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INTERSPECIFIC COMPETITION AND COEXISTENCE IN A GUILD OF CORAL-DWELLING FISHES

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Abstract. We investigated the effects of interspecific competition on abundance, habitat partitioning, and coexistence of six closely related species of gobies (genus *Gobiodon*) that inhabit a range of coral species at Lizard Island, Great Barrier Reef, Australia. After documenting the extent of overlap in habitat use among pairs of species in the field, we used a combination of field and laboratory experiments to investigate the relationship between these patterns and the occurrence of interspecific competition. Experiments in aquaria tested the ability of five of the species to compete against *Gobiodon histrio,* the apparent competitive dominant, including the effects of body size and prior residency. A manipulative field experiment, in which abundance of *G. histrio* was reduced, tested whether competition with this species limits the abundance of the other five species.

Two species competed for space with *G. histrio* in the field, yet overlap in habitat use with *G. histrio* was high for one of these species (*G. axillaris*) and low for the other (*G. brochus*). In aquaria, *G. axillaris* and *G. histrio* preferred the same species of coral and had equivalent, size-based, competitive abilities. The coexistence of *G. axillaris* and *G. histrio* at the scale of tens of meters on the reef can thus be explained by a competitive lottery model. However, differential distributions of these two species across the reef flat and reef crest suggest that resource partitioning or habitat selection at larger spatial scales may also be important to their coexistence. In aquaria, *G. brochus* was an inferior competitor to *G. histrio* and could only gain access to the preferred species of coral through an advantage in body size or prior residency. Low overlap in habitat use between *G. brochus* and *G. histrio* in the field appears to result from niche shifts by the subordinate competitor only.

The field experiment indicated that the other three species did not compete for space with *G. histrio.* Experiments in aquaria demonstrated that *G. rivulatus* and *G. histrio* exhibited low overlap in habitat use and did not compete, because they preferred different species of coral. In contrast, *G. unicolor* and *G. histrio* exhibited high overlap in habitat use but did not compete, because they were able to cohabit the same coral colonies without affecting each other. In aquaria, *G. quinquestrigatus* and *G. histrio* preferred the same coral species; however, in a field recolonization experiment, coral colonies previously occupied by *G. quinquestrigatus* were rarely recolonized by *G. histrio,* indicating that these species coexist because they use different types of coral colonies in the field. The study demonstrates that there is no single relationship between overlap in resource use and the occurrence of interspecific competition and that species within a guild can coexist by a diversity of mechanisms.

Key words: Acropora; *body size; competition; coral reef fish; Gobiidae;* Gobiodon; *Great Barrier Reef, Australia; habitat use; interspecific interactions; lottery model; niche; residency.*

INTRODUCTION

Few generalizations are available on the relationship among overlap in resource use, relative competitive ability, and mechanisms by which competing species coexist in high-diversity faunas (Morin 1999). A fundamental prediction of competition theory is a positive relationship between interspecific overlap in resource use and the intensity of interspecific competition. That is, species with high overlap in the range of resources they can exploit (the fundamental niche) are expected to compete more strongly than species with low over-

lap, provided that at least one overlapping resource is limiting. Testing this prediction with field data has proven difficult because patterns of resource use observed in the field (the realized niche) are not necessarily related to competitive interactions (Colwell and Futuyma 1971, Schoener 1982). Species with high overlap in resource use may compete strongly when resources are limited but not when there is an oversupply of resources. Conversely, species may exhibit low overlap in resource use either because competition has led to resource partitioning or because they exhibit different resource preferences and, therefore, compete only weakly or not at all. Determining the relationship between overlap in resource use and the intensity of interspecific competition requires a combination of careful description of resource use and experimental

manipulations to demonstrate the occurrence of competition for these resources (Colwell and Futuyma 1971, Connell 1983).

Although field experiments have detected significant effects of interspecific competition on the populations of many different organisms (reviews by Connell 1983, Schoener 1983, Roughgarden 1986, 1989, Goldberg and Barton 1992), little is known about the link between overlap in resource use and the occurrence of interspecific competition. Where a link has been established there have been conflicting results. For example, Hairston (1980) detected strong interspecific effects on the density of salamanders in a location where two species overlapped very little in their altitudinal distributions and weaker effects in a location where the two species overlapped extensively. In contrast, Pacala and Roughgarden (1985) demonstrated competitive effects between pairs of *Anolis* lizards in a location where there was high overlap in resource use but not in a location where there was low overlap. These different results might reflect the different taxa, locations, spatial scale, or even types of resource considered. In any case these studies demonstrate that both low and high overlap in resource use can be associated with the occurrence of interspecific competition.

According to niche-based competition theory, the coexistence of competing species is achieved largely through resource partitioning (Colwell and Fuentes 1975, Diamond 1978). The effect of competition on the fundamental niches of competing species depends to a large extent on the initial degree of overlap in these niches and the competitive ability of each species. For example, where two species have similar fundamental niches and similar competitive abilities, niche contraction is expected for both species (e.g., coextensive niche model of Colwell and Fuentes 1975). In contrast, where a dominant species' fundamental niche is a subset of the fundamental niche of a subordinate generalist, niche contraction is expected to be greater in the subordinate species (e.g., included niche model of Colwell and Fuentes 1975). An alternative theory does not rely on resource partitioning to explain competitive coexistence. In the competitive lottery model (Sale 1974, 1977, 1978), species with similar fundamental niches and similar competitive abilities can coexist through chance recolonization of vacant space by juveniles and fluctuations in the relative abundances of recruits of the various species, provided that adults survive between successive recruitment events (Chesson and Warner 1981, Warner and Chesson 1985). Therefore, various combinations of resource overlap, competitive abilities, and competitive outcomes can theoretically occur, but their relative importance in natural systems is poorly understood.

Determining the relationships between patterns of resource use, competitive ability, and coexistence despite interspecific competition requires studies of guilds of species amenable to experiments in which these relationships can be tested. Coral-dwelling gobies of the genus *Gobiodon* (family Gobiidae) provide an excellent opportunity to explore these relationships. These gobies comprise a widely distributed guild of small (<60 mm total length [TL]) coral reef fishes that mostly inhabit coral colonies of the genus *Acropora* (Munday et al. 1999). At Lizard Island on the Great Barrier Reef, Australia, species of *Gobiodon* have narrow but often overlapping patterns of habitat use and, for most of these species, patterns of abundance are correlated with the abundance of the coral species they usually inhabit (Munday et al. 1997). This correlation is consistent with the notion that preferred corals are a limited resource for *Gobiodon* species and, therefore, species might compete for habitat space.

