressus</i>	<i>Apogon fragilis</i>	<i>Apogon leptacanthus</i>	<i>Apogon nigrofasciatus</i>	<i>Archamia fucata</i>	<i>Archamia zosterophora</i>	<i>Cheilodipterus artus</i>	<i>Cheilodipterus quinquelineatus</i>	<i>Sphaeramia nematoptera</i>
<b>(a)</b>									
<i>Apogon bandanensis</i>	100	99.0	98.7	8.9	96.1	96.1	86.1	86.0	98.1
<i>Apogon compressus</i>	100	100	99.5	9.4	96.7	96.7	86.6	88.7	99.6
<i>Apogon fragilis</i>		100	98.2	10.7	94.5	94.5	88.1	95.6	100
<i>Apogon leptacanthus</i>			100	9.1	100	100	86.2	85.8	100
<i>Apogon nigrofasciatus</i>				100	6.3	6.3	10.0	10.7	6.3
<i>Archamia fucata</i>					100	100	81.9	81.5	100
<i>Archamia zosterophora</i>						100	81.9	81.5	100
<i>Cheilodipterus artus</i>							100	94.2	86.2
<i>Cheilodipterus quinquelineatus</i>								100	85.8
<b>(b)</b>									
<i>Apogon bandanensis</i>	66.8	75.1	65.5		67.0	75.7	59.5	50.2	68.3
<i>Apogon compressus</i>	100	58.8	71.1		53.0	57.0	71.5	71.5	54.6
<i>Apogon fragilis</i>		100	90.4		86.5	93.4	62.2	43.1	89.9
<i>Apogon leptacanthus</i>			100		92.9	86.3	59.3	35.9	89.8
<i>Archamia fucata</i>					100	100	54.7	33.3	94.1
<i>Archamia zosterophora</i>						100	57.5	39.1	89.7
<i>Cheilodipterus artus</i>							100	59.0	55.9
<i>Cheilodipterus quinquelineatus</i>								100	34.6

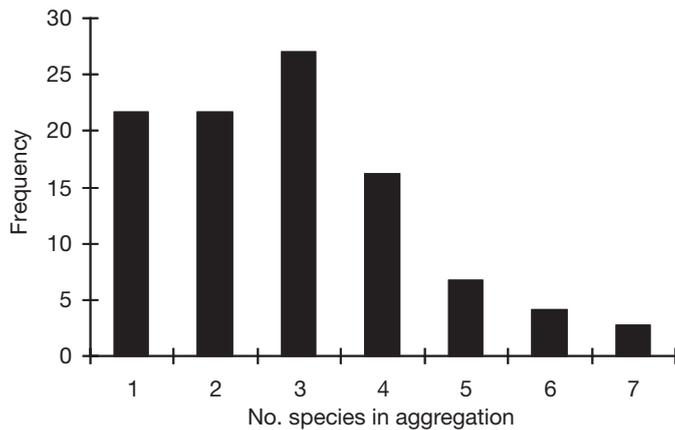


Fig. 6. Frequency distribution of multispecific aggregations of cardinalfish associated with *Porites cylindrica* outcrops (based on 74 observed aggregations). An aggregation is defined as more than 10 individuals resting together in the same coral head

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 almost all cardinalfish species were positively associated with it. A number of factors could explain the convergence in apparent selection for branching corals and this particular species. Firstly the quality of shelter has a strong influence on coral reef fish survivorship (e.g. Beukers & 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 & 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 postsettlement mortality compared to other reef fish groups (Beukers-Stewart & 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 & Bellwood 2002). Small eddies could concentrate availability of plankton within branching corals as well as minimise the energy fish expend in maintaining resting positions.

Our 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 & Johnson 1990). However, patterns described for particular species are supported by the literature where they are known. For example, Marnane (2001) and Nanami & Nishihira (2003) describe a similarly broad use of microhabitat types by *Cheilodipterus quinquelineatus*

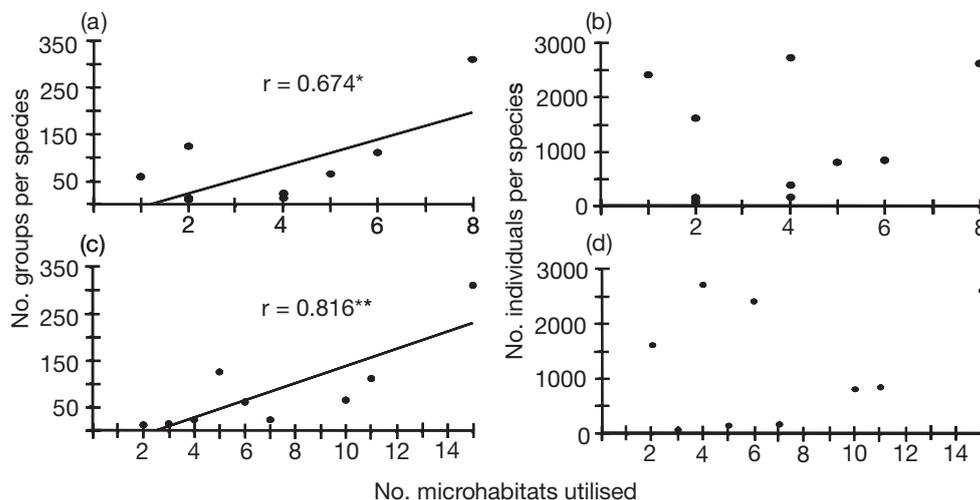


Fig. 7. Relationship between microhabitat specialisation and abundance of 10 common cardinalfish species. Habitat specialisation is defined as the number of habitats utilised. Abundance measured both by no. groups and no. individuals per species. (a) Coarse substrata and total no. of groups. (b) Coarse substrata and total no. of individuals. (c) Live coral substrata and total no. of groups. (d) Live coral substrata and total no. of individuals. \*\* $p < 0.01$ , \* $p < 0.05$

and the similarity in microhabitat associations between it and *C. artus* (Marnane & 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 our 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 8 yr due to a variety of factors (Jones et al. 2004, Munday 2004). 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 daytime resting sites was associated with a high overlap among species. Previous studies have emphasised limited diurnal segregation amongst reef zones (Greenfield & Johnson 1990, Marnane 2001, Marnane & Bellwood 2002), but here we show this extends to depths and microhabitats within zones. This low level of habitat partitioning does not follow from competition theory (Hutchinson 1957, Hardin 1960, MacArthur & 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 microhabitat partitioning among fish species and the high frequency of multispecific colony formation all suggest that competition for shelter may be minimal (see also Greenfield & 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 and predator evasion and diluting the individual's mortality risk (Pitcher 1986). However, coral reef piscivores prey heavily on apogonids (Kingsford 1992, Beukers-Stewart & 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 intraspecific aggregative behaviour, as this leaves space available to weak competitors (Atkinson & 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 & 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 *Apogon leptacanthus* was found in branch tips (Ida & 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 microhabitat 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 2004). 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 2004). *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) suggest that the family's vulnerability is comparable to, 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. Our hypothesis that 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) is deserving of a high research priority.

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