Habitat specialisation and the distribution and abundance of coral-dwelling gobies

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ABSTRACT· Many fishes on coral reefs are known to associate with particular microhabitats. If these associations help determine population dynamics then we would expect (1) a close association between the abundances of these fishes and the abundances of the most frequently used microhabitats, and (2) changes in the abundance of microhabitats would result in a corresponding change in fish population sizes. We examined habitat associations among obligate coral-dwelling gobies (genus Gobiodon) and then investigated relationships between the spatial and temporal availability of habitats and the abundances of Gobiodon species among locations and among zones on the reef at Lizard Island (Great Barrier Reef). Out of a total of 11 Acropora species found to be used by Gobiodon, each species of Gobiodon occupied 1 or 2 species of Acropora significantly more often than expected from the availability of these corals on the reef. Across reef zones, the abundance of most species of Gobiodon was closely correlated with the abundance of coral species most frequently inhabited. However, the abundance of 1 species, G. axillaris, was not correlated with the availability of most frequently used corals across reef zones or among locations. For G. axillaris, therefore, factors other than habitat availability were more important in determining differences in abundance among zones and locations. Also, correlations between the abundance of 2 species, G. histrio and G. quinquestrigatus, and the coral species they most frequently used was less consistent among locations than among zones. This suggests that the relative importance of habitat availability in determining the abundance of these species of Gobiodon is reduced at the spatial scale of locations around Lizard Island. The population dynamics of Gobiodon during this study were closely linked to the population dynamics of host corals. Because of a crown of thorns starfish (Acanthaster planci) outbreak the abundance of corals declined in particular reef zones. Corresponding with this loss of habitat was a decline in Gobiodon abundance. This study demonstrated that the abundance of habitat specialised fishes can be closely correlated with the spatial and temporal availability of suitable habitats among and within reefs.

KEY WORDS: Gobiidae · Gobiodon · Acropora · Acanthaster · Habitat associations · Specialisation · Species abundances

INTRODUCTION

Animals are typically associated with characteristic habitats or microhabitats and the abundance of these habitats may influence the distribution and abundance of species on various spatial or temporal scales. Although microhabitat associations are commonly observed among coral-reef fishes, the importance of these associations in determining patterns of distribution and abundance remains unclear (Sale 1991). The distributions and abundances of some coral-reef fishes have been correlated with coral cover (Bell & Galzin 1984, Bouchon-Navaro et al. 1985, Bouchon-Navaro & Bouchon 1989, Jennings et al. 1996), availability of shelter holes (Roberts & Ormond 1987, Hixon & Beets 1989, Buchheim & Hixon 1992), structural complexity (Luckhurst & Luckhurst 1978, Carpenter et al. 1981, Caley & St. John 1996) and microhabitat heterogeneity (Kaufman & Ebersole 1984). In contrast, other studies have found that the abundances of coral-reef fishes are not closely related to microhabitat characteristics (Robertson & Sheldon 1979, Wellington 1992, Sale et al. 1994, Green 1996). Similarly, temporal changes in

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microhabitat availability have influenced the abundance of some species of coral-reef fishes (Williams 1986, Sano et al. 1987, Clarke 1996) but not others (Wellington & Victor 1985, Williams 1986, Sano et al. 1987). Therefore, the influence of microhabitat availability on species abundances varies widely among coral reef fishes. It may only be among the more habitat specialised species that microhabitat availability will substantially influence patterns of distribution and abundance.

Many fishes on coral reefs have a close association with live corals and if this association is an important determinant of population distributions and population dynamics, we would expect, (1) a correlation between the distributions and abundances of these fishes and the distributions of the corals they most frequently use and, (2) that changes in abundance of corals would result in a corresponding change in fish population sizes. The abundance of coral species typically differs greatly among reef zones and among reef types (Glynn 1976, Done 1983). Also, the abundances of corals may change temporally as a result of disturbances such as cyclones and outbreaks of crown of thorns starfish *Acanthaster planci* (Done 1985, Moran 1986, Hughes 1989). Therefore, if the abundance of different coral species can influence the abundance of coral-reef fishes, this should be apparent among reef zones and locations, or following coral depletion as a result of storms or *Acanthaster* outbreaks.

If relationships between coral abundances and fish abundances are to be detected it is essential that appropriate taxonomic scales are used. For example, measures of live coral cover which are frequently used to examine the distribution of butterflyfishes (Chaetodontidae) may be unreliable predictors of abundance for species that associate with only certain coral species. This may explain why some studies have found strong correlations between coral abundance and fish abundances (Bell & Galzin 1984, Bouchon-Navaro 1986, Bouchon-Navaro & Bouchon 1989, M. Pratchet, T. P. Hughes & G. P. Jones unpubl. data), whilst others have found only weak relationships (Bell et al. 1985, Findley & Findley 1985). Also, some species of coral-reef fishes exhibit similar microhabitat associations throughout their lives (Williams 1980, Sweatman 1983, Leis 1991, Booth 1992, Elliott et al. 1995), whereas the habitat associations of others change with ontogeny (Clarke 1977, Helfman 1978, Shulman & Ogden 1987, Lirman 1994). Therefore, habitat associations and ontogenetic patterns of habitat use must be known before spatial or temporal relationships between coral abundances and fish abundances can be reliably assessed.

If microhabitat availability can influence the spatial or temporal distributions and abundances of coral-reef fishes, then this should be most apparent among habitat-specialised species. Coral-dwelling gobies of the genus *Gobiodon* exhibit an obligate association with branching corals from the family Acroporidae and may be among the most habitat-specialised fishes on coral reefs. If the availability of corals influences the distribution and abundance of *Gobiodon* species, then the abundance of *Gobiodon* species should be correlated with coral abundances across reef zones or among reef types and also *Gobiodon* abundances should fluctuate in response to temporal changes to coral abundances. *Gobiodon* species use a range of *Acropora* species (Tyler 1971, Patton 1994), but the degree of habitat specificity is largely unknown. Therefore, in order to examine relationships between *Gobiodon* abundances and coral abundances it was first necessary to identify the degree of habitat specialisation exhibited by each species of *Gobiodon*. Having identified the species of coral used most frequently by these species, we then examined relationships between the abundances of *Gobiodon* species and the abundance of these coral species among locations and across reef zones at Lizard Island. During the latter part of the study, there was an observable decline in the number of *Acropora* coral colonies on northern reefs on Lizard Island. This decline was caused by an increase in the number of *Acanthaster planci* (Stump 1996), which feed preferentially on acroporid corals of the types also used by *Gobiodon* species (Moran 1986). We used this phenomenon to examine the response of *Gobiodon* populations to temporal changes in coral abundances.

