

Diversity in coral reef fish communities: the effects of habitat patchiness revisited

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ABSTRACT: Explanations for the association between habitat patchiness and diversity in coral reef fish communities are often conflicting among studies, and no consensus has been reached. We investigated patterns in diversity and structure of fish communities associated with large and small coral patch reefs at Glover's Reef, Belize. The abundance of fish was greater on large reefs (mean size 2300 m²) than on small reefs (mean size 740 m²), but species richness was less consistent among the different sizes of reefs. Results from rarefaction analyses indicated that both species richness and species evenness were similar between a single large reef and 3 smaller reefs of equivalent total area to the large reef. Furthermore, the density of species on standardized sizes of reef habitat was similar or greater on small reefs than species density on large reefs. The nested subsets hypothesis predicts that species assemblages on small isolated habitat patches will constitute only a subset of the assemblage on a large patch. However, reef fish communities in our study did not show any nested patterns when they were ordered by species richness, reef size, or reef isolation. To further evaluate why the fish communities on small reef patches were so diverse, we compared the number of numerically rare species and the spatial segregation of species within large and small reefs. More rare species, including both transients and resident species, occupied the combined small reefs than the large reefs. A greater number of species occupied reef edge habitats than the reef top and thus contributed to greater species density on small patches with larger perimeter:area ratios. Diversity in coral reef fish communities may be associated with the spatial distribution of species over the physical structure of reef habitat, but these patterns may be highly scale-dependent.

KEY WORDS: Species diversity · Patchiness · Coral reef fish · Community structure · Sloss · Nestedness

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INTRODUCTION

The effects of habitat patchiness on species diversity in coral reef fish communities have been the subject of considerable and often conflicting debate. The influence of physical characteristics of a reef patch on reef fish diversity has been widely studied, but results have been contradictory (Sale 1980). For example, some studies indicated that reef surface complexity (rugosity) was significantly associated with diversity (Risk 1972, Luckhurst & Luckhurst 1978, Gladfelter et al.

1980, Carpenter et al. 1981, Clarke 1988, McLain & Pratt 1999), whereas other studies found no such relationship (Sale & Douglas 1984, Roberts & Ormond 1987, Ault & Johnson 1998). At the larger scale among reef patches, habitat area has been a reliable predictor for fish species diversity (Gladfelter et al. 1980, Sale & Douglas 1984, Clarke 1988, Ault & Johnson 1998). The species-area relationship on insular habitats provides a firm basis for predicting that diversity will be greater on a large patch than on a small patch (Preston 1962, MacArthur & Wilson 1967). However, there is no simple extension of this relationship for predicting diversity on a large patch versus a group of smaller patches of total area equal to that of the large patch (Simberloff

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& Abele 1982). Several empirical studies suggested that species diversity will be similar on a 'Single Large patch Or on Several Small patches' of equal total area (i.e. the 'sloss' debate) (e.g. Quinn & Harrison 1988). This premise was based on observations that the reduction in the number of patches may have a less than proportional reduction in the number of species, due to microhabitat influences on species assemblages (Gilpin & Diamond 1980).

If the species assemblage on each small patch is simply a subset of the species assemblage on the large patch, however, the community structure of the large patch may effectively incorporate the combined diversity of the smaller patches. The 'nested subsets hypothesis' predicts that small species-poor communities will simply be subsets of large species-rich communities in patchy habitats (Darlington 1957, Patterson & Atmar 1986, Cook 1995). Nested patterns may be produced by the interacting mechanisms of extinction influenced by patch size and colonization influenced by patch isolation (Darlington 1957, Lomolino 1996). McLain & Pratt (1999) suggested that 'nestedness' occurred only in select families of obligate reef fishes and that this pattern was associated with recruitment limitation but not with patch size.

