

A multi-scale study of the relationships between habitat use and the distribution and abundance patterns of three coral reef angelfishes (Pomacanthidae)

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ABSTRACT: The degree to which species partition resources often depends on the spatial scale of the study. To investigate this, we examined the distribution and abundance patterns of 3 relatively rare pygmy angelfishes (family Pomacanthidae: *Centropyge*) among reef locations, depths and microhabitats at Lizard Island on the Great Barrier Reef. A strong association among species and between species and their habitat was found at some scales, but not others. On a broad scale, the abundances of the 3 species were highest at the same 4 sites (kilometres apart). These sites were all located at headlands, suggesting that the patterns of abundance may be in response to the topographic features of the island at this scale. Differences among species occurred at intermediate scales (10s to 100s of metres), where species were associated with different depth zones or reef locations. *Centropyge vroliki* occurred shallower than *C. bicolor*, while the depth distribution of *C. bispinosa* overlapped with both of these species. Laterally along the fringing reef, *C. vroliki* were more abundant in areas where both *C. bicolor* and *C. bispinosa* were also abundant, but these 2 latter species were not correlated with each other. The proportions of substratum types present in home patches differed among species, to some extent reflecting the benthic composition of the reef area where each occurred. However on a fine scale (metres), all 3 species appeared to use the same substratum type, which consisted of dead branching coral covered in algae, and occasionally formed multi-species groups. Species abundances were not correlated with this commonly used microhabitat, but rather the availability of the substrata characterizing the reef areas in which they were most abundant. Here, although *Centropyge* species use the same type of microhabitat, they may be an example of species that partition space on the basis of non-preferred resources. For example, all 3 species used home patches containing high proportions of overgrown corals; however where this habitat was not available, *C. bicolor* used sand and rubble habitat at the reef base, while *C. vroliki* used coral habitat on the reef crest. Most importantly, this study emphasizes that a multi-scale approach is necessary to determine appropriate scales for examining species associations and resource partitioning in reef fishes.

KEY WORDS: *Centropyge* · Pomacanthidae · Great Barrier Reef · Habitat use · Distribution patterns · Multi-scale analysis · Spatial scale · Species associations

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INTRODUCTION

The importance of resource partitioning to the coexistence of ecologically similar coral reef fish species

and its relationship to the high diversity that characterizes these assemblages have been the subject of much debate. Early studies on reef fish communities not only found them to be highly speciose assemblages, but also to be relatively generalised in terms of both diet and space requirements (Roughgarden 1974, Sale

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1975, 1977, 1978). This appeared to conflict with competition theory, which argued that coexistence in diverse assemblages results from the partitioning of resources among species (Pianka 1966, MacArthur 1969, Colwell 1973). Early attempts to demonstrate that competition plays a role in habitat partitioning on coral reefs repeatedly failed (Doherty 1983, Roberts 1987, Jones 1988). As an alternative, it has been argued that diversity may be related to the variability in the supply of pelagic larvae and juvenile recruitment, at levels below which space would become saturated (Talbot et al. 1978, Doherty 1983, Victor 1983, Sale et al. 1984, Doherty & Williams 1988). This variability may act to reduce the capacity for a competitively dominant species to eliminate an inferior competitor.

Since the pioneering work on reef fishes, numerous studies have documented distinct patterns of food and habitat utilisation among similar species. Examples can be found in a range of coral reef fish families including surgeonfishes (Robertson 1980, Waldner & Robertson & Gaines 1986, Robertson & Lassig 1980), blennies (Clarke 1994), groupers (Shpigel & Fishelson 1989), sandperch (Sano 1990), damselfishes (Ormond et al. 1996), butterflyfishes (Pitts 1991, McAfee & Morgan 1996) and gobies (Munday et al. 1997). In addition, there is increasing evidence that inter-specific competitive interactions play a role in maintaining species-specific patterns in habitat use (Robertson 1984, 1996, Ebersole 1985, Robertson & Gaines 1986, Clarke 1989).

There are a number of reasons why some studies emphasize ecological similarities among species, while others highlight their differences. Coral reef fishes are found in an environment which is structurally complex on a hierarchy of spatial scales (Sale 1991, 1998) and reef fish appear to respond to the environment at all spatial scales that have been examined (Williams 1991). For example, the species composition of fish assemblages have been found to vary across continental shelves (Williams 1991), along gradients of wave exposure (Talbot 1965, Williams 1982, Victor 1986), and depth (Waldner & Robertson 1980, Eckert 1985, Fowler 1990, McCormick 1994, Green 1996), and among microhabitats (Itzkowitz 1977, Jones 1988, Jennings et al. 1996, Ormond et al. 1996). However, not all species respond to all gradients in habitat structure, and species may partition resources at some scales and not others. Consequently, multi-scale approaches should be used to identify appropriate scales to measure ecological similarity and differences among species.

Different levels of resource partitioning may be characteristic of different taxa. Ecological theories regarding processes which contribute to high diversity in coral reef fish assemblages have been constructed pri-

marily on the results of studies on relatively common and speciose taxa, such as damselfish (Doherty 1983, Sale et al. 1984). However, coral reefs contain a large number of species that are locally rare even though the dispersive larval stage ensures relatively wide geographic distributions (Jones & Kaly 1995). Patterns of resource partitioning in common taxa may not be representative of their rarer counterparts. If rarity results from low availability of preferred resources, then competition for these resources may be more intense among closely related rare species compared with more common ones. Alternatively, if rarity is due to inherent life history characteristics such as low reproductive output, recruitment rates, or mortality rates, then shared resources may be in abundant supply, and thus resource use among rare species may overlap to a greater degree than expected. An examination of patterns of resource use by rare species and their subsequent effects on distribution and abundance may give some indication of whether coexistence in rare species is maintained through resource partitioning. In addition, investigations of rare species may provide further clues as to the causes of diversity in reef fish assemblages as a whole.