In this study we tested the effects of interspecific competition for coral habitats on the abundance and coexistence of six species of *Gobiodon* at Lizard Island. Between pairs of species we examined the relationships between pairwise overlap in habitat use, competitive abilities of these species in acquiring habitat, and the effects of interspecific competition in the field. First, we estimated the degree of overlap in habitat use among species of *Gobiodon* in the field. We then used experiments in aquaria to estimate the competitive ability of five of these species against their apparent competitive dominant, *G. histrio*. The ability to acquire and defend space can also depend on body size or prior residency (Maynard Smith and Parker 1976, Hammerstein 1981, Robertson 1984, Itzkowitz et al. 1998). Therefore, we also tested the effects of body size and prior residency on the outcome of interspecific interactions. We then used a competitor reduction experiment in the field to determine whether interspecific competition can influence the abundance of *Gobiodon* species. Finally, we determined whether characteristics of individual coral colonies can influence competitive outcomes in the field by removing gobies from coral colonies and comparing the species that recolonized these colonies to the species removed.

METHODS

Study species and location

This study was conducted between March 1996 and December 1998 at Lizard Island (14°40′ S, 145°28′ E) on the Great Barrier Reef, Australia. There are 13 recognized species and at least two undescribed species of coral-dwelling goby (genus *Gobiodon*) on the Great Barrier Reef (Munday et al. 1999). In this study we concentrated on the six most common species of *Gobiodon* on reefs around Lizard Island (Table 1; Munday et al. 1997). One species, *G. histrio,* has two color morphs, a "histrio" form, which is green with red stripes and an "erythrospilus" form, which is green with red spots (Munday et al. 1999). These two colors forms have indistinguishable patterns of habitat use in the field (P. L. Munday, *personal observation*) and are

TABLE 1. Species of *Gobiodon* considered in this study, maximum recorded lengths, and the coral species usually inhabited at Lizard Island, Great Barrier Reef, Australia.

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

† Source: Munday et al. 1997, 1999.

considered together here as *G. histrio*. Different species of *Gobiodon* are rarely found together on the same coral colony and within-species social groups are usually restricted to a single fish or a pair per coral colony (Nakashima et al. 1996, Munday et al. 1998). Only one species, *G. unicolor*, is frequently found to cohabit coral colonies with other species of *Gobiodon* (Munday et al. 1999).

Habitat use

Overlap in the pattern of habitat use was estimated for these six species of *Gobiodon* from visual census of coral colonies of 10 species of *Acropora* inhabited by *Gobiodon* species at Lizard Island. These species of coral were *A. cerealis*, *A. digitifera*, *A. gemmifera*, *A. humilis*, *A. loripes*, *A. nasuta*, *A. millepora*, *A. secale*, *A. tenuis*, and *A. valida*. All colonies of these coral species within a total of 75 randomly placed 10 × 1 m transects at nine sites around Lizard Island were searched for the presence of *Gobiodon* (see Munday et al. 1997 for further details). Overlap in habitat use

among species pairs of *Gobiodon* was estimated using the percent similarity index (Krebs 1989).

Competitive ability

The ability of each species of *Gobiodon* to compete for habitats was tested in aquaria. First, to determine habitat use in the absence of competitors, individuals of each species of *Gobiodon* were given the choice of two coral colonies, one of a species that was commonly used in the field and one of a species that was rarely used in the field. At Lizard Island *Acropora nasuta* was commonly used by most species of *Gobiodon* whereas *A. gemmifera* was only occasionally used (Munday et al. 1997). Therefore, these two coral species were used in all the choice experiments. Small colonies (15–20 cm diameter) of these two coral species were carefully removed from the reef, transported alive to the laboratory, and then cleared of all infauna (gobies, crabs, and shrimps). One colony of each coral species (approximately equal sized) was placed at opposite ends of six glass aquaria. Each aquarium measured ~800 × 300 × 300 mm (Fig. 1). The position of each coral species on either the left or right side of each aquarium was changed regularly during the experiment and coral colonies were replaced if their condition visibly deteriorated. The bottom of each aquarium was covered with coarse beach sand and fresh seawater entered from both ends. An outlet, slightly above the level of the sand was positioned at the front and center of each aquarium and an external standpipe controlled water depth in the tank.

Fish for these trials were collected from the species of coral most frequently occupied in the field by anesthetizing them with clove oil (Munday and Wilson 1997). New individuals were collected every 1–2 d and
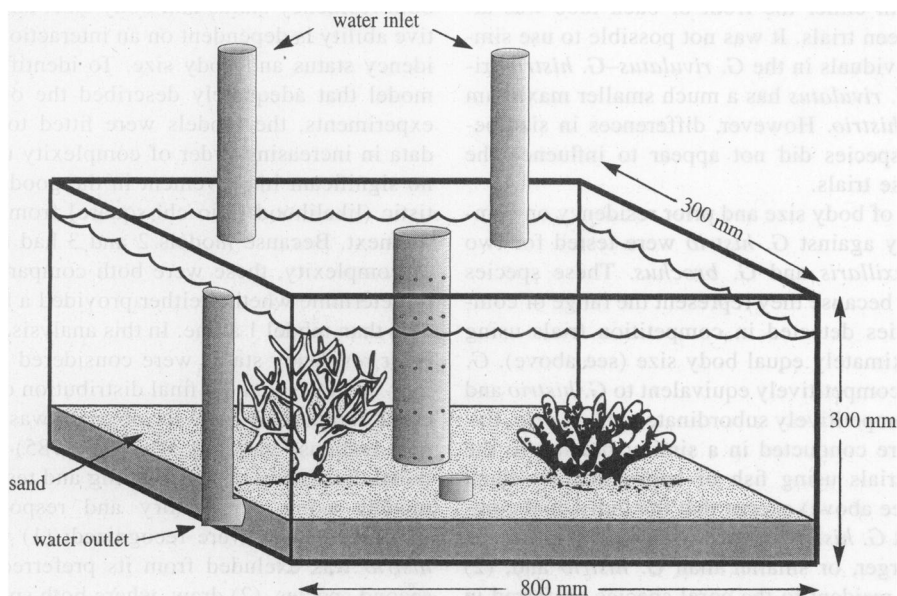

FIG. 1. Design of aquaria used to test coral habitat use and competitive ability of *Gobiodon*.

individuals of different species were held in separate aquaria until used. Each holding aquarium had a continual flow of fresh seawater and contained only small plastic tubes for shelter. At the beginning of each trial one fish was transferred to an acclimatization tube in the middle of each test aquarium. This tube extended from the sand to above the water surface so that the fish could not escape. The tube also had small holes around its circumference to enable water to flow through the tube. These holes were provided to aid in the acclimatization of fish to the experimental apparatus. After 45 min the tubes were carefully lifted from the aquaria and each fish was allowed to choose between the two corals. Fish were released from the acclimatization tubes between 1800 and 1900 and their choice of coral recorded between 0600 and 0700 the following morning. Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 h.