MATERIALS AND METHODS

Study species. *Gobiodon* species are small obligate coral-dwelling gobies (family Gobiidae), that live among the branches of corymbose and digitate corals from the genus *Acropora* (Patton 1994). Eight species of *Gobiodon* that inhabit acroporid corals were recognised during this study (Table 1). One other species, *G. ceramensis*, inhabits corals from the family Pocillo-

Table 1 Species of *Gobiodon* recognised at Lizard Island during this study

Species	Source
Gobiodon axillaris	Patton (1994)
Gobiodon histrio (including erythrospilus form)	Randall et al. (1990), D. F. Hoese unpubl.
Gobiodon micropus	Randall et al. (1990)
Gobiodon oculolineatus	Masuda et al. (1984)
Gobiodon okinawae	Randall et al. (1990)
Gobiodon quinquestrigatus	Myers (1991), Patton (1994)
Gobiodon rivulatus	Winterbottom & Emery (1986), Myers (1991)
Gobiodon unicolor	Winterbottom & Emery (1986)

poridae, rather than corals from the family Acroporidae (Tyler 1971, Russell 1983, pers. obs.) and, therefore, was not included in this study. The taxonomic identity of small *Gobiodon* species with lines on the head and body has been questioned by Winterbottom & Emery (1986). D. F. Hoese (unpubl.) suggested that there may be several species of *Gobiodon* with lines on the body, but lines are only retained in adults of *G. rivulatus*. Histological examination of gonads from 6 specimens with lines on the head and body confirmed that they were mature individuals and, therefore, conformed to the diagnosis for *G. rivulatus*.

With few exceptions *Gobiodon* species were easily identified *in situ*. It was, however, difficult to separate *G. unicolor* and *G. occulolineatus* without collection, therefore these species were grouped as 'others'. *G. micropus* was sometimes difficult to distinguish from *G. unicolor* without collection and where any doubt existed about the taxonomic identity of an individual it was pooled with 'others' for analyses.

Sampling design and visual census method. This study was conducted between March 1995 and February 1996 at Lizard Island (14° 40' S, 145° 28' E) on the northern Great Barrier Reef, Australia. Lizard Island is a high continental island with extensive fringing and lagoonal reef formation. To determine if *Gobiodon* inhabits some species of *Acropora* more frequently than others, we compared the observed distribution of *Gobiodon* among *Acropora* corals at Lizard Island with that expected if each species of *Acropora* was used in proportion to its availability on the reef. The species of *Acropora* to be censused for *Gobiodon* were determined during a 3 d preliminary investigation of habitat use by *Gobiodon*, where all species of *Acropora* occurring at Lizard Island (38 species) were carefully searched for the presence of *Gobiodon*. We then censused *Gobiodon* in all coral colonies of *Acropora* species used by *Gobiodon*, within random transects at 3 locations around Lizard Island. The 3 locations differed in their exposure to the prevailing south easterly trade winds and were (1) an exposed southern location, (2) a moderately exposed northern location and (3) a protected western location (Fig. 1). Three sites were sampled at each of these locations (Fig 1). In addition to determining habitat preferences among *Gobiodon*, this sampling design also allowed us to examine relationships between the abundances of *Gobiodon* and the abundances of coral species among locations. To examine relationships between the abundances of *Gobiodon* and the abundances of coral species across reef zones, we extended the sampling design to the reef crest and slope at each of the 3 moderately exposed sites (Fig. 1).

At each site, 5 replicate 10 × 1 m belt transects were established on the outer reef flat, running roughly
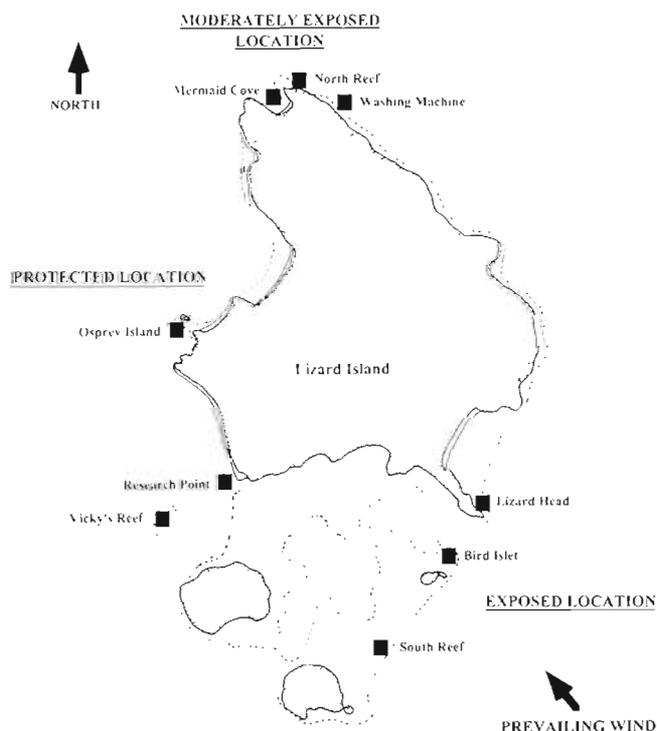

Fig. 1 Lizard Island sampling locations (exposed, moderately exposed and protected) and sites

parallel to the reef crest. At each moderately exposed site, 5 transects were also laid along the contour of the reef crest and along the middle of the reef slope. The starting position of each transect was haphazardly selected. A 10 m tape was placed along the center of the transect and a 1 m plastic measuring bar was used to measure the transect width. Each coral colony of acroporid species used by *Gobiodon*, located at least half within the transect and with a diameter greater than 5 cm, was carefully searched for *Gobiodon* with the aid of a small underwater light. Gobies remained within coral colonies during the census and, therefore, corals could be repeatedly censused if there was any uncertainty about the accuracy of any census. Because patterns of habitat use may differ with ontogeny, all *Gobiodon* observed were grouped by size as either juveniles or adults. Histological examination of gonad maturity indicated that 3 size classes were sufficient to classify species as either juveniles or adults (Table 2).