We revisited the effects of patch size on diversity and structure of coral reef fish communities. To isolate reef patchiness as a factor, reefs were deliberately selected to reduce variability in physical factors other than reef size. Null models were used to test the associations between the number of reef patches and fish species richness, species evenness, and species density in groups of a single large and 3 smaller reefs of total area equal to that of the large reef. The null hypothesis that fish assemblages on large and small patches are similar was also tested. To determine whether fish assemblages on the small reefs were nested subsets of the fish assemblages on larger patches, reefs were sorted by size, isolation, and species richness, and the degree of nestedness was compared among the individual reef fish communities. Finally, to further compare the spatial distribution of species, we assessed the number of fish species preferentially occupying the edge and top surface of reefs, and we compared the distribution of numerically rare species (suffusive rarity, *sensu* Schoener 1987) on large and small reefs. We assessed the community patterns that are consistently influenced by habitat patchiness.

MATERIALS AND METHODS

Site selection and fish surveys. Fish surveys were conducted on discrete coral patch reefs at Glover's Reef, Belize, from May to July 1998. Glover's Reef

(87° 48' W, 16° 50' N) is a coral atoll, 28 × 20 km, that is ringed by an emergent crest reef. More than 700 patch reefs occur in the lagoon, and many of these rise to near the surface from the lagoon floor 2 to 18 m deep. Patch reef formations are mostly elliptical or circular in shape with distinct vertical walls 2 to 3 m in height from the sand or seagrass floor (Wallace & Schafersman 1977). For fish surveys, 4 groups of reefs were selected, with each group containing 1 large patch and 3 small patches of total area equal to that of the large patch. Reefs were selected to minimize the variability in reef size ('small' or 'large'), reef shape, surface complexity (rugosity), the distance between reef patches, proximity to the reef crest, current flow, and depth of the water column over the reef. The distance between reefs within a group averaged 0.5 km, and groups of reefs were separated by at least 3 km. All reef groups were oriented north-south, 1 to 2 km from the eastern reef crest.

To check the variability of the physical reef structure, we analyzed data from detailed reef measurements. The perimeter of reefs was measured using fiberglass measurement tapes fitted around the edge. To calculate the area of the reef, the patch was approximated as a circle, with the radius estimated from the measured circumference. Water depth was measured at 3 m intervals on across-reef transects, adjusted for tidal difference (mean tidal fluctuation 0.5 m), and averaged across replicate transects (4 transects across a small reef and 8 across a large reef). Rugosity of the reef was estimated from the across-reef transects. A measurement tape was fitted closely to the contours of the reef and then stretched taut over the same transect; rugosity was calculated as the ratio of the fitted-to-taut measurements (Risk 1972). Data on reef size were log-transformed to conform to assumptions of normality and homoscedasticity, and *t*-tests were used to compare within- and among-differences in large and small reefs at an adjusted significance level of $p = 0.01$ (Sokal & Rohlf 1981).

Surveys were conducted in the conservation zone of the Glover's Reef Marine Reserve that is closed to commercial fishing. Fish communities were surveyed by 2 divers swimming crossing patterns over the entire reef, starting at opposite ends of the reef. Divers identified fish to species level (Böhlke & Chaplin 1993, Humann 1994) and counted the number of each species; fish that could not be identified in the field were photographed for later identification. All species sighted on reefs were included in surveys, except gobies (Gobiidae), blennies (Blenniidae), and cardinalfishes (Apozonidae). These species are highly cryptic and difficult to accurately census by this non-destructive method. A census for species occurrence on a reef was compiled from the combined diver surveys, and the abundance

of each species was obtained by taking the higher value from the surveys (Sale & Douglas 1984).