Pygmy angelfishes (genus *Centropyge*) are a group of relatively rare but conspicuous reef fishes, with several congeners occurring on almost all tropical coral reefs. These characteristics make the pygmy angelfishes an ideal genus to compare resource utilization traits and determine how they may affect patterns of distribution. Pygmy angelfishes are known to be highly site-attached with the females holding foraging territories, while the males defend females from other males throughout the year (Lobel 1978, Moyer & Nakazono 1978, Bauer & Bauer 1981, Moyer et al. 1983, Aldenhoven 1984, Sakai & Kohda 1997). Although some information has been published on the habitat requirements of particular *Centropyge* species (Moyer & Nakazono 1978, Moyer et al. 1983, Aldenhoven 1984, Sakai & Kohda 1997), there are no quantitative studies to date that compare habitat use among more than 1 species of *Centropyge*.

This study investigated the distribution and abundance patterns of 3 pygmy angelfishes, *Centropyge bicolor*, *C. vroliki* and *C. bispinosa*, at multiple spatial scales. The aim was to determine appropriate scales for examining ecological partitioning among these species. The spatial scales examined were (1) a large spatial scale (≥ 1000 m) encompassing an exposure gradient, (2) a medium spatial scale (10 to 100 m) along a depth gradient, and (3) fine-scale (1 to 10 m) patterns of dispersion within habitats. The first 2 scales relate to environmental gradients which reef fish are known to respond to, while the smallest scale relates to the extent of movement of *Centropyge* individuals based

on the behavioural observations of a previous study (Aldenhoven 1986). Using this sampling hierarchy, we were able to identify scales at which habitat resources appear to influence patterns of angelfish abundance and distribution.

METHODS

Study location and species. This study was carried out at Lizard Island, a continental island located approximately 35 km off the coast of Australia in the northern sector of the Great Barrier Reef ($14^{\circ}40'S$, $145^{\circ}28'E$). The fringing reefs surrounding the island were divided into 3 sites according to their exposure to the prevailing southeasterly trade winds (Fig. 1a): sheltered (S), moderately exposed or oblique to the prevailing wind (M) and directly exposed (D) (Choat & Bellwood 1985). At Lizard Island, pygmy angelfishes (genus *Centropyge*) are rare in terms of local abundance (*sensu* Gaston 1994) comprising less than half a percent of the demersal reef fish community (Syms & Jones unpubl.). They are, however, easily identifiable by their small size and distinct colour patterns. Three species, *C. bicolor*, *C. vroliki* and *C. bispinosa*, were found in the sites surveyed for this study.

Sampling design. A total of 9 sites, 3 within each of the 3 exposures at Lizard Island (i.e. S1–S3, M1–M3 and D1–D3) were censused visually for *Centropyge*. Four replicate 100×10 m transects were conducted at each of the 9 sites surveyed, except for one site (D3), where only 3 transects were censused due to adverse weather conditions. For each transect, a 100 m long tape was placed approximately 3 m below and parallel to the reef crest, and pygmy angelfish occurring within 5 m either side of the tape were counted (Fig. 1b). Such a large sampling unit was required due to the rarity of *Centropyge* species. Along each transect, the depth of each *Centropyge* was recorded, and their locations within the transect were mapped to provide comparative information on the degree of dispersion for each species. Data from 2 additional sites, 1 sheltered (Mermaid Cove) and 1 exposed (Bird Islet), were included in the analysis of the smaller scale distribution patterns.

The availability of microhabitats at 7 of the 9 sites used in the fish censuses were quantified by sampling in 3 reef zones: crest, slope and base. Two sites (D2 and D3) were excluded from the data collections due to adverse weather conditions. The same sampling design was used to survey the available habitat as was used for the visual censuses. Four transects 100 m long were carried out at each site, and within these transects the habitat was surveyed separately for each of 3 reef zones, the crest, slope and base (Fig. 1b). Ten ran-