Habitat associations. Chi-square homogeneity tests were used to compare juvenile and adult patterns of habitat use for each species of *Gobiodon*. In these tests, the frequency distribution of coral colonies occupied by juveniles was compared to the frequency distribution of coral colonies occupied by adults. Using chi-squared goodness-of-fit tests, the observed distribution of each *Gobiodon* species (juveniles and adults) among

Table 2. Size categories used to group *Gobiodon* as juveniles or adults. Allocation to life history stages was determined by histological examination of gonad maturity of a large species (*G. histrio*) and small species (*G. rivulatus*)

Species	Total length		
	0–15 mm	15–25 mm	>25 mm
G. axillaris	Juvenile	Juvenile	Adult
G. histrio	Juvenile	Juvenile	Adult
G. micropus	Juvenile	Adult	Adult
G. okinawae	Juvenile	Adult	Adult
G. quinquestrigatus	Juvenile	Adult	Adult
G. rivulatus	Juvenile	Adult	Adult
G. unicolor (others)	Juvenile	Adult	Adult

Acropora corals was then compared to the frequency distribution of all *Acropora* colonies censused to determine if *Gobiodon* used coral species disproportionately to their availability. Because inclusion of rare and infrequently used species of coral may increase the likelihood of a significant result, 3 uncommon and rarely used coral species (*A. cerealis*, *A. valida* and *A. yongei*) were excluded from these analyses. Where *Gobiodon* species used corals disproportionately to their abundance, Bonferroni z-statistics were used to test which particular coral species were used disproportionately by each species of *Gobiodon*. For each *Gobiodon* species, the proportion of each coral species used ± a 95% confidence interval was compared to the proportion of that coral species in the overall sample. Following Alldredge & Ratti (1992), confidence intervals were calculated using the formula:

$$Z_{\alpha/2k} \sqrt{(p_i(1 - p_i)/n)}$$

where p_i is the proportion of the total coral colonies occupied by a species of *Gobiodon* for coral species i, n is the total number of coral colonies occupied by the species of *Gobiodon*, $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $\alpha/2k$, $\alpha = 0.05$, and k = the number of coral species. The use of a coral species was considered to be proportional to its availability when the proportion of that species used, ± its 95% confidence interval, encompassed the proportion of that habitat available in the environment. A species of coral was considered to be used disproportionately to its availability when the proportion of that habitat used, ± its 95% confidence interval, did not encompass the proportion available in the environment. Application of chi-square and Bonferroni z-statistics to analysis of habitat use requires that observations for one animal are independent of observations of other animals (Alldredge & Ratti 1992). Aggregations of *Gobiodon* individuals from the same species within coral colonies would violate this assumption if total abundance data

were used. Therefore, to ensure independence of habitat use observations, presence or absence of each *Gobiodon* species per colony was used, as recommended by Thomas & Taylor (1990). Comparison of results using presence/absence data with results using total abundance data confirmed that this method did not alter the outcome of habitat association analyses.

Relationships between abundance of *Gobiodon* and abundance of corals. Canonical correlation analysis, a multivariate technique that analyses linear relationships between 2 sets of variables (Tabachnick & Fidell 1989), was used to examine the relationship between the abundance of each species of coral and the abundance of each species of *Gobiodon*. Separate analyses were conducted to examine the relationships between fish and coral abundances across zones (reef flat, crest and slope) and among locations (exposed, moderately exposed and protected). For each analysis the abundance of each *Gobiodon* species (fish variables) and each coral species (coral variables) was pooled within transects.

The reliability of canonical correlation depends on the number of variables being examined and the distribution of each variable (Tabachnick & Fidell 1989). Two coral species, *Acropora cerealis* and *A. valida*, occurred infrequently and preliminary analysis showed they had little influence on the results, therefore, they were dropped from the final analysis. Square root transformations were applied to all variables to reduce moderate skewness.

Where a significant relationship between variables was detected the results of the canonical correlation were displayed as a reduced space biplot. Relationships between fish and coral abundances were examined by plotting interset (between variables) correlation coefficients of both the fish variables and the coral variables in the multivariate space defined by the coral variables. The coral space was used because of an *a priori* expectation that the abundance of *Gobiodon* species may respond to the abundance of particular coral species. In canonical correlation the correlation coefficients are generally regarded as reliable when the coefficient exceeds 0.3 and this protocol was adopted when examining correlations between variables.

Response of *Gobiodon* populations to declining coral cover. There was an observable decline in the number of live coral colonies on northern Lizard Island reefs during the latter part of 1995. This was apparently due to an increase in the number of *Acanthaster planci* present on these reefs during 1995 (Stump 1996). To determine the response of *Gobiodon* species to this decline in habitat availability, the 3 reef zones (flat, crest and slope) at the 3 northern (moderately exposed) sites were re-censused in January 1996. An

identical sampling protocol was used to that of the initial census and results analysed using ANOVA (fixed effects model). Homogeneity of variances was improved by data transformation [log(x + 1)] and significant differences among means were examined using Tukey's Honest Significant Difference tests.

If the population dynamics of *Gobiodon* species are influenced by the availability of the most frequently inhabited coral species we would expect changes in the abundance of *Gobiodon* species to be correlated with changes in the abundance of these corals. Therefore, we used Pearson's correlations to compare the change in abundance of each *Gobiodon* species with the change in abundance of each coral species. Because different transects were sampled on each occasion, the abundances of corals and gobies were pooled for each combination of time, site and zone. To determine the change in abundance for each coral species and goby species the abundance at the first sampling occasion was subtracted from the abundance at the second occasion. As for previous analyses, 2 rare corals, *Acropora cerealis* and *A. valida*, had little influence on the analysis and, therefore, were not included.

RESULTS

Habitat associations

A total of 1373 coral colonies from 11 species of *Acropora* were censused and 1593 *Gobiodon* were observed within these colonies (Fig. 2). The total number of coral species used by each species of *Gobiodon* varied, from 3 species for *G. micropus* to 10 species for *G. rivulatus* (Fig. 2). Juveniles and adults had very similar patterns of habitat use (Fig. 2). The distributions of juveniles and adults among coral species were not significantly different for *G. rivulatus*, *G. histrio*, *G. quinquestrigatus*, *G. micropus* and 'others'. The distributions of juvenile and adult *G. axillaris* among coral species were significantly different (χ^2 = 17.2, df = 8, p < 0.05). However, juvenile and adult *G. axillaris* used the same coral species and differences between their distributions occurred primarily because juveniles occurred relatively more frequently than adults in colonies of *A. gemmifera* and *A. digitifera*. No juvenile *G. okinawae* were observed during this study. Although juveniles and adults of all *Gobiodon* species had very similar patterns of habitat use, juveniles were occasionally found in coral species not used by adults. For example, juvenile *G. histrio* were

found in *A. loripes*, *A. digitifera* and *A. valida* but adults were never observed in these corals (Fig. 2). All *Gobiodon* were found on live coral colonies and during additional, unrecorded, observations no *Gobiodon* were observed on dead coral colonies.