Having determined the relative use of *A. nasuta* and *A. gemmifera* by each species of *Gobiodon* in the absence of a competitor we then examined the use of these coral species in the presence of a competitor. *G. histrio* was chosen as the competitor because it is numerically dominant on *Acropora nasuta*, which appeared to be the preferred coral species for at least three species of *Gobiodon* at Lizard Island (Munday et al. 1997). Experiments used to estimate competitive ability were conducted using a similar protocol to the previous experiment described above, except that two acclimatization tubes and two fish were used in each trial. The second tube was positioned directly in front of the first. One *G. histrio* was placed in one of the acclimatization tubes and one approximately equal-sized individual (within 5 mm total length [TL]) of another species was placed in the other tube. The location of each species in either the front or back tube was alternated between trials. It was not possible to use similar-sized individuals in the *G. rivulatus–G. histrio* trials because *G. rivulatus* has a much smaller maximum size than *G. histrio*. However, differences in size between these species did not appear to influence the results of these trials.

The effects of body size and prior residency on competitive ability against *G. histrio* were tested for two species, *G. axillaris* and *G. brochus*. These species were selected because they represent the range of competitive abilities detected in competition trials using fish of approximately equal body size (see above). *G. axillaris* was competitively equivalent to *G. histrio* and *G. brochus* competitively subordinate to *G. histrio*. Experiments were conducted in a similar manner to the competition trials using fish of approximately equal body sizes (see above) except that the individual competing against *G. histrio* in each trial was (1) either the same size, larger, or smaller than *G. histrio* and, (2) either a prior resident to the coral species preferred in aquaria or had no prior residency status. All combi-

nations of body size and residency status were used. Individuals of different body size were a minimum of 5 mm and a maximum of 10 mm different in TL. This size difference was found to be sufficient to detect effects of body size on competitive interactions. Where an individual of *G. axillaris* or *G. brochus* was a prior resident to the coral species preferred in aquaria, it was released directly onto that coral 12 h prior to the release of *G. histrio*.

Data analysis

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

Log-linear modeling was used to test the influence of body size and prior residency on competitive ability. Models were constructed to test five specific hypotheses: (1) competitive ability is independent of body size or residency status, (2) competitive ability is dependent on residency status, (3) competitive ability is dependent on body size, (4) competitive ability is dependent on both residency status and body size, and (5) competitive ability is dependent on an interaction between residency status and body size. To identify the simplest model that adequately described the outcome of the experiments, the models were fitted to the observed data in increasing order of complexity until there was no significant improvement in the goodness-of-fit statistic (likelihood ratio chi-square) from one model to the next. Because models 2 and 3 had the same level of complexity, these were both compared to model 1 to determine whether either provided a better fit to the data than model 1 alone. In this analysis, body size and prior residency status were considered to be explanatory variables and the final distribution of fish between coral colonies in each set of trials was considered to be a response variable. Wrigley (1985) provides a detailed discussion of constructing and testing log-linear models using explanatory and response variables. Three responses were recognized: (1) win, where *G. histrio* was excluded from its preferred coral by the second species, (2) draw, where both species occupied the preferred coral and, (3) lose, where the second spe-

cies was excluded from its preferred coral by *G. histrio.* Separate analyses were conducted to test the outcomes between *G. histrio* and *G. axillaris* and between *G. histrio* and *G. brochus.* Analyses were performed using SPSS for Windows version 7.0 (SPSS 1997).

Competitor reduction experiment

To test whether competition with *G. histrio* influences the abundance of other species of *Gobiodon* in the field, we reduced the abundance of *G. histrio* in replicate plots of reef and compared the changes in abundance of the other five species of *Gobiodon* to changes in their abundances in control plots. A total of 16 plots, each ~25 m² in area, were established on the reef flat at Horseshoe Reef and surrounding reefs on the leeward side of Lizard Island in January 1998. These reefs had patches of acroporid corals separated by areas of dense soft coral cover. We exploited this natural patchiness of coral distribution to help segregate plots and to reduce the potential for fish to move among experimental plots and from surrounding areas. All *G. histrio* were removed from eight randomly selected plots by anesthetizing the fish with clove oil and carefully removing them from the corals. Eight other plots were assigned as controls where *G. histrio* was not removed. Any *G. histrio* that colonized the removal plots were removed again in May 1998. *G. histrio* rarely cohabited coral colonies with other species of *Gobiodon;* however, in the few cases where other species were found in the same coral as *G. histrio* they were not removed. The abundance of all species of *Gobiodon* in these plots was recensused at the end of the experiment in December 1998.

Because the initial number of *G. histrio* and other species of *Gobiodon* varied considerably among plots, it was not possible to compare the absolute changes in abundance among control and treatment plots using a parametric test. Mann-Whitney *U* tests were used instead to test the rank order of changes in abundance in control vs. treatment plots. We did not include new recruits in the analysis because a recruitment pulse could mask effects of removing *G. histrio* on the abundance of juvenile and adults of each species. Recruits were classed as small individuals (<15 mm TL) that appeared to have settled within the month preceding the final census. Coral-dwelling gobies have rapid juvenile growth and can mature within a few months of settling to the reef (Kuwamura et al. 1996); therefore the effects of competition on adult abundance should be detected earlier in these small fish than in larger, slower growing species of reef fish.

To determine whether changes in abundance following competitive release could be predicted from competitive abilities of species estimated in aquaria, the mean change in abundance between control and removal plots for each species in the field experiment was compared to the percentage change in habitat use of these species in the laboratory-based competitive ability trails. The percentage change in habitat use in the presence vs. the absence of *G. histrio* in the laboratory was regarded as a measure of the ability of each species to compete against *G. histrio* for habitat space.