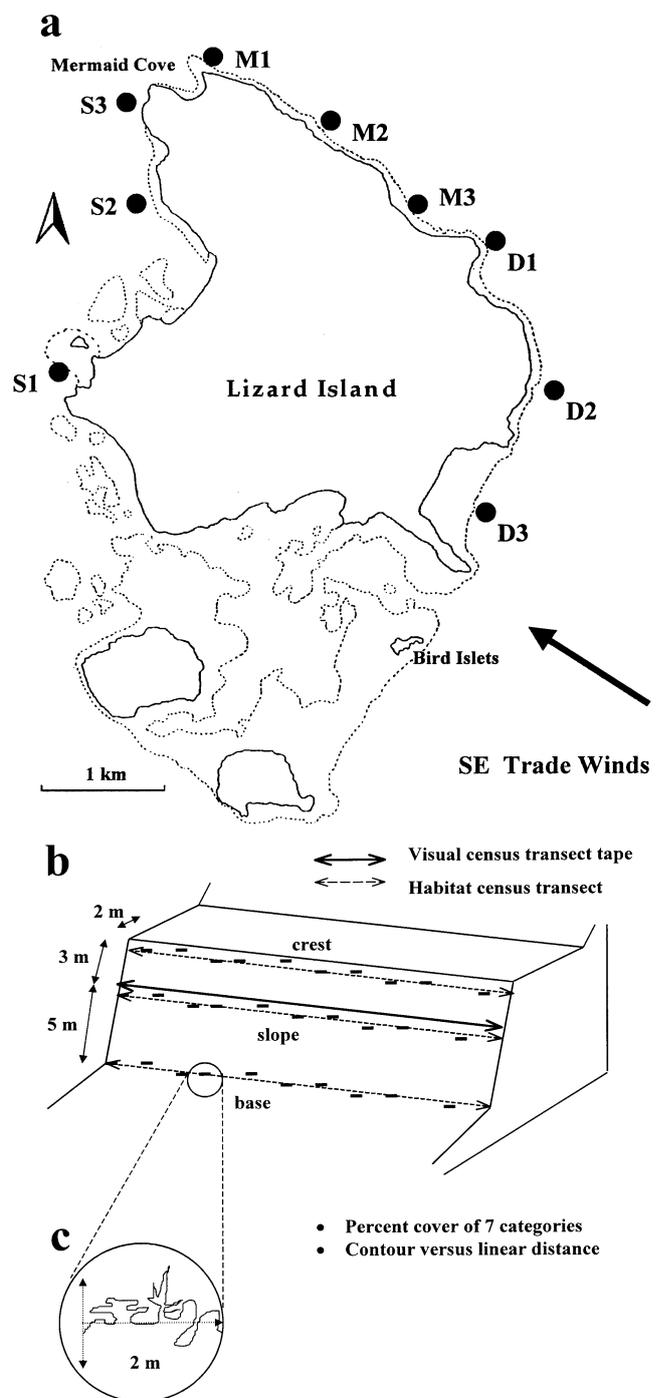


Fig. 1. (a) Map of Lizard Island ($14^{\circ}40'S$, $145^{\circ}28'E$), showing the main sites used in this study and the direction of the prevailing wind. Codes refer to the relative degree of exposure: S = sheltered, M = moderately exposed, D = directly exposed. (b) Overlay of fish census and habitat availability transects. Within each 'fish' transect, 3 'habitat' transects were laid out along the reef crest, slope and base, in which 10 discrete 2 m sections were surveyed. (c) Data recorded for each 2 m section of habitat surveyed included the topographical complexity (contour vs linear distance) and percentage cover of 7 substratum categories (see Table 1)

domly selected 2 m sections were surveyed along each of these zones. For each 2 m section, the topographic complexity (ratio of contoured length to 2 m) was measured and the intercept lengths of 7 substratum categories (Table 1) along the 2 m section were quantified to estimate percentage composition (Fig. 1c).

To determine the characteristics of the reef substrata used by each of the 3 species of *Centropyge*, 2 m line transects laid parallel to the reef crest were surveyed over the home patches of 45 groups of *Centropyge vroliki*, 43 of *C. bicolor* and 22 of *C. bispinosa*. The home patch was defined as the area of reef into which members of a particular social group would retreat most often when disturbed, and around which most of their foraging was based. Home patches were usually based around an outcrop of rock or coral and contained portions of territories of individual fish. In addition, 13 home patches were surveyed which were occupied by 2 or more species of *Centropyge*.

Analysis of distribution and abundance. Total abundance estimates of the 3 species of *Centropyge* were compared among exposures and sites (nested in exposures) using MANOVA followed by a non-metric multidimensional scaling (MDS). To examine the relative abundances of each species of *Centropyge* among sites, an MDS was carried out using a Quantitative Symmetric Kulezynski (QSK) matrix to preserve the rank order of dissimilarities. A complete linkage cluster analysis using Ward's method on the dissimilarities from the matrix was used to group sites according to their similarity in relative abundance of the 3 species, and this was superimposed on the first 2 dimension axes.

Pairwise Pearson's correlations were used to test for associations between species of *Centropyge* at the transect level. Data were $\log_{10}(x + 1)$ transformed to reduce the variation resulting from low numbers. To assess patterns in inter-specific associations at an even smaller spatial scale (within 10 × 10 m sections of reef), the presence of each species relative to the presence of

the others were compared using chi-square test of independence with an adjusted alpha value (Bonferroni method) for multiple comparisons. At this fine scale, the presence and absence of each species were compared rather than absolute numbers to overcome the bias of different group sizes among the species. Distributions which were found not to be independent were tested for the nature of their association (positive or negative) using the phi coefficient of association (Sokal & Rohlf 1995). These data were obtained from the mapped distributions of fish within each transect using the co-ordinates recorded during visual censuses.

To compare the relative depth distributions among the 3 species of *Centropyge*, the depths recorded for each individual were standardised to mean low water tide. The depth frequency distributions across all sites were then compared among species using Kolmogorov-Smirnov tests with an adjusted alpha value (Bonferroni method) for multiple comparisons (Sokal & Rohlf 1995).

Analysis of habitat use. Similarities in the habitat occurring in home patches among *Centropyge* species were examined by comparing the relative proportion of substratum categories, and the variability in the micro-topographic reef profiles. Out of the 13 shared patches censused, 6 were occupied by groups of both *Centropyge bicolor* and *C. vroliki*, 3 by all 3 species, and 2 each by *C. bispinosa* with *C. bicolor*, and *C. bispinosa* with *C. vroliki*. To determine whether the 3 species differed significantly in their habitat use, data were analysed using a 1-way MANOVA. Pillais Trace statistic was used to determine significance. A canonical discriminant analysis (CDA) was used to display similarities in habitat use by plotting each of the 3 species in a 2-dimensional space. Confidence ellipses (95%) were calculated for all the group mean centroids using the formula:

$$95\% \text{ CL} = \sqrt{(\chi^2_{2, 0.05/n})}$$

where n = the number of replicates (Seber 1984).

Table 1. Seven broad substratum categories used to define reef microhabitat

Algae	1. Algae (flat): Non-complex reef substrata (e.g. massive corals, reef base) overgrown with epilithic algae or macroalgae
	2. Algae (compl): Complex reef substrata (e.g. branching corals) overgrown with epilithic algae or macroalgae
Sand & rubble	3. Calcareous or silicious sediment, live and dead coral rubble
Encrusting organisms	4. Benthic categories with an encrusting morphology, including scleractinian corals, algae and sponges
Alcyonarians	5. Includes all soft corals
Scleractinians	6. Complex corals: Corals with complex morphologies, including branching, corymbose, digitate, foliose and tabular forms
	7. Massive corals: Corals with a massive morphology, or solitary forms

Electivity indices were used to determine if *Centropyge* species incorporated particular substratum categories into their home patches disproportionately to their availability in the environment. The Vanderploeg & Scavia (1978) electivity index (E^*) was used because it is considered to be one of the most robust electivity indices (Lechowicz 1982). Positive values indicate that a particular category is used in greater proportions than expected from its availability. Negative values indicate that categories are used less than expected.

An electivity coefficient (E^*) was calculated separately for each species of *Centropyge* for every substratum category using the formula

$$E^* = [W_i - (1/n)]/[W_i + (1/n)]$$

where n = the number of resource types (substratum categories), $W_i = (r_i/p_i)/\sum(r_i/p_i)$, r = the proportion of resource utilised, and p = the proportion of resources available (Vanderploeg & Scavia 1978). To compensate for potential variability in the habitat associations exhibited by *Centropyge* across reef zones, electivities were calculated for the average composition of available habitat types for the reef zone in which the territory occurred. Therefore, mean electivities and standard errors could be calculated for each species.