Habitat use of all species of *Gobiodon* was disproportionate to habitat availability. Ninety-five percent confidence intervals around proportions of habitats used indicated that all species of *Gobiodon* inhabited at least 1 coral species more frequently than expected, occurred significantly less frequently than expected in a range of coral species, and inhabited a number of other species approximately in accordance with their availability (Table 3). *G. micropus* most frequently inhabited *Acropora loripes*. *G. histrio* and *G. quinquestrigatus* inhabited *A. nasuta* significantly more frequently than other species of *Acropora*. *G. axillaris* most frequently inhabited *A. nasuta* and *A. millepora*. *G. rivulatus* most frequently inhabited *A. gemmifera*. The group 'others', which was composed primarily of *G. unicolor*, most frequently used *A. millepora* but the presence of more than 1 species of *Gobiodon* in this group means that the result must be interpreted with caution. Habitat use was not statistically tested for *G. okinawae* because it was recorded from only 6 coral colonies during the visual census and this sample size was considered too small for a reliable test.

Relationships between abundance of *Gobiodon* and abundance of corals

Across reef zones, the abundance of most species of *Gobiodon* was positively correlated with the abundance of coral species most frequently inhabited. The abundance of *Gobiodon micropus* was correlated with the abundance of *Acropora loripes* (Fig. 3) and both species were most abundant on the reef slope (Fig. 4). *G. histrio* and *G. quinquestrigatus* abundances were correlated with the abundance of *A. nasuta* (Fig. 3), which was most abundant on the reef crest (Fig. 4).

Table 3. Significance of habitat use by *Gobiodon* species determined using Bonferroni *z*-statistics (alpha = 0.05). U = unused, NS = non significant, +: habitat used significantly more than expected, –: habitat used significantly less than expected

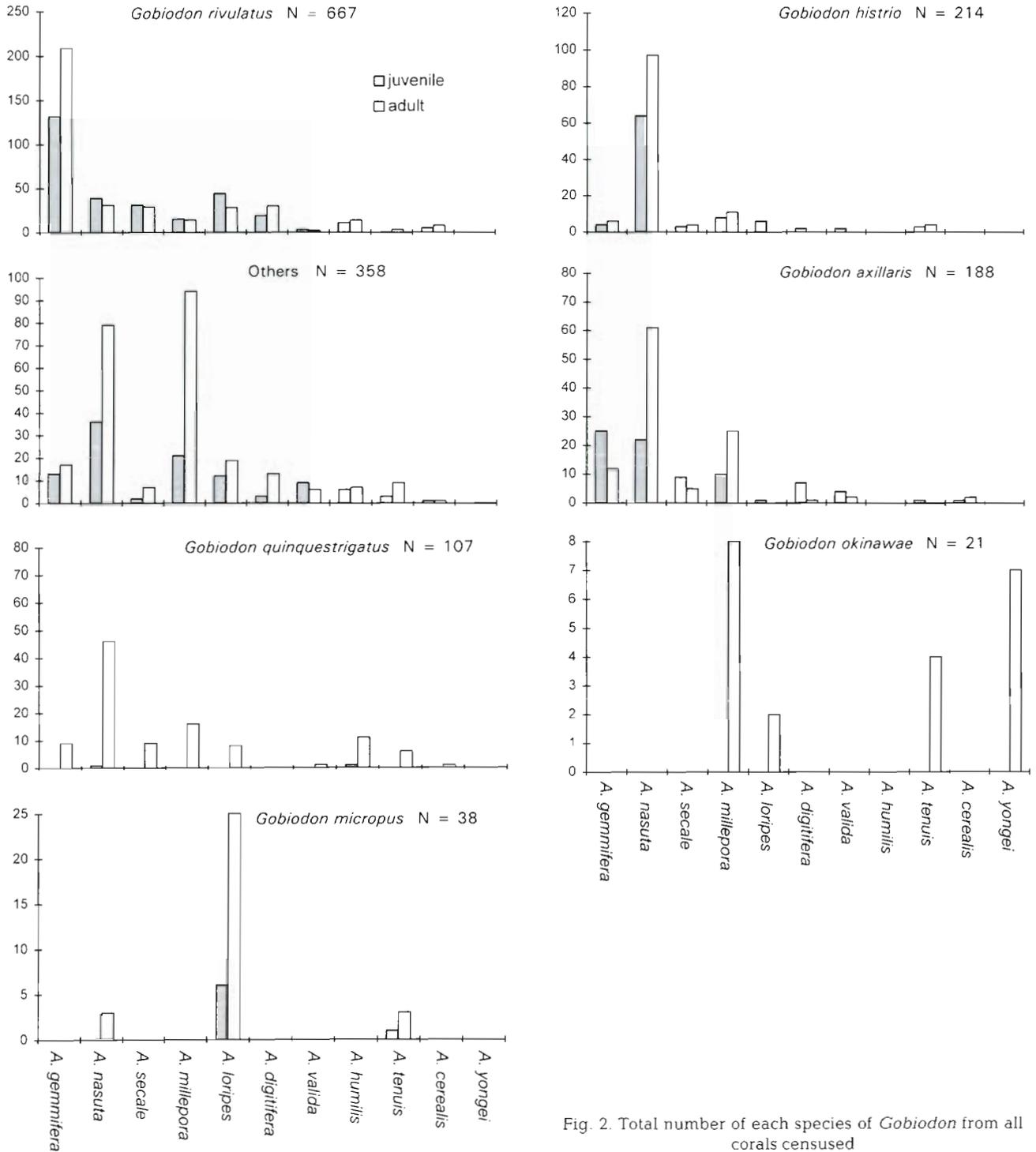|	G. micropus	G. histrio	G. axillaris	G. quinque.	G. rivulatus	Others
A. gemmifera	U	–	–	–	+	–
A. nasuta	NS	+	+	+	–	NS
A. secale	U	–	NS	NS	NS	–
A. millepora	U	NS	+	NS	–	+
A. loripes	+	–	–	NS	NS	NS
A. digitifera	U	–	NS	U	NS	NS
A. humilis	U	U	U	NS	NS	NS
A. tenuis	NS	NS	–	NS	–	NS

Fig. 2. Total number of each species of *Gobiodon* from all corals censused

G. *rivulatus* was most abundant on the reef flat in conjunction with *A. gemmifera* (Figs. 3 & 4). In contrast, G. *axillaris* was strongly correlated with corals on the reef flat rather than the reef crest where *A. millepora* and *A. nasuta* were most abundant (Figs. 3 & 4). Also, the abundance of 'others' was not strongly correlated with the abundance of *A. millepora* (Fig. 3).