Recolonization experiment

Although *G. histrio* and *G. quinquestrigatus* appeared to have high percent similarity in habitat use and *G. quinquestrigatus* was an inferior competitor to *G. histrio,* the abundance of *G. quinquestrigatus* did not increase significantly following the reduction of *G. histrio* in the field experiment (see *Results: Competitor reduction experiment*). *G. quinquestrigatus, G. histrio,* and *G. axillaris* all mostly occupied *A. nasuta* at Lizard Island (Munday et al. 1997); however, the *A. nasuta* colonies used by *G. quinquestrigatus* were often more finely branched and browner than those used by *G. histrio* and *G. axillaris* (P. L. Munday, *personal observation*). This apparent habitat partitioning might help explain how these competitively dominant and subordinate species can coexist using the same species of coral. To test this possibility, we removed gobies from approximately equal-sized coral colonies of *A. nasuta* that were inhabited by *G. histrio, G. axillaris,* or *G. quinquestrigatus,* and then observed natural patterns of recolonization by gobies to these coral colonies. If morphological differences of corals are irrelevant to these gobies, recolonization should be characterized by a random reassortment of goby species among the cleared colonies. Alternatively, if some characteristics of the corals influence habitat preferences and competitive interactions, then recolonization should be biased toward the species that had previously inhabited each coral colony. Fish were removed from coral colonies after anesthesia with clove oil on reefs near the lagoon entrance on the leeward side of Lizard Island. Coral colonies used in this experiment were located on the reef flat and separated from each other by ~2–15 m. These colonies were visually censused 3 mo later and the recolonizing species recorded.

RESULTS

Habitat overlap

Gobies inhabiting 1368 colonies of 10 species of acroporid corals were censused. *G. axillaris* and *G. quinquestrigatus* exhibited a high percent similarity in habitat use with *G. histrio* (69% and 72%, respectively, Table 2). This similarity was largely due to the frequent use of *A. nasuta* by all three of these species. In contrast, *G. brochus* and *G. rivulatus* exhibited low percent similarity in habitat use with *G. histrio* (18% and 29%, respectively, Table 2). *G. brochus* most frequently inhabited *A. loripes,* which was rarely used by *G. histrio.* However, the largest individuals of *G. brochus* are usually found in *A. nasuta* (P. L. Munday, *personal observation*), the coral species usually inhabited by *G.*

TABLE 2. Percentage similarity in habitat use between species of *Gobiodon* at Lizard Island.

Species	G. histrio	G.a.	G.b.	G.r.	G.u.
G. axillaris (G.a.)	69				
G. brochus (G.b.)	18	25			
G. rivulatus (G.r.)	29	48	30		
G. unicolor (G.u.)	60	68	35	46	
G. quinquestrigatus	72	86	32	45	70

TABLE 3. Number of binary habitat-choice trials in which species of *Gobiodon* chose either *A. nasuta* or *A. gemmifera* corals.

Species	A. nasuta	A. gemmifera	P
G. axillaris	16	1	***
G. brochus	15	0	***
G. histrio	26	0	***
G. quinquestrigatus	15	2	**
G. rivulatus	6	11	NS
G. unicolor	16	0	***

Notes: The rightmost column reports results of a chi-square comparison against the null expectation of equal habitat use: $**P < 0.01$; $***P < 0.001$; NS = not significant ($P < 0.05$).

histrio. G. rivulatus mostly inhabited *A. gemmifera,* which was rarely used by *G. histrio. G. unicolor* exhibited moderate percent similarity in habitat use with *G. histrio* (60%, Table 2) and cohabited coral colonies with *G. histrio* more than twice as frequently (17 occurrences) than all other species combined (eight occurrences).

Competitive ability

In binary-choice trial in aquaria, *G. axillaris, G. brochus, G. histrio, G. quinquestrigatus,* and *G. unicolor* all showed very strong preference for *A. nasuta* in the absence of a competitor (Table 3). In contrast, *G. rivulatus* used both species of coral available but tended to prefer *A. gemmifera* (Table 3). The presence of *G. histrio* influenced patterns of habitat use in some species of *Gobiodon* but not others (Fig. 2). For both *G. axillaris* and *G. histrio* the use of the coral preferred in aquaria (*A. nasuta*) was significantly reduced in the presence of the other species (Fig. 2a), indicating that these two species were approximately equivalent competitors. The presence of *G. histrio* significantly reduced the use of *A. nasuta* by *G. brochus* but not vice-versa (Fig. 2b) indicating that *G. brochus* was an inferior competitor to *G. histrio.* The presence of *G. histrio* also significantly reduced the use of *A. nasuta* by *G. quinquestrigatus* but not vice-versa (Fig. 2c), indicating that *G. quinquestrigatus* was also an inferior competitor to *G. histrio.* In contrast, the presence of *G. histrio* did not significantly influence the habitat use of *G. rivulatus* (Fig. 2d) or *G. unicolor* (Fig. 2e); therefore these species did not appear to compete directly for habitat space with *G. histrio.*

Both body size and prior residency significantly affected the outcomes of competition trials between *G. axillaris* and *G. histrio* (Table 4, model 4 was the best fitting model). However, when sequentially fitting the models, the inclusion of body size resulted in a much greater improvement in the fit of the model (models 1 vs. 3, Table 4) than the inclusion of residency status (models 1 vs. 2, Table 4). Therefore, although outcomes of competition trials were dependent on both body size and residency status, body size had a greater effect than prior residency on competitive ability of *G. axillaris. G. axillaris* was approximately an equivalent competitor to *G. histrio,* and where *G. axillaris* and *G. histrio* were of equal size and neither species was a prior res-