Finally, canonical correlations were calculated to detect any relationships between the abundance estimates [$\log_{10}(x + 1)$] of the 3 species of pygmy angelfish and the availability of habitat types in each site/zone across all exposures. No relationship was detected between the abundance of any species with the habitat available at the site level. Therefore, both abundance and habitat were separated into the 3 reef zones at each site to incorporate the effect of depth into the analysis. Canonical coefficients of the species (intersets) were then plotted into the space defined by the canonical coefficients of the habitat variables (intrasets).

RESULTS

Distribution and abundance patterns

Over the 9 sites censused, a total of 910 individuals from the genus *Centropyge* were recorded around Lizard Island. Relative abundance patterns of the 3 species found were extremely consistent, with *Centropyge bicolor* always being the most abundant, and *C. bispinosa* the least abundant (Fig. 2a). There were significant differences in the abundances of *Centropyge* among exposed, oblique and sheltered sites, and also in the abundances of *Centropyge* among sites within each exposure (Table 2). Within each exposure type, 2 out of 3 sites tended to be similar in their abun-

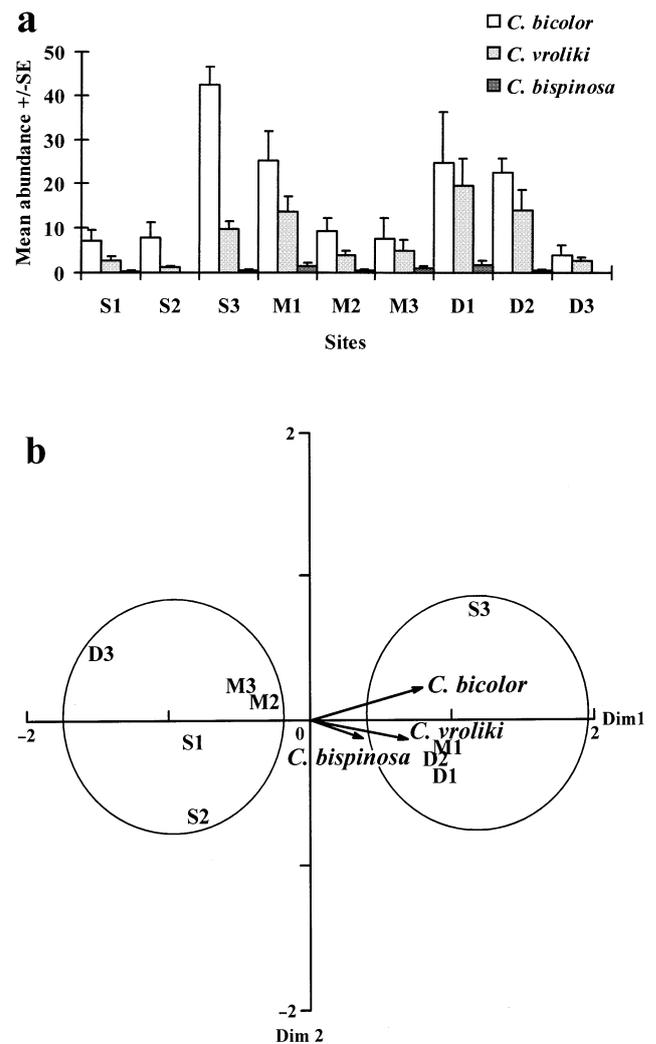


Fig. 2. (a) Mean abundances (\pm SE) 1000 m⁻² of the 3 *Centropyge* species at 9 sites including 3 sheltered sites (S1–S3), 3 moderately exposed sites (M1–M3) and 3 directly exposed sites (D1–D3). (b) Non-metric multidimensional scaling of *Centropyge* mean abundances. Sites are represented by their exposure codes and plotted on a dissimilarity matrix described by the 3 species vectors. The 2 clusters show the results of a complete linkage cluster analysis using Ward's method on the dissimilarities from the matrix

dance and composition of the 3 angelfish species while the third site differed markedly in each case (Fig. 2b). Furthermore, 2 main groups within the 9 sites, separated along dimension 1 of the MDS, were identified by the cluster analysis which do not correspond to exposures (Fig. 2b). Sites S3, M1, D1 and D2 were characterized by high abundances of all 3 species of *Centropyge*, while sites S2, S3, M2, M3 and D3 exhibited relatively low abundances (see also Fig. 2a). Interestingly, sites with high abundances of *Centropyge* correspond to reefs that are adjacent to headlands

Table 2. MANOVA result comparing distribution patterns of *Centropyge* species among exposure regimes and sites nested within exposures. $\alpha = 0.05$, *significant effects

Source of variation	Pillais trace	Hypoth. df	Error df	F	Significance of F
Exposure	1.360	6	10	3.544	0.038*
Site(Exposure)	0.887	18	78	1.8194	0.037*

around Lizard Island and sites of low abundance corresponded to reefs located in bays (Fig. 1a).

Although all 3 species of *Centropyge* were most abundant at the same sites, a similar pattern was not observed at the 2 smaller scales examined. At the scale of transects (100 × 10 m), high abundances of *Centropyge vroliki* coincided with high abundances of *C. bicolor* and also *C. bispinosa*, but the abundance estimates of the latter 2 species were not correlated (Table 3). Similarly, *C. vroliki* were more often seen in 100 m² quadrats, where either *C. bicolor* and *C. bispinosa* were also found, than would have been expected if the species were distributed independently (Table 3), while the occurrences of the latter 2 species were independent.

The 3 species of *Centropyge* largely overlapped in their depth distributions over the range surveyed in this study (Fig. 3). All 3 species were found between depths of 1 and 6 m; however *Centropyge vroliki* and *C. bicolor* were also found as deep as 9 and 10 m respectively. Kolmogorov-Smirnov tests using the total frequency of counts for each depth found that there was a significant difference in the depth distribution between *C. bicolor* and *C. vroliki* ($D = 0.369$, $\alpha = 0.017$, $p < 0.001$), but not between *C. bispinosa* and *C. bicolor* ($D = 0.200$, $\alpha = 0.017$, $p < 0.025$), or *C. bispinosa* and *C. vroliki* ($D = 0.197$, $\alpha = 0.017$, $p < 0.05$). *C. vroliki* was generally found in shallower sections of the reef, with over a quarter of individuals (26%) between 0 and 1 m (around the crest) and with the frequency of observation generally declining with depth. In contrast, the depth distribution of *C. bicolor* approximates a normal distribution, with the greatest frequency of observation between 4 and 5 m, and 31% seen below 6 m.