The relationship between the abundance of each species of *Gobiodon* and the abundance of corals most frequently inhabited was not as clear among locations as that found in the analysis across zones. The abundance of G. *micropus* was strongly correlated with the abundance of *Acropora loripes* (Figs. 5 & 6). The abundance of G. *rivulatus* was strongly correlated with the
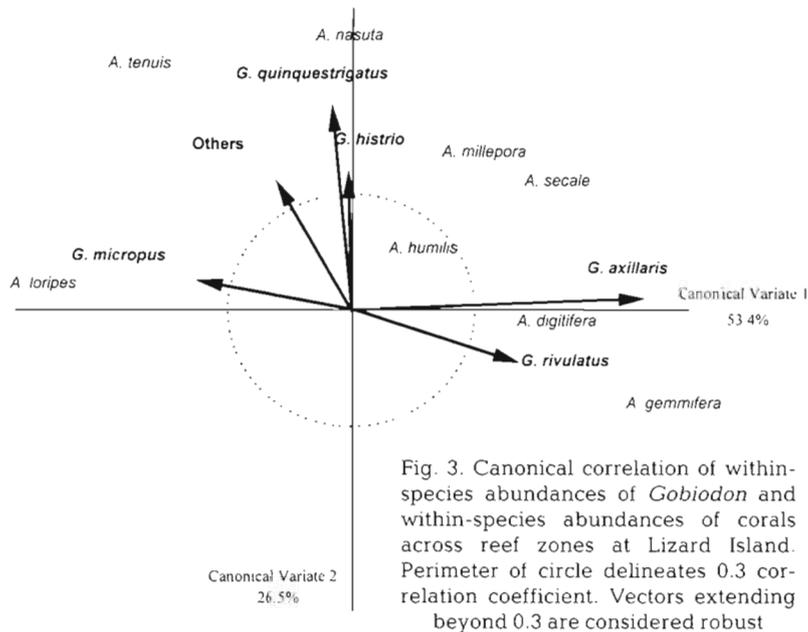
Fig. 3. Canonical correlation of within-species abundances of *Gobiodon* and within-species abundances of corals across reef zones at Lizard Island. Perimeter of circle delineates 0.3 correlation coefficient. Vectors extending beyond 0.3 are considered robust

the abundance of *A. nasuta*, the coral species it inhabited most frequently, and 'others' were not strongly associated with *A. millepora*. Once again, *G. axillaris* was correlated with *A. gemmifera* rather than the abundance of *A. nasuta* and *A. millepora*, the species it usually inhabited (Fig. 5). *G. axillaris* was most abundant at moderately exposed and exposed locations and had a low abundance relative to habitat availability in the protected location (Fig. 6). The analysis was strongly influenced by transects at Research Point (sheltered location), where *G. okinawae* was abundant on *A. yongei* and *A. tenuis*. *G. okinawae* was frequently observed at other sheltered sites during this study, but was not found in exposed or moderately exposed locations.

abundance of *A. gemmifera* (Fig. 5) and both species were most abundant in the moderately exposed location (Fig. 6). The abundance of *G. histrio* was not strongly correlated with the abundance of *A. nasuta* (Fig. 5). *G. histrio* was most abundant in the sheltered location and had a low abundance relative to habitat availability at the exposed location (Fig. 6). The abundance of *G. quinquestrigatus* was not correlated with

Response of *Gobiodon* to declining coral cover

The number of live *Acropora* colonies of coral species used by *Gobiodon* decreased significantly on the 3 moderately exposed reefs between March 1995 and January 1996. However, coral cover at each site and zone was not impacted equally (Table 4). The number of colonies of coral species used by *Gobiodon* declined
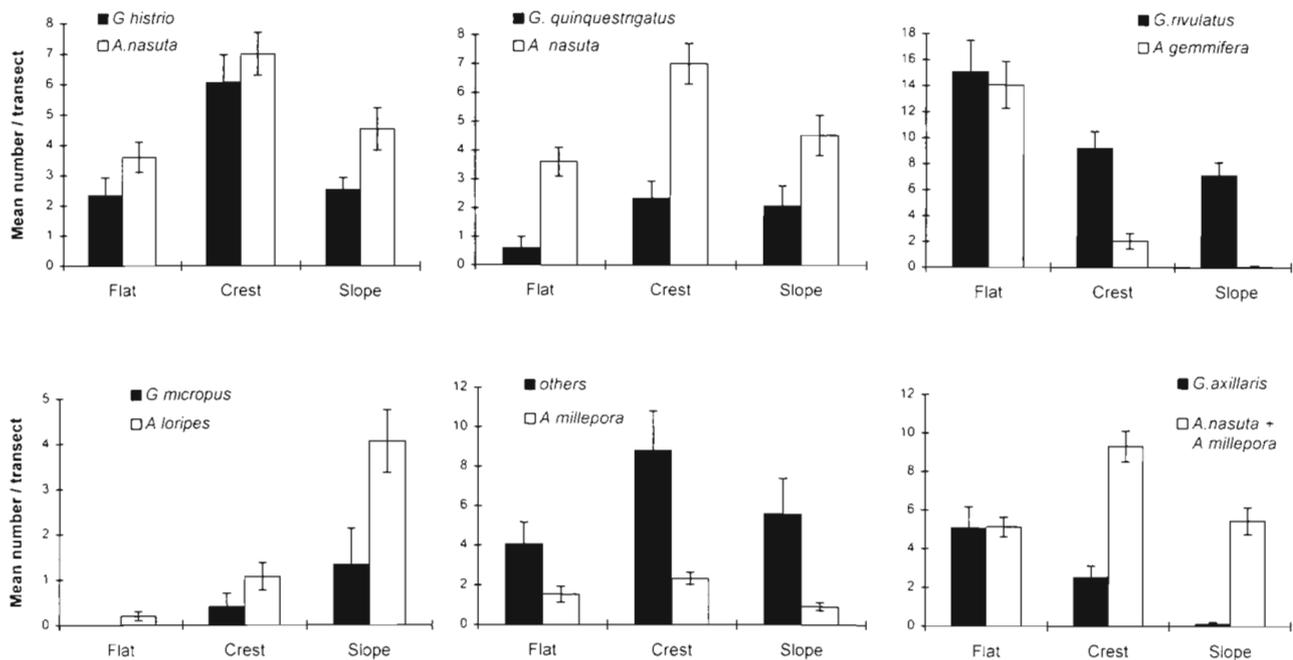