ident of the preferred coral colony (*A. nasuta*), the results of competition trials were approximately equally spread among the possible outcomes (Table 5). Larger individuals of *G. axillaris* almost always won and smaller individuals of *G. axillaris* almost always lost competition trials where neither species was a prior resident of the preferred coral colony (Table 5). When *G. axillaris* was a prior resident of the preferred coral colony, individuals of an equal or greater size to *G. histrio* nearly always won the preferred coral (Table 5).
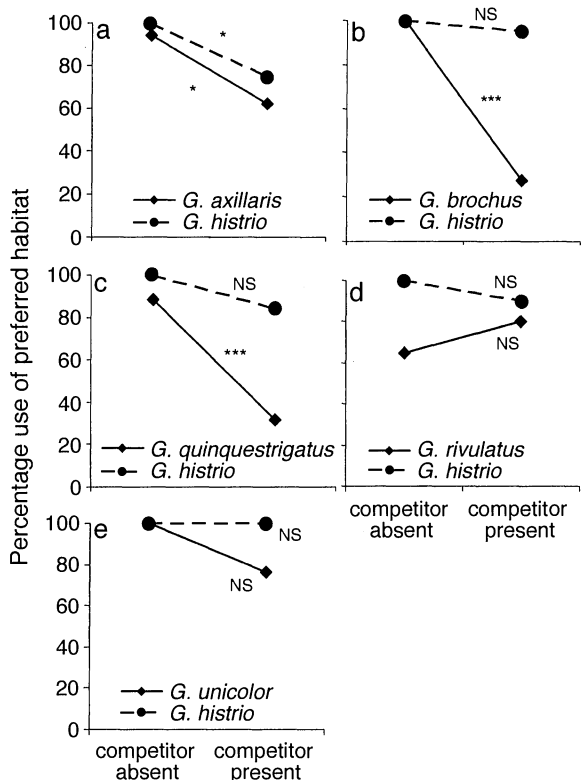

FIG. 2. Percentage of trials in which preferred coral habitat in aquaria was used by each species of *Gobiodon* in the absence and presence of *G. histrio.* Significance of change in habitat use: $*P < 0.05$; $***P < 0.001$; NS = not significant ($P > 0.05$).

TABLE 4. Log-linear analysis of relationships between competitive ability, body size, and prior residency for *G. histrio* and *G. axillaris*.

Model	Hypothesis: competitive ability is	Likelihood ratio χ^2	df	Difference between models	df
1) R × B + C					
	independent of body size or residency status	86.37***	10	1 and 2, 10.34**	2
2) R × B + R × C	dependent on residency status	76.03***	8	1 and 3, 62.63***	2
3) R × B + B × C	dependent on body size	13.37*	6	3 and 4, 12.38**	2
4) <u>R × B + R × C + B × C</u>	dependent on both residency status and body size	0.99 NS	4	4 and 5, 0.99 NS	4
5) R × B × C	dependent on an interaction between residency status and body size	0.0	0		

Notes: R = residency status, B = body size, C = competitive outcome. The best fitting model is underlined.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS = not significant ($P > 0.05$).

Both body size and prior residency also significantly affected the outcome of competition trials between *G. brochus* and *G. histrio* (Table 6, model 4 was the best fitting model). As was the case with *G. axillaris,* the inclusion of body size in the model resulted in the greatest improvement in the fit of the log-linear model (models 1 vs. 3, Table 6) compared to the inclusion of residency status in the model (models 1 vs. 2, Table 6). Therefore, although the outcomes of competition trials were dependent on both body size and residency status, body size had a greater influence than prior residency on competitive ability of *G. brochus. G. brochus* was an inferior competitor to *G. histrio* and equal-sized or smaller individuals of *G. brochus* were nearly always excluded from the preferred coral by *G. histrio* (Table 7). However, in trials where *G. brochus* individuals were larger than *G. histrio,* they nearly always excluded *G. histrio* from the preferred coral (Table 7). Also, when *G. brochus* had prior residency of the preferred coral colony, individuals equal in size to *G. histrio* retained the preferred coral in approximately half the trials (Table 7).

TABLE 5. Results of competition trials between *G. histrio* (H) and *G. axillaris* (A) for preferred (*A. nasuta*) and non-preferred (*A. gemmifera*) coral habitats in aquaria.

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

Notes: In prior residency trials, *G. axillaris* was placed on the preferred coral 12 h prior to releasing *G. histrio.* Outcomes are displayed for *G. axillaris.* Win = *G. axillaris* defended preferred coral from *G. histrio*; lose = *G. axillaris* displaced from preferred coral by *G. histrio*; draw = both species used preferred coral.

Competitor reduction experiment

The removal of *G. histrio* was successful in reducing the abundance of this species in treatment plots compared to controls (Fig. 3, Mann-Whitney $U = 60.5$, n_1, $n_2 = 8$ plots, $P < 0.001$). The reduction of *G. histrio* resulted in an increase in the abundance of *G. axillaris* (Fig. 3, Mann-Whitney $U = 49.5$, n_1, $n_2 = 8$ plots, $P < 0.05$) and *G. brochus* (Fig. 3, Mann-Whitney $U = 52$, n_1, $n_2 = 8$ plots, $P < 0.025$) in treatment plots compared to control plots. In addition, the combined change in abundance of *G. axillaris* and *G. brochus* in all removal and control plots was closely correlated with the change in abundance of *G. histrio* in these plots (Fig. 4). These results demonstrated that *G. axillaris* and *G. brochus* competed for habitat space with *G. histrio.* Although 62% of the change in abundance of *G. axillaris* and *G. brochus* was explained by the change in abundance of *G. histrio,* the slope of the relationship between these factors was <1 (Fig. 4), indicating undercompensation in the response of *G. axillaris* and *G. brochus* to competitive release.

The abundance of *G. quinquestrigatus* (Fig. 3, Mann-Whitney $U = 43$, n_1, $n_2 = 8$ plots, $P > 0.1$) did not change in treatment plots compared to control plots despite this species exhibiting high overlap in habitat use and being an inferior competitor to *G. histrio.* The abundances of *G. rivulatus* (Fig. 3, Mann-Whitney $U = 44$, n_1, $n_2 = 8$ plots, $P > 0.1$) and *G. unicolor* (Fig. 3, Mann-Whitney $U = 37$, n_1, $n_2 = 8$ plots, $P > 0.1$) did not change in removal plots compared with control plots. The abundances of *G. rivulatus* and *G. unicolor* were not expected to change because the laboratory experiments indicated that they did not compete directly with *G. histrio.*

Overall, the results of the competitor reduction experiment exhibited a predictable trend in relation to the competitive interactions observed in the laboratory. The difference between the mean change in abundance in control plots and the mean change in abundance in

TABLE 6. Log-linear analysis of relationships between competitive ability, body size, and prior residency for *G. histrio* and *G. brochus*.