Habitat availability and use

The characteristics of the habitat found in home patches varied significantly among species of *Centropyge* (Table 4). These results reflect the depth distribution of each species and corresponding depth-related changes in the benthic cover. In a CDA of home patch habitat composition (Fig. 4) the first 2 canonical axes explained 84% of the variation among habitat characteristics. Differences in depth and the

cover of living complex corals accounted for approximately 46% of the variation among home patches (Can 1, Fig. 4). Complex overgrown corals and topographical complexity of habitats accounted for approximately 38% of the variation among home patches (Can 2, Fig. 4). In general *Centropyge bicolor* home patches differed significantly from those of *C. vroliki*, in that they occurred at greater depths and contained proportionately less amounts of live complex corals. *C. bispinosa* territories occurred in areas

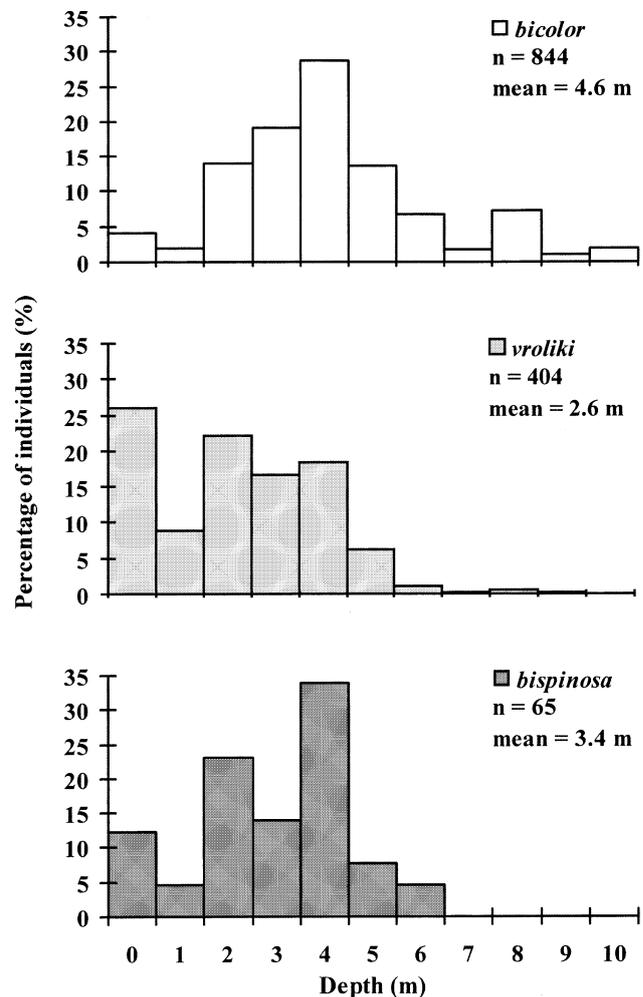


Fig. 3. Depth frequency distributions for the 3 *Centropyge* species across all sites

that were intermediate between the other 2 species in depth and the percent cover of living complex corals. However territories were topographically more complex and contained higher proportions of overgrown complex corals than either *C. vroliki* or *C. bicolor* sites. Shelter sites shared by more than 1 species of *Centropyge* similarly consisted of a higher percentage cover of complex corals overgrown with algae than *C. bicolor* and *C. vroliki* territories.

A comparison of microhabitat use and availability showed that all 3 species appeared to use the same microhabitat (Fig. 5). Overall, home patches for all of the species contained a higher percentage cover of overgrown complex corals than would be expected from the proportion available. Interestingly, there is strong use of overgrown rather than living complex coral substrata, which was not used by any species. Furthermore, all 3 species used non-complex substrata overgrown with algae in approximately the same proportions to which it was available, while most other categories were present in lower proportions in home patches than available.

Correlations between abundance and habitat

While all 3 *Centropyge* species appeared to associate with reef patches which had high proportions of complex reef substrata covered in algae, only the abundance of *Centropyge bispinosa* correlated with the availability of this habitat type (Fig. 6) The canonical correlation indicates that higher numbers of *C. bispinosa* occur where this type of habitat occurs, regardless of the site or reef zone. In contrast, the abundances of *C. bicolor* and *C. vroliki* were not correlated with this commonly used microhabitat. Instead, their abundances were related to the features of depth strata with which each were related (Fig. 4). *C. bicolor* was more abundant at site/zones where there were increased amounts of sand and rubble, while *C. vroliki* was more abundant in site/zones where there were more complex corals. On a fine scale, these species did not appear to be closely associated with these substrata and used them in lower proportions than expected on the basis of their availability (Fig. 5).

Table 3. Analysis of intermediate and small-scale dispersion patterns of *Centropyge* species. Values in the top right section are correlation coefficients and p-values (parentheses) between the log abundance at the transect level (1000 m⁻²). *Significant correlations. Values in the bottom left section are chi-square values for the within transect distribution of *Centropyge* species (100 m⁻²). *Significant non-independence at $\alpha = 0.013$. The values in parentheses are phi coefficients of association ($-1 < \phi < +1$), where a positive value indicates a positive association, and a negative value would indicate negative association

	<i>C. bicolor</i>	<i>C. vroliki</i>	<i>C. bispinosa</i>
<i>C. bicolor</i>		0.56 (0.001)*	0.31 (0.070)
<i>C. vroliki</i>	10.64* (+0.17)		0.44 (0.008)*
<i>C. bispinosa</i>	0.92	17.87* (+0.31)	

DISCUSSION

The numerical relationships among the 3 *Centropyge* species, and their patterns of association with features of the habitat, varied depending on the spatial scale examined. Species were positively associated