Fig. 4. Mean abundance (±SE) per transect of *Gobiodon* species and the coral species they most frequently inhabit across reef zones at Lizard Island
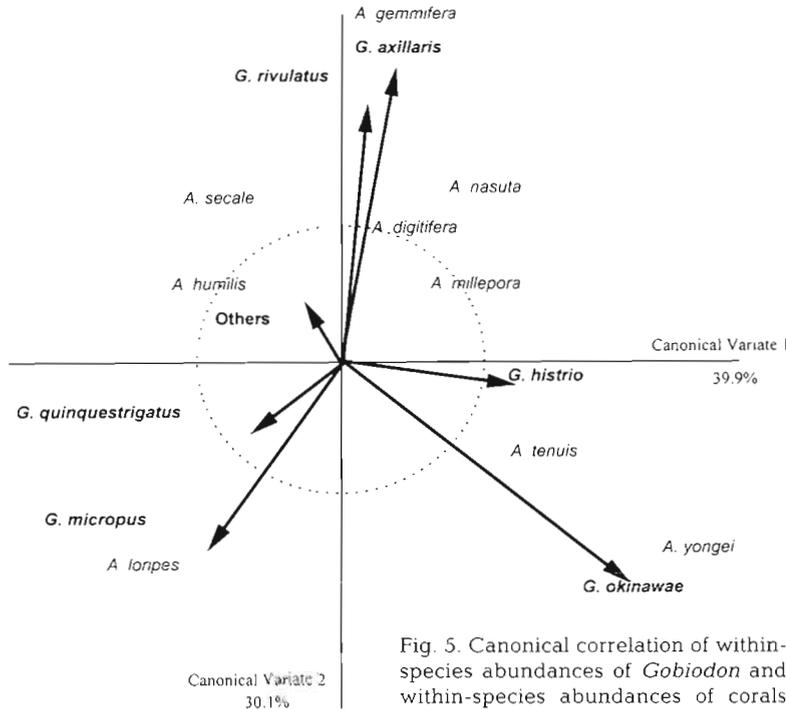
Fig. 5. Canonical correlation of within-species abundances of *Gobiodon* and within-species abundances of corals among reef locations at Lizard Island. Perimeter of circle delineates 0.3 correlation coefficient. Vectors extending beyond 0.3 are considered robust

decline in coral colonies at North Reef (Fig. 7). There was no significant difference in coral abundance between times on the reef crest at Washing Machine and on the reef flat at all 3 sites.

Corresponding with the decline in coral cover there was a decline in the total number of *Gobiodon* at the 3 moderately exposed sites (Table 4, Fig. 7). The pattern of decline in *Gobiodon* numbers closely followed the pattern of decline in corals among sites and zones (Fig. 7). *Gobiodon* numbers declined significantly on the slope at all sites, as occurred for corals. Similarly, there was a significant reduction in the number of *Gobiodon* on the crest at Mermaid Cove, and an observable but non-significant decline on the crest at North Reef. There was little change in *Gobiodon* numbers on the crest at Washing Machine and on the reef flat at all sites.

Changes in abundance of *Gobiodon* species were generally correlated with changes in the abundance of the corals most frequently inhabited by each species (Table 5). Changes in the abundance of *G. micropus* were significantly correlated

significantly on the slope at all 3 sites (Fig. 7). On the reef crest, a significant reduction in the number of suitable coral colonies occurred at Mermaid Cove and there was an observable, but just non-significant,

with changes in abundance of *G. loripes* and changes in abundance of *G. rivulatus* were significantly correlated with changes in abundance of *Agropora gemmifera*. Others were correlated with changes in abun-
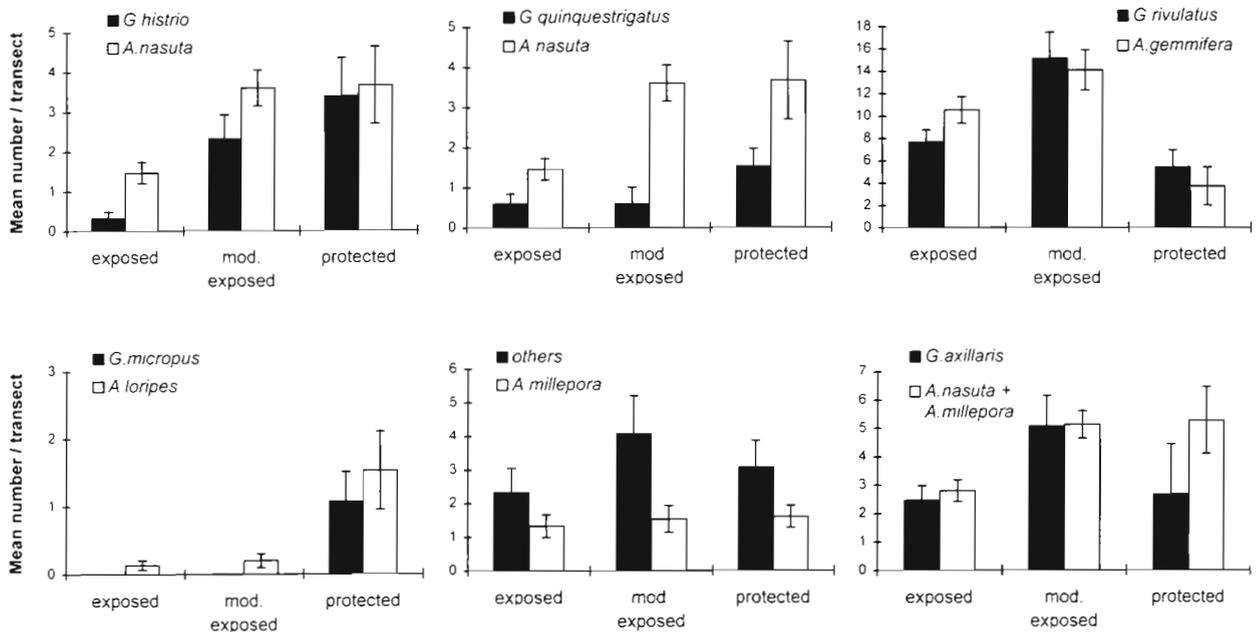

Fig. 6. Mean abundance (±SE) per transect of *Gobiodon* species and the coral species they most frequently inhabit among reef locations at Lizard Island

Table 4. ANOVA results for coral and *Gobiodon* numbers [log(x+1)-transformed] in transects on the reef flat, crest and slope at moderately exposed sites in March 1995 and February 1996. ⋅⋅ $p < 0.001$, ⋅ $0.001 < p < 0.05$; NS: not significant