Model	Hypothesis: competitive ability is	Likelihood ratio χ^2	df	Difference between models	df
1) R × B + C	independent of body size or residency status	68.41***	10	1 and 2, 9.38**	2
2) R × B + R × C	dependent on residency status	59.03***	8	1 and 3, 48.58***	2
3) R × B + B × C	dependent on body size	19.83**	6	3 and 4, 12.69**	2
4) <u>R × B + R × C + B × C</u>	dependent on both residency status and body size	7.14 NS	4	4 and 5, 7.14 NS	4
5) R × B × C	dependent on an interaction between residency status and body size	0.0	0		

Notes: R = residency status, B = body size, C = competitive outcome. The best fitting model is underlined.

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; NS = not significant ($P > 0.05$).

removal plots for each species tended to be positively correlated with the percentage change in preferred habitat use by these species in the presence of *G. histrio* in the competitive ability trails (Fig. 5); however, the results of the regression analysis were not statistically significant. Although *G. quinquestrigatus* fit this general pattern, the competitive interactions in the laboratory experiment did not predict the response of this species in the field experiment. Therefore, the trend for a relationship between competitive ability detected in the laboratory and the response to competitive release in the field may have been even less robust than suggested by the regression analysis.

Recolonization experiment

The pattern of recolonization varied among corals that were previously occupied by *G. histrio*, *G. axillaris*, or *G. quinquestrigatus*. Colonies of *A. nasuta* previously inhabited by *G. histrio* were mostly recolonized by *G. histrio*, but also by *G. axillaris* and *G. brochus* and infrequently by *G. quinquestrigatus* and *G. unicolor* (Fig. 6). Colonies of *A. nasuta* previously

inhabited by *G. axillaris* were mostly recolonized by *G. histrio* and *G. axillaris*, but also by *G. quinquestrigatus* and *G. unicolor*. In contrast, colonies of *A. nasuta* previously occupied by *G. quinquestrigatus* were almost exclusively recolonized by *G. quinquestrigatus* and only infrequently by *G. histrio* and *G. unicolor*. This result suggested that colonies of *A. nasuta* had characteristics preferred by *G. quinquestrigatus* and avoided by *G. histrio* and *G. axillaris*.

DISCUSSION

Few studies have experimentally shown that interspecific competition can influence the abundance of coral reef fishes (Robertson 1996, Schmitt and Holbrook 1999), even though patterns of resource partitioning consistent with niche-based models of competition theory are frequently observed among these species (Ross 1986, Jones 1991, Williams 1991). In general, patterns of resource use in the field are often difficult to reconcile with competition theory (Colwell

TABLE 7. Results of competition trials between *G. histrio* (H) and *G. brochus* (B) for preferred (*A. nasuta*) and non-preferred (*A. gemmifera*) coral habitats in aquaria.

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

Notes: In prior residency trials, *G. brochus* was placed on the preferred coral 12 h prior to releasing *G. histrio*. Outcome is displayed for *G. brochus*. Win = *G. brochus* defended preferred coral from *G. histrio*; lose = *G. brochus* displaced from preferred coral by *G. histrio*; draw = both species used preferred coral.
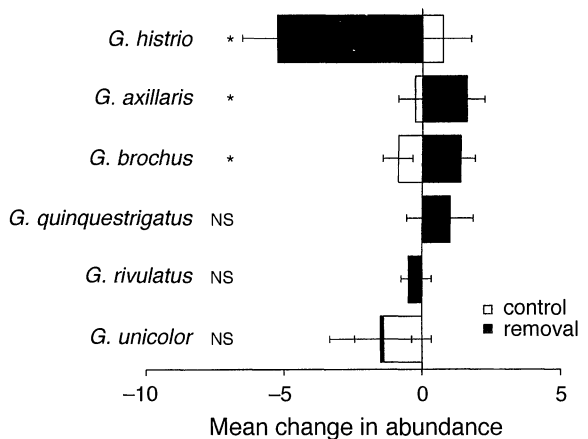

FIG. 3. Mean change in abundance (±1 SE) of each species of *Gobiodon* in removal and control plots following the removal of *G. histrio*. Mann-Whitney *U* tests: * $P < 0.05$, NS = not significant ($P > 0.05$).
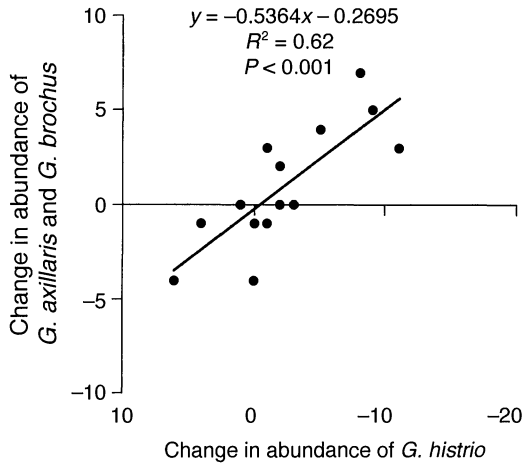
FIG. 4. Relationship between change in abundance of *G. histrio* and combined change in abundance of *G. axillaris* and *G. brochus* in all plots (removals and controls) between the start and end of the competitor reduction experiment.
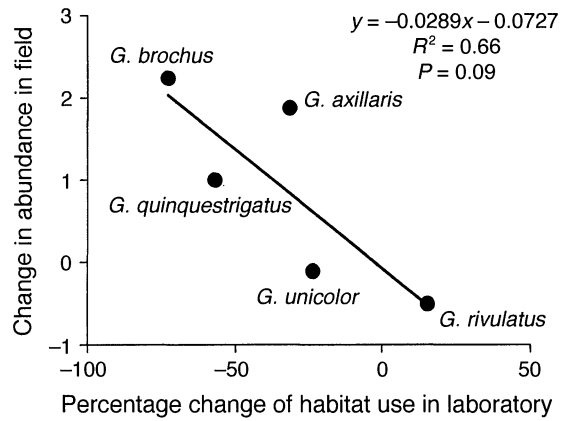

FIG. 5. Relationship between the percentage change of preferred habitat use in the presence of *G. histrio* in the laboratory experiment and the mean change in abundance between control plots and removal plots, following the reduction of *G. histrio* in the field experiment.

and Futuyma 1971), because species with overlapping realized niches may compete strongly if resources are limiting, but not compete if there is a surplus of resources. In addition, resource partitioning may occur as a result of current competition or simply because species prefer different resources.