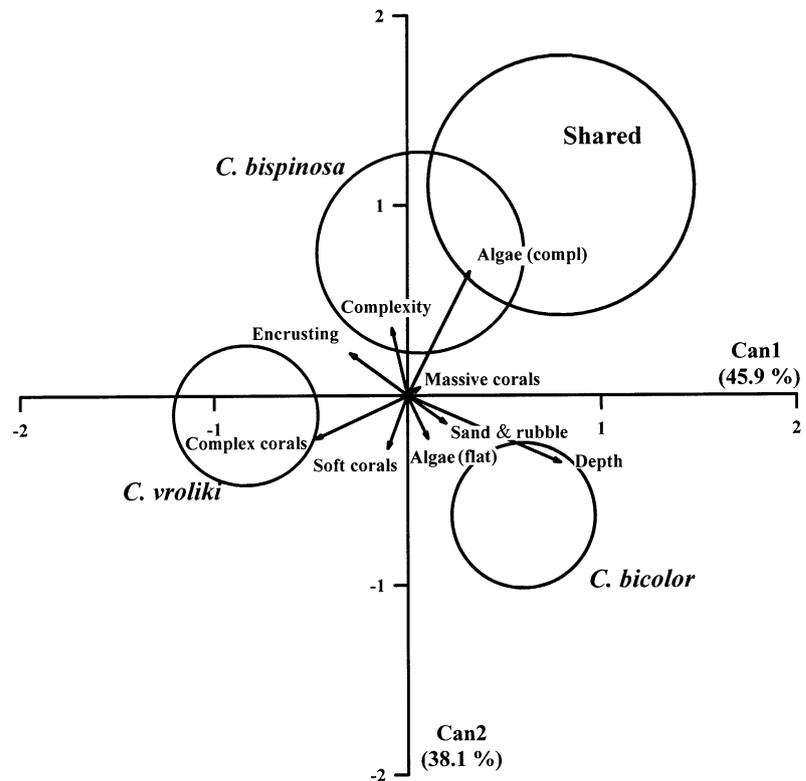


Fig. 4. CDA of the characteristics of shelter sites used by each species of *Centropyge*. Circles are plotted around the means and the size corresponds to the 95% confidence ellipses of the canonical scores for the substratum composition and profile characteristics of each species. The proximity of circles indicates the similarity in the habitat used. Vectors are structural coefficients of response variables. Axis labels show the proportion of the variation explained by the plot. Can1 and Can 2 = canonical variates 1 and 2

Table 4. MANOVA results for differences in percentage composition of benthic categories, complexity and depth of shelter sites inhabited by *Centropyge* species. n = 43, 45, 22 for *C. bicolor*, *C. vroliki* and *C. bispinosa* respectively, and n = 13 for shared sites. $\alpha = 0.05$, *denotes significant effects

Source of variation	Pillais trace	Hypoth. df	Error df	F	Significance of F
Species	0.733	27	339	4.061	0.0001*

with each other at some scales but abundances were inversely related at others. Likewise, each species could be positively associated with particular habitat variables at one scale, but appeared not to associate with these habitats at others. Hence studies of these species carried out at different spatial scales could lead to opposite conclusions.

At the largest scale examined, the 3 species of *Centropyge* recorded the greatest abundance at the same

sites around Lizard Island. This suggests that they were responding to the same features of the environment and that there is no partitioning of resources among species at this scale. The factors affecting the distribution and abundance around whole reefs may be phylogenetically conservative in this group. While the species composition for other fish groups has been found to vary at the scale of wind exposures around Lizard Island (Choat & Bellwood 1985, Kingsford 1992, Meekan et al. 1995, Munday et al. 1997), this was not the case for *Centropyge*, which appeared to be associated with headlands. The increased abundance of *Centropyge* at these sites may be the result of preferential settlement by larvae (Victor 1986, Milicich et al. 1992, Tolimieri 1995, Doherty et al. 1996, Light & Jones 1997) or post-settlement survival (Doherty & Sale 1985, Shulman & Ogden 1987, Robertson 1988, Tupper & Hunte 1994), both of which may result in higher population abundances in more favourable habitats.

There could be several reasons why abundances are greater at headlands. Studies of the distribution of fish larvae around reefs have found that specific wind and current regimes can result in larval retention in particular reef areas (Leis 1986, Kingsford et al. 1991, Sponaugle & Cowen 1996). Wave refraction and the formation of slicks and eddies may be concentrating larvae at headlands, and densities of *Centropyge* may be reflecting these differential levels of passive larval supply. Alternatively, high abundances of *Centropyge* at headlands could be due to the preferential settlement of larvae. However, there is currently no information available on large-scale habitat preferences in *Centropyge*.

The headlands at Lizard Island may have upwellings or greater current speeds that are known to sustain higher densities of planktivorous fish (Kingsford & MacDiarmid 1988). It has been observed that populations of *Centropyge interrupta* at Miyake-jima (Japan) are greater in density along cliff areas where upwelling currents attract aggregations of plankton feeders (Moyer & Nakazono 1978). It was suggested that this may be due to the faecal materials of planktivores providing an important percentage of the diet of *C. interrupta*. *C. bicolor*, *C. vroliki* and *C. bispinosa* may be more abundant here because they consume detritus directly, however there is no evidence to sug-