Source of variation	df	Corals			Gobiodon		
		MS	F	p	MS	F	p
Time	1	2.8	102.8	⋅⋅	3.32	62.39	⋅⋅
Site	2	0.2	7.21	⋅	0.01	0.191	NS
Zone	2	3.34	122.4	⋅⋅	2.21	41.5	⋅⋅
Time × Site	2	0.004	0.164	NS	0.099	1.87	NS
Time × Zone	2	0.948	34.81	⋅⋅	1.00	18.9	⋅⋅
Site × Zone	4	1.93	7.091	⋅⋅	0.108	2.04	NS
Time × Site × Zone	4	0.117	4.288	⋅	0.205	3.85	⋅
Residual	72	0.027			0.053		

Table 5. Correlations between changes in abundance of *Gobiodon* species and changes in abundance of coral species between March 1995 and February 1996 on northern reefs at Lizard Island. All correlation coefficients over 0.5 are shown. ⋅Significant correlations, $p < 0.05$

	G. micropus	G. histrio	G. axillaris	G. quinque.	G. rivulatus	Others
A. gemmifera	NS	NS	NS	NS	0.78⋅	NS
A. nasuta	NS	0.59	NS	0.50	NS	NS
A. secale	NS	NS	0.64	NS	0.56	NS
A. millepora	NS	0.58	0.50	NS	NS	0.70⋅
A. loripes	0.67⋅	NS	NS	0.71⋅	NS	NS
A. digitifera	NS	NS	0.83⋅	NS	NS	NS
A. humilis	NS	NS	NS	NS	NS	NS
A. tenuis	NS	NS	NS	NS	NS	0.70⋅

dance of the most frequently used species, *A. millepora*, and 1 other species, *A. tenuis*. *G. quinquestrigatus* was significantly correlated with changes in abundance of *A. loripes*, an infrequently used coral species. However, a strong, but non-significant correlation, was also detected between *G. quinquestrigatus* and change in abundance of the most frequently inhabited species, *A. nasuta* (Table 5). Although no significant correlations were detected for *G. histrio*, strong correlations did occur between this species and the most frequently used species, *A. nasuta* and *A. millepora* (Table 5). Change in abundance of *G. axillaris* were most strongly correlated with change in abundance of *A. digitifera* and *A. secale* which were most abundant on the reef flat.

DISCUSSION

All species of *Gobiodon* used a range of *Acropora* species but used 1 or 2 species more frequently than expected by chance. Therefore, there is
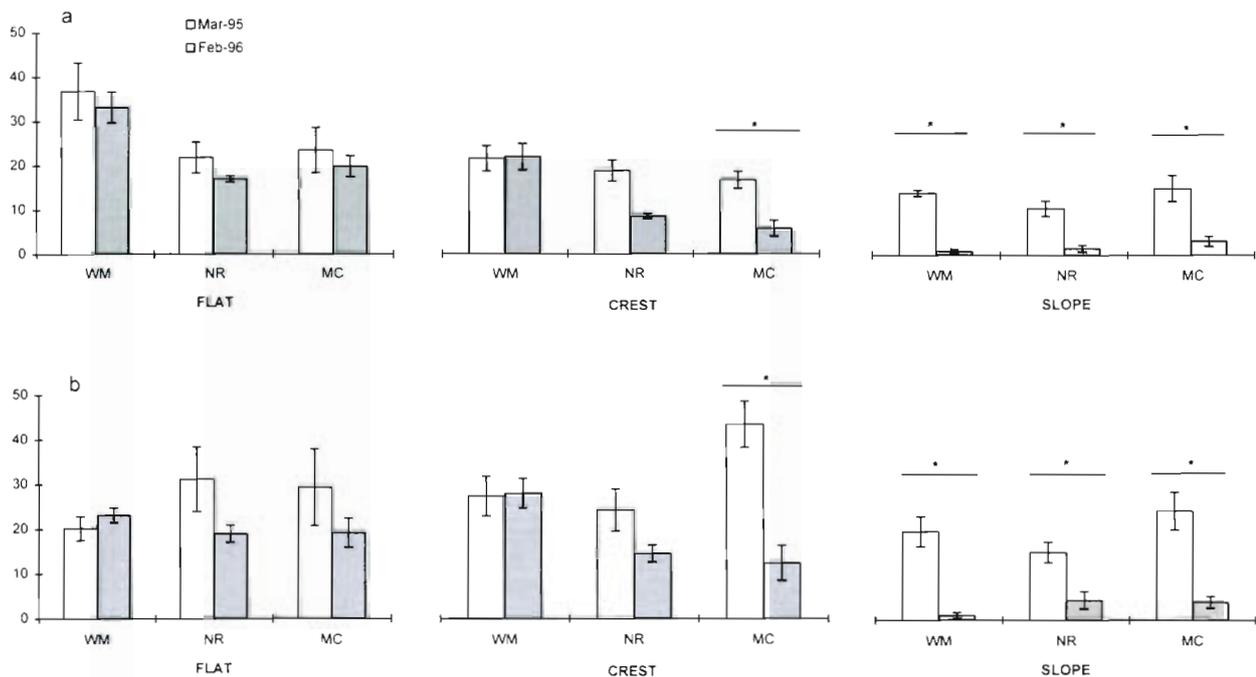

Fig. 7. Mean abundance (±SE) per transect of (a) corals and (b) *Gobiodon* at moderately exposed reefs at Lizard Island in March 1995 and February 1996. WM: Washing Machine, NR: North Reef, MC: Mermaid Cove. (±) Significantly different

specialisation for habitats at the level of coral species, among species of *Gobiodon* at Lizard Island. The spatial and temporal patterns of *Gobiodon* abundances across zones were generally closely associated with the abundance of the most frequently inhabited coral species. The abundance of other habitat specialists such as *Paragobiodon echinocephalus* (Kuwamura et al. 1994), *Amphiprion* species (Ross 1978) and *Acanthemblemaria* species (Buchheim & Hixon 1992, Clarke 1996) have also been found to be closely associated with the availability of habitats. In addition, close associations have been found between the abundance of coral colonies and the abundance of chaetodontids that feed exclusively on coral polyps (Bell & Galzin 1984, Bouchon-Navaro 1986, Bouchon-Navaro & Bouchon 1989, Pratchet et al. unpubl. data). Therefore, it appears that the availability of habitat can influence the relative abundance and population dynamics of specialised species of fishes, not just their presence or absence on coral-reefs. In contrast, for many species of reef fishes it appears that habitat availability is relatively unimportant in determining species abundances (Sale & Douglas 1984, Sale et al. 1994). These different results indicate that the relative importance of microhabitat availability in determining the distribution and abundance of coral-reef fishes varies considerably among species. It may only be among the more specialised species of fish that associations between abundance and habitat availability will be apparent.