This study demonstrates that all these alternatives can occur within a single guild of animals (Table 8). Reducing the abundance of a competitive dominant, *G. histrio,* resulted in a significant increase in the abundances of two species, *G. axillaris* and *G. brochus.* These two species clearly compete for space with *G. histrio.* However, *G. axillaris* exhibited high overlap in habitat use with *G. histrio,* whereas *G. brochus* exhibited low overlap in habitat use. Three other species did not compete for space with *G. histrio* and exhibited either low (*G. rivulatus*) or high (*G. quinquestrigatus* and *G. unicolor*) overlap in habitat use with *G. histrio.* These different relationships between overlap in resource use and the occurrence of interspecific competition indicate that guild members coexist through a range of different mechanisms (Table 8). A full appreciation of the differing roles of competition may require a pairwise comparison of resource overlap and competitive interactions among all species in a guild.

The hypothesis that competitive lotteries allow coexistence of competing species that do not partition resources was developed from studies of territorial coral reef fishes (Sale 1974, 1977, 1978), but there has previously been little experimental evidence to support the existence of such lotteries (Robertson 1995). At the scale of tens of meters (i.e., within plots) in this study, the coexistence of *G. histrio* and *G. axillaris* conforms to a competitive lottery. These two species had high overlap in habitat use in the field and had approximately equal competitive abilities as estimated from aquarium trials. Many of the new *G. axillaris* individ-
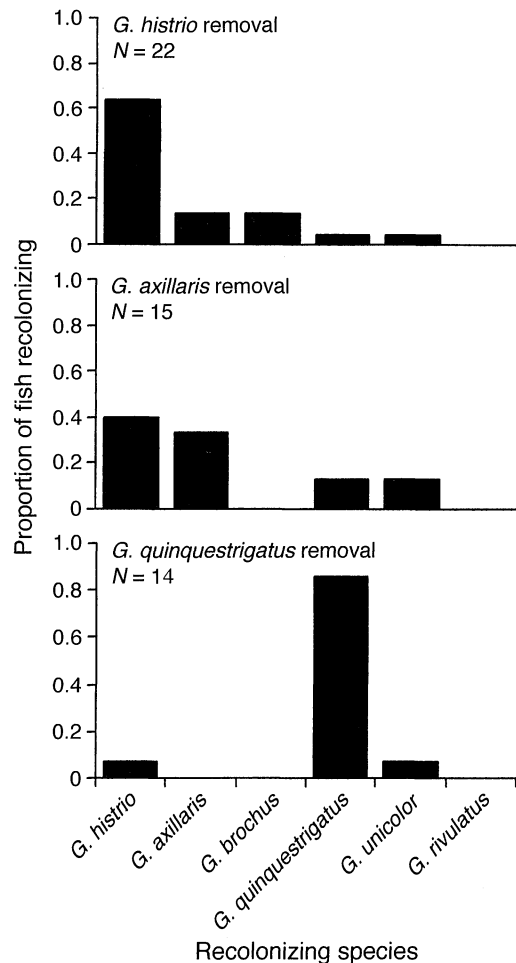

FIG. 6. Proportion of colonies of *Acropora nasuta* recolonized by each species of *Gobiodon. N* = number of coral colonies previously occupied by *G. histrio, G. axillaris,* and *G. quinquestrigatus.*

TABLE 8. Possible mechanisms of coexistence between *G. histrio* and other species of *Gobiodon* in relation to overlap in habitat use and competitive ability against *G. histrio*.

Species	Overlap in nabitat use with *G. histrio*	Competitive ability vs. *G. histrio*	Competes for space with *G. histrio*?	Mechanism of coexistence
G. axillaris	high	equal	yes	competitive lottery or coextensive niches
G. brochus	low	subordinate	yes	included niches
G. quinquestrigatus	high	subordinate	no	different microhabitat preferences
G. rivulatus	low	no interaction	no	different habitat preferences
G. unicolor	high	no or weak interaction	no	cohabitation of territories

uals observed in the plots had not reached full adult size and had apparently recruited from the larval pool between the survey periods. Also, the plots in this study were surrounded by areas of reef with relatively few suitable habitats for these fish, so movement of adult fish into the plots is likely to have been minimal. Although vacant space is recolonized by recruitment, there is also likely to be competition among established residents on the reef, especially for superior habitats. Our assays of competitive abilities suggest that the outcomes of competitive interactions between juvenile or adult *G. axillaris* and *G. histrio* are largely determined by the relative sizes of competing individuals. Because *G. axillaris* and *G. histrio* have almost identical size-based competitive abilities and attain similar maximum sizes (Table 1), these competitive interactions between established residents apparently do not lead to the numerical dominance of one species.

Although a lottery model might explain coexistence of *G. axillaris* and *G. histrio* within experimental plots, there is clear habitat partitioning by these species between reef zones. *G. axillaris* is most abundant on reef flats whereas *G. histrio* is most abundant on reef crests (Munday et al. 1997). This distribution pattern is consistent with the coextensive niche model (Colwell and Fuentes 1975), where species may have overlapping fundamental niches, but can coexist because each species is a superior competitor in a different subregion of the shared niche space. At the scale of whole reefs, *G. axillaris* and *G. histrio* could potentially coexist by differential competitive ability in the reef flat and the reef crest habitats, respectively. Alternatively, the distribution of *G. axillaris* and *G. histrio* across reef zones might be the result of habitat selection for different reef zones, as observed in other coral reef fishes (Wellington 1992, Doherty et al. 1996, Gutierrez 1998). Removal experiments in both reef zones are needed to determine whether the distribution pattern of *G. axillaris* and *G. histrio* is a result of current competition or other ecological and/or evolutionary processes.

Both the theories of competitive lotteries and coextensive niches provided inadequate explanations of the patterns of coexistence observed between *G. histrio* and *G. brochus*. These species appear to coexist through a niche shift by the subordinate competitor

only, conforming to the broad context of the included niche model (Colwell and Fuentes 1975). In the field, *G. brochus* usually inhabits *A. loripes* (Munday et al. 1997, 1999) and only the largest individuals are found in colonies of *A. nasuta* (P. L. Munday, *personal observation*). The competitive ability experiments demonstrated that *G. brochus* was an inferior competitor and individuals were only able to gain access to *A. nasuta* if they were larger than *G. histrio*, or if an equal size, were prior residents of the coral colony. The removal of *G. histrio* gave *G. brochus* access to colonies of *A. nasuta* from which it was previously excluded. Competition between *G. histrio* and *G. brochus* appears to involve a niche shift by the subordinate species only because adult *G. histrio* are rarely observed on colonies of *A. loripes* (Munday et al. 1997) despite being the superior competitor. Asymmetrical competitive effects of this type are common among animals (Connell 1983, Schoener 1983) and have been demonstrated for other coral reef fish (Ebersole 1985, Robertson and Gaines 1986, Clarke 1992, Robertson 1996).