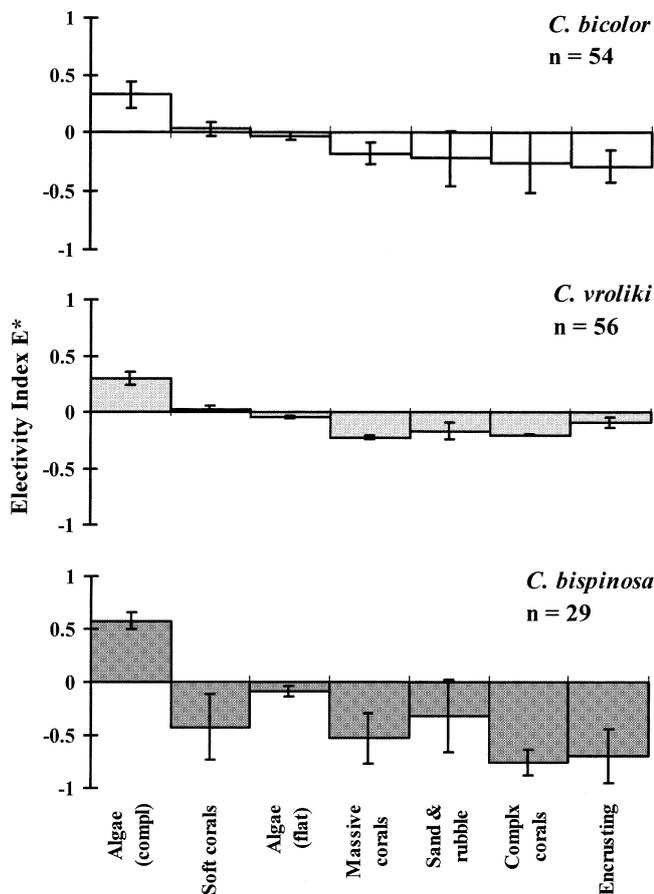


Fig. 5. Patterns of habitat selectivity for *Centropyge* species. Values are mean electivities (Vanderploeg & Scavia's E^*) and standard errors. Positive values represent greater use of a habitat type than was available. Negative values represent use of a habitat category less than would be expected from its availability

gest this at present. Alternatively, densities may be higher because increased levels of detritus may enhance the productivity of turf algae that they are known to consume (Moyer & Nakazono 1978, Aldenhoven 1984, Sakai & Kohda 1997, Eagle unpubl. data). However, no relationship was found between the abundance of species at headland sites and the presence of turf algae in this study.

It is possible that site-specific differences in mortality, if correlated among species, may also contribute to the distribution patterns observed. Mortality rates have been estimated to vary 10-fold among sites for *Centropyge bicolor* at Lizard Island (Aldenhoven 1986); however, further investigation is required, with a direct comparison between headland and bay sites.

The greatest species-specific differences in patterns of abundance and habitat-use occurred at the intermediate spatial scale examined. It appears that the species may be partitioning reef areas at scales of 10s to 100s of metres by depth and lateral location. *Centropyge vroliki* was most abundant on the reef crest, and *C. bicolor* was found deeper. There was no significant difference in the depth distribution between *C. bispinosa* and either of these 2 species. This may have been due to the relatively small number of observations of this rarer species obscuring patterns, or its relatively low abundance reducing the need for ecological partitioning. However laterally along the reef margin, *C. bispinosa* was not found in the same areas as *C. bicolor* at either the 1000 or 100 m² scale, even though *C. vroliki* was found where either *C. bicolor* or *C. bispinosa* were present. Depth partitioning has been reported for 2 cohabiting *Centropyge* species in Guam, where *C. shepardi* replaces *C. flavissimus* at depths greater than 20 m, with a zone of overlap from 20 to 24 m (Moyer 1981). Similar depth segregation has been reported for congeners of many other coral reef fishes, such as *Chaetodon* spp. (Bouchon-Navaro 1986, Fowler 1990), *Cephalopholis* spp. (Shpigel & Fishelson 1989), *Acanthemblemaria* (Clarke 1989), *Stegastes* spp. (Wellington 1992) and *Gobiodon* spp. (Munday et al. 1997).

The patterns of abundance of adult *Centropyge* in these reef zones may reflect differential recruitment to particular reef areas as a result of larval habitat selection. Distribution patterns may correspond with the availability of the reef substrata from which recruits emerge, as found for a number of other reef fishes

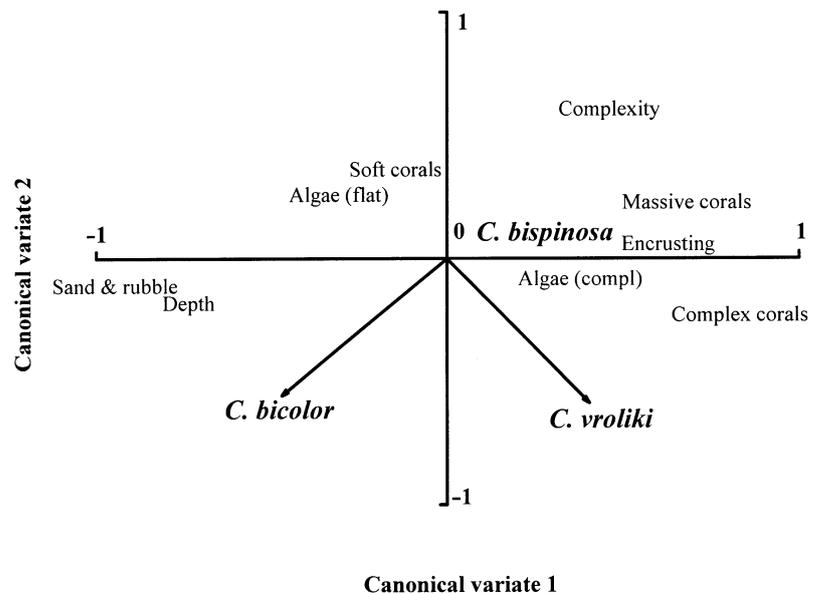


Fig. 6. Canonical correlation of *Centropyge* species abundances and availability of habitat types. Species and habitat projection biplots are shown in the space defined by the canonical variates of the habitat variables. See Table 1 for habitat codes

(Tolimieri 1995, Booth & Wellington 1998, Gutierrez 1998). Previous studies have found that adult densities of some reef fish are correlated with recruit densities (Victor 1986) and also that abundances of recruits are correlated with the availability of preferred shelter sites (Shulman 1984, 1985, Victor 1986, Jones 1987, Light & Jones 1997, Nemeth 1998, Booth & Wellington 1998). It is thought that *Centropyge bicolor* individuals recruit to deeper rubble substrata, whereas *C. vroliki* recruit to the reef flat (D. R. Bellwood pers. comm.). This suggests that *Centropyge* may have subtle ontogenetic shifts in resource use after settlement, in particular a habitat shift towards the reef proper from the reef edges. Post-settlement events such as niche shifts are not uncommon for coral reef fishes (McCormick & Makey 1997, Munday & Jones 1998, St. John 1999).