Positive correlations between the spatial abundances of fish and habitats support the notion, but do not demonstrate, that habitats are important in determining abundances. However, in this study, correlations between changes in the abundance of *Gobiodon* species and changes in the abundance of the most frequently used corals demonstrates that the availability of habitats helps determine abundances. The abundance of another coral goby, *Paragobiodon echinocephalus*, is also strongly influenced by the availability of habitats on a local scale. Kuwamura et al. (1994) found that the abundance of juveniles fluctuated with pulses of recruitment but adult population dynamics were largely determined by the availability of suitable sized corals.

In contrast to the other species of *Gobiodon*, the abundance of *G. axillaris* across reef zones was not closely associated with the abundance of coral species it most frequently inhabited. *G. axillaris* was more abundant on the reef flat, rather than the crest where *Acropora nasuta* and *A. millepora* tended to be most abundant. Interspecific competition (Ebersole 1985, Robertson & Gaines 1986, Clarke 1992), settlement patterns (Eckert 1985, Wellington 1992) and differential mortality (Connell & Jones 1991, Caley & St. John 1996) can influence distribution patterns of reef fishes

and the 2 former processes are important in determining among-zone distributions of some coral-reef fishes (Eckert 1985, Robertson & Gaines 1986, Wellington 1992). The corals used most frequently by *G. axillaris* are also used by *G. histrio* and *G. quinquestrigatus* and the occupation rate of these corals at Lizard Island is between 70 and 80% (Munday unpubl. data). Therefore, competition for habitats might be expected among these species. Larger species are typically better competitors (Robertson 1996) and *G. histrio* is the largest species of *Gobiodon* at Lizard Island. Therefore, *G. axillaris* could be excluded from corals on the reef crest by competitive interactions with *G. histrio*. Settlement patterns may also contribute to the observed distribution of *G. axillaris*. This species may prefer to settle on the reef flat rather than the crest or slope. In addition, settlement patterns may explain the very low abundance of *G. axillaris* on the reef slope.

Correlations between the abundance of fish and the coral species they most frequently inhabited were less consistent among locations than among zones for *Gobiodon quinquestrigatus* and *G. histrio*. This suggests that the relative importance of habitat availability in determining the abundance of these species is reduced at the spatial scale of locations. Factors that reduced the association between the abundance of these species and the abundance of their preferred corals among locations are unknown but differences in the availability of larvae, settlement preferences, different post-settlement mortality regimes, or competitive interactions could all potentially be important. The distribution and abundance of larvae is likely to be particularly important in determining the distributions of fishes among reefs or among locations on contiguous reef (Williams 1991). Strong correlations have been observed between larval distribution and the distribution of sedentary reef-fishes among location on contiguous reef (Sponaugle & Cowen 1996) and larvae may also influence their abundances among locations by broadscale habitat selection before settlement (Doherty et al. 1996). Broadscale habitat selection by larvae may explain the greater abundance of *G. histrio* in protected locations at Lizard Island. Both juvenile and adult *G. histrio* were less commonly found on corals in the exposed location than on corals in the protected location, indicating that broadscale selection at settlement is more likely than differential post-settlement mortality to determine the distribution of this species among locations. Broadscale habitat selection may also explain the distribution of *G. okinawae*, which typically occurs only in sheltered lagoonal habitats (Myers 1991, this study) even though suitable habitats occur in other reef locations.

The similarity between juvenile and adult habitat use suggests that ontogenetic habitat shifts are rare among species of *Gobiodon*. Other habitat specialist such as *Dascyllus aruanus* (Sweatman 1983), *Paragobiodon* spp. (Kuwamura et al. 1994) and *Amphiprion* spp. (Leis 1991, Fautin 1992) settle directly to adult habitat types and this may enhance juvenile survivorship (Jones 1988). Fine-scale habitat selection at settlement may explain the patterns of habitat use observed in this study. However, the occurrence of juveniles in coral species not used by adults indicates that larvae occasionally settle into inappropriate corals.

The general association between the distribution and abundance of each species of *Gobiodon* and the abundance of particular coral species in this study demonstrates the importance of an appropriate categorisation of habitats in studies comparing the abundance of fish and habitat. Measures such as percent coral cover or even broad taxonomic groups for corals used in many previous studies are unlikely to detect relationships between fish and habitat for fish species that are associated with specific coral species. In addition, differences among spatial scales (zones, locations) in the strength of relationships between the abundances of *Gobiodon* species and the corals they most frequently inhabit demonstrates that the scale of analysis can influence the results of habitat association studies, even among habitat specialised fishes.

To examine patterns of habitat use among *Gobiodon*, in relation to the availability of habitats, we used a random sampling design and a predetermined suite of coral species. As a result, rare coral species, or those used infrequently by *Gobiodon* may not have been sampled. For example, observations subsequent to this study have revealed that some species of *Gobiodon* may occasionally inhabit species of *Acropora* not included in this study. However, these occurrences are infrequent and their inclusion would have no effect on the results of this study. Also, in this study *G. micropus* used few species of *Acropora* and was typically found in *A. loripes*. Patton (1994) found a similar pattern of habitat use but identified the coral used as *A. elseyi*, rather than *A. loripes*. There is considerable morphological variation among *Acropora* species (Wallace & Willis 1994) and *A. loripes* and *A. elseyi* have similar general morphologies. It is likely that the corals identified as *A. loripes* in this study and *A. elseyi* in Patton's study contain at least some individuals of both species and that *G. micropus* will use both of these similar species.

This study has demonstrated that reef fish may exhibit habitat specialisation at the level of individual coral species on coral reefs. In addition, the relative abundances and population dynamics of these fishes can be closely linked to the abundance of these corals.

This contrasts with other studies that have found a poor relationship between the abundance of coral-reef fishes and the abundance of habitats. Therefore, the influence of habitat availability on reef fish populations varies considerably among species. Even within habitat specialised groups there may be species, such as *Gobiodon axillaris*, where factors other than availability of suitable habitats have a major influence on distribution patterns. This study also illustrates the importance of appropriate habitat categorisation and scale of analysis in studies of habitat associations among reef fishes. Both these factors can alter the perceived relationship between the abundance of fishes and the abundance of habitats.

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