Asymmetrical effects of competition were also expected between *G. quinquestrigatus* and *G. histrio*. Because *G. quinquestrigatus* exhibited high overlap in habitat use with *G. histrio*, but was a subordinate competitor in aquaria, we expected that *G. quinquestrigatus* would increase in abundance following the reduction in abundance of *G. histrio*. Contrary to expectation, *G. quinquestrigatus* did not appear to compete with *G. histrio* in the field. In the recolonization experiment, the colonies of *A. nasuta* inhabited by *G. quinquestrigatus* were nearly always recolonized by *G. quinquestrigatus*. In contrast, colonies of *A. nasuta* inhabited by *G. histrio* and *G. axillaris* were recolonized by a range of species, but mostly by *G. histrio*. These results suggest that *G. quinquestrigatus* uses a different component of the *A. nasuta* population than that used by *G. histrio* and *G. axillaris*. Therefore, competition between *G. histrio* and *G. quinquestrigatus* might not occur because of preferences of these species for different types of coral colonies. Also, in comparison to other species, *G. quinquestrigatus* has a more generalist pattern of habitat use within and among geographic locations (Munday et al. 1997, Munday 2000). This generalist pattern of habitat use might reduce the com-

petitive effects experienced by this species through use of a greater variety of corals for which competition with other species of *Gobiodon* does not occur.

G. rivulatus and *G. unicolor* also did not compete for space with *G. histrio,* but the mechanism for coexistence with *G. histrio* differs between these two species. *G. rivulatus* had a low overlap in habitat use with *G. histrio* because it prefers different species of coral. In the field *G. rivulatus* usually inhabits *A. gemmifera,* whereas *G. histrio* usually inhabits *A. nasuta* (Munday et al. 1997) and the laboratory experiments demonstrated that this pattern was due to habitat preference rather than competitive interactions by either species. In contrast, *G. unicolor* exhibited high overlap in habitat use with *G. histrio* but appeared to coexist by the ability to cohabit the same coral colonies without substantial interactions. *G. unicolor* is frequently observed to cohabit coral colonies with *G. histrio* and other species of *Gobiodon* in the field (Patton 1994, Munday et al. 1999), especially on larger coral colonies (Munday et al. 1998).

Because species can coexist by different mechanisms, different combinations of resource overlap, competitive abilities, and competitive outcomes are to be expected. This study clearly demonstrates there can be a number of relationships between resource overlap and the occurrence of interspecific competition, even among closely related species. There was, however, a trend in the relationship between competitive ability, as measured by the change of habitat use in the presence of a competitor in laboratory trials, and the response to competitive release in the field. This result suggests that the competitive interactions between individuals observed in aquaria might be useful for predicting population level responses. However, this relationship will only hold where the resources used in laboratory experiments are limiting in the field, as demonstrated by the contradictory result for *G. quinquestrigatus.* Indeed, interactions between individuals of territorial species are frequently observed in the field but these interactions need not control population abundances because space or other resources may not be limiting (Doherty 1983, Doherty and Williams 1988, Mapstone and Fowler 1988, Jones 1991).

At the spatial scales of our study, populations of gobies are demographically open. While the role of competition in determining patterns of abundance and coexistence remains controversial in general, its role is particularly unclear in open populations. Because at small spatial scales reef fishes generally have open populations coupled with highly variable patterns of recruitment (Doherty and Williams 1988, Doherty 1991), it is likely that populations of some species are often below levels where resources such as habitat space are limiting. Furthermore, experimental density manipulations have often not detected effects of interspecific competition among coral reef fishes (Doherty 1982, 1983, Jones 1987, 1988). Consequently, interspecific

competition is often considered to be relatively unimportant in structuring populations and communities of reef fishes. This study, in conjunction with others (Robertson 1996, Schmitt and Holbrook 1999, Srinivasan et al. 1999), provides increasing evidence from manipulative experiments that interspecific competition for space can influence patterns of abundance of coral reef fishes.

Despite the clear effects of competition with *G. histrio* on the abundance of *G. axillaris* and *G. brochus,* the increase in abundance of these species did not fully compensate for the reduction in abundance of *G. histrio* in the field. Such undercompensation has been frequently observed in competition experiments and may be explained by a variety of mechanisms, including differences in fundamental niches of the competitors, competition with other species not recorded in the experiment, or insufficient time for complete compensation to occur (Holbrook and Schmitt 1995). Delays in compensatory effects are especially likely in open populations where recruitment can be highly variable (Forrester 1990, Hixon 1991, Jones 1991, Caley et al. 1996). This appears to be the most likely explanation for undercompensation in this study. Species of *Gobiodon* usually form breeding pairs on coral colonies of sufficient size (Patton 1994, Nakashima et al. 1996, Munday et al. 1998). However, by the end of the competitor removal experiment, some coral colonies from which pairs of *G. histrio* had been removed had been recolonized by only a single *G. axillaris.* Some other coral colonies from which pairs of *G. histrio* were removed were reoccupied by only a single *G. histrio.* The presence of a single adult prevented the space being occupied by other species of *Gobiodon,* but did not fully compensate for the number of *G. histrio* removed. This study ran for just under 12 mo and it seems likely that the experiment was terminated before *G. axillaris* and *G. brochus* fully responded to the reduction in the abundance of *G. histrio.*

Studies of interspecific competition in reef fishes have mostly demonstrated effects on the abundances of relatively small, sedentary or territorial fishes (Hixon 1980, Larson, 1980, Schmitt and Holbrook 1990, 1999, Robertson 1996, Srinivasan et al. 1999). The species studied here are very small, site-attached species with specialized habitat requirements. Experimental manipulations of habitat availability (Buchheim and Hixon 1992) and predictable changes in abundances following natural changes to habitat availability (Kuwamura et al. 1994, Clarke 1996) indicate that other small, habitat-specialized species are also limited by the availability of habitats. Small species are among the most diverse and numerically dominant fishes on coral reefs (Munday and Jones 1998). Therefore, it may be among these species that the effects of interspecific competition for space will be most apparent. Perhaps the most important message from this study is that

diverse roles of competition can be expected in complex communities.

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