Depth distributions may also be maintained by preferential settlement of larvae to areas where adult conspecifics are already located (Sweetman 1983, 1985, Wellington 1992, but see Forrester 1995, 1999, Schmitt & Holbrook 1999). Or similarly, juvenile persistence may be confined to adult habitats, as has been found for cohabiting *Stegastes* congeners with complementary depth distributions (Wellington 1992). Thus adult distribution patterns may be driven by a combination of patterns of recruitment, subsequent habitat selection by juveniles and patterns of post-settlement mortality.

On the finest scale examined, all 3 species of *Centropyge* shared the same pattern of high use of algal-

covered substratum with a complex morphology, presumably because this type of habitat provides both food and shelter. Aldenhoven (1984) has previously noted that *Centropyge bicolor* at Lizard Island tended to use patches of habitat which contained both food (algae and detritus) and shelter (corals and crevices). Specific habitat associations have been noted for a number of other species of *Centropyge*. *C. interrupta* reportedly prefers areas such as tunnels and caves lacking in *Acropora* cover (Moyer & Nakazono 1978). In contrast, *C. argi* territories were found primarily in areas of 'lush coral growth' (Moyer et al. 1983), and similarly, *C. ferrugata* territories were found to contain higher coral coverage than the surrounding reef (Sakai & Kohda 1997).

It is as yet unknown whether species actively select particular patches of microhabitat, or simply survive and persist in these areas. One study has quantified *Centropyge* abundance in a comparison between reefs infested with *Acanthaster planci* and reefs that were unaffected (Sano et al. 1987). The feeding activities of these coral predators result in reefs retaining their structural complexity but becoming overgrown with turf algae. Interestingly, on living reefs means of 20 individuals (all *Centropyge vroliki*) 1000 m⁻² were recorded, while on affected reefs 30 individuals (of 2 species *C. vroliki* and *C. heraldi*) 1000 m⁻² were recorded. The same dead reefs were surveyed again after 2 yr, by which time they had been reduced to rubble with 0 fish 1000 m⁻² recorded. Notably, the living and affected reefs may have had naturally varying abundances of *Centropyge* which were not due to the effects of *A. planci*. However, it appears possible that overgrown complex habitat is desirable to species of *Centropyge* elsewhere, and that the availability of this type habitat may affect patterns of distribution and abundance.

In our study, however, no significant correlations were found between abundances of 2 of the *Centropyge* species and their commonly used micro-habitat, as has been found for other coral reef species (Tolimieri 1998, but see Robertson & Sheldon 1979). Instead, *Centropyge bicolor* abundances were correlated with the percentage cover of sand and rubble, a substratum category found in lower proportions in home patches than elsewhere. Similarly, *C. vroliki* abundances were positively correlated with the percentage cover of complex living corals, which was also present in lower proportions within home patches than elsewhere. Only abundances of *C. bispinosa* were correlated with the micro-habitat type all species were associated with. These patterns of abundance appear to reflect the species' differing broader-scale habitat use patterns rather than their common microhabitat use patterns.

If competition is involved in the determination of patterns of resource use, then it may involve both phylogenetic constraints in the use of some habitat features and partitioning of others. Competition theory predicts greater specialization and partitioning of resource use among species as competition becomes more intense. Conversely, optimal foraging theory predicts that species will become more generalized in their use of resources when competition becomes more intense and resource availability declines (Stephens & Krebs 1986). This contradiction between competition theory and optimal foraging theory in the role that competition plays in ecological specialization, and thus resource partitioning, has been termed Liem's Paradox. Robinson & Wilson (1998) proposed that because some resources are easy to use and widely preferred, while others require specialized traits by the consumer, optimally foraging consumers evolve specializations to use non-preferred resources without compromising their abilities to use preferred resources. Therefore, the evolution of specializations to use non-preferred resources can be driven by competition, but the specialists act as generalists whenever their preferred resources are available. It is possible that studies so far have not distinguished between preferred and non-preferred resources, which may be partitioned differently, in their examination of resource partitioning and its subsequent effects on distribution and abundance.

Patterns observed for *Centropyge* are consistent with Robinson & Wilson's (1998) proposed solution to Liem's Paradox. For pygmy angelfishes at Lizard Island, the commonly used and possibly preferred microhabitat for all species, overgrown corals, provides both food and shelter and may be easy to use by all species. However, because species tend to be abundant at the same sites, it is possible that this resource is limited in supply and, subsequently, *Centropyge vroliki* and *C. bicolor* have diverged to specialize on the reef top and base respectively. Additionally, these 2 species are more abundant in areas with higher proportions of usable habitat, (i.e. complex corals, and sand and rubble respectively) rather than the most used microhabitat. *C. bispinosa* does not appear to use alternative habitats, which may explain why it is extremely rare at this location, as ecological factors which correlate with rarity include specialised habitat requirements and their availability (Brown et al. 1995) and a poor ability to establish in new areas (Glazier 1980, Rabinowitz 1981).

At some sites, individuals of more than 1 species of *Centropyge* were observed to share the same home patches and to forage together. This has also been observed for cohabiting *Centropyge* species elsewhere (Moyer & Nakazono 1978, Thresher 1982). Significantly, these shared home patches also contained greater proportions of the most used habitat type than

the single species patches inhabited by groups of *C. bicolor* or *C. vroliki*. Very little aggression among cohabiting species was observed and this suggests that the intermediate-scale resource partitioning apparent among the species of *Centropyge* at Lizard Island may not be due to direct competitive displacement among individuals. Instead, it may be the result of the so-called 'ghost of competition past' (Connell 1980) or simply 'individualistic responses' to resources (Ebeling & Laur 1986).

The results from our study demonstrate that patterns of distribution and abundance among closely related coral reef fishes vary among spatial scales. Species tended to be positively associated and ecologically similar at the largest and smallest spatial scales examined, but divergent at an intermediate scale. Although all species are relatively rare, they tend to be concentrated at a small number of sites and are virtually absent elsewhere. Because they have similar fine-scale habitat use patterns, they are often found sharing the same territorial sites. It is only at an intermediate scale that the species have complementary distribution and abundance patterns. The role of inter-specific competition in the formation of these patterns needs further investigation. While it is unclear exactly how much habitat partitioning is necessary before competitive interactions are reduced enough to allow coexistence, the partitioning of *Centropyge* species on intermediate scales might enable all 3 species to coexist in relatively small areas of reef where they reach their greatest abundance.

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