Fish diversity and community composition. We first examined patterns of similarity in the number of species and abundance of each species among all reefs using non-metric multidimensional scaling (MDS) (Legendre & Legendre 1983). Bray-Curtis similarities were analyzed on matrices of presence-absence data for species richness and standardized species abundance data. Abundance of each species was standardized as the ratio of local abundance of a species to maximum abundance among all sites, in order to remove the influence of absolute values (Jackson 1993). We then examined patterns in species richness, species evenness, and species density within 4 reef groups consisting of a single large and 3 small reefs using distribution-free randomization tests (Gotelli & Graves 1996). Species richness was compared using rarefaction with 100 replicate simulations on the 2 reef sizes in each group (Gotelli & Entsminger 1997). The rarefaction procedure estimates expected species richness and the associated variance in random subsamples based on the same number of individuals (Sanders 1968, Heck et al. 1975), allowing for direct comparisons of fish species richness on different sizes of reefs. To compare species evenness, we used Hurlbert's (1971) probability of an interspecific encounter (PIE), i.e. the probability that 2 individuals drawn randomly from a reef will be different species. To assess how many species were expected on a fixed area of reef (i.e. species density on a standardized area of reef habitat), we applied rarefaction to determine the expected number of species on standardized 200 m² plots up to the maximum size of small reefs (James & Wamer 1982). The means of the numbers of species and sizes of small reefs were used for comparison with the large reef in each of the 4 reef groups. No assumptions or extrapolations were made for areas larger than actual patches surveyed.

We tested the null hypothesis that the species composition on one reef is not different from that on another reef, regardless of local species richness, patch size, or patch isolation. Fish assemblages were evaluated for nested patterns using the algorithm by Lomolino (1996) that uses species presence-absence data to quantify nested patterns in communities ordered by species richness, patch size, or patch isolation. Matrices of species presence-absence data were ordered by species richness, regardless of reef size or isolation. Area-ordered matrices were constructed by sorting reefs by size in descending order. Matrices of reef isolation were constructed by sorting small reefs by distance from the large reef in the group, instead of the reef crest which may have distinctly different fish assemblages (Clarke 1977, Molles 1978, Acosta &

Robertson, unpubl. data). Species common to all 16 reefs were excluded because this may inflate the degree of nestedness (Simberloff & Martin 1991). The deviation (D) from perfect nestedness is calculated by counting the number of times a species present on a lower reef in a matrix is absent on the higher reefs. The statistical significance of nestedness was evaluated by comparing the observed D value to expectations from Monte-Carlo simulations of 1000 randomly ordered matrices (Lomolino 1996).

To further assess the species compositions within reef patches, we compared the number of numerically rare species occurring on only 1 reef in the 4 reef groups and the number of rare species encountered on only 1 reef during the entire study. These data were analyzed using the Mann-Whitney U -statistic. Fishes were also classified by their spatial distribution on a reef; a species was classified as occupying the edge/wall of a reef, the top of a reef, or both zones when observed in a zone during 95% of all surveys. The Kruskal-Wallis rank statistic (H) was used to compare the number of species occupying different reef zones. Due to the paucity of autecological information for most species, no other attempts were made to classify species by vagility or microhabitat use.

RESULTS

A total of 11 273 fishes of 85 species was surveyed on 4 large reefs (average size 2303 m²; range 2056 to 2574 m²) and 12 small reefs (average size 738 m²; range 664 to 871 m²). Reef area and the perimeter:area ratios were significantly different between reefs classified as large or small, but mean rugosity of all reefs was similar (Table 1). Results from the MDS analysis indicated that the number of species was not consistent among reefs, with the large reefs clustered

Table 1. Comparisons of physical structural attributes between large and small reefs in the lagoon at Glover's Reef, Belize. Log₁₀-transformation was used on area measurements in order to conform to assumptions of normality and homoscedasticity of variance. There were no significant differences in the parameters within the 4 large or 12 small reefs

Attribute	Large reefs Mean (± SE)	Small reefs Mean (± SE)	t	p
Log area	3.398 (± 0.038)	2.785 (± 0.038)	11.597	<0.001
Rugosity	1.183 (± 0.06)	1.134 (± 0.026)	0	0.42
Perimeter:area	0.071 (± 0.003)	0.145 (± 0.005)	8.364	<0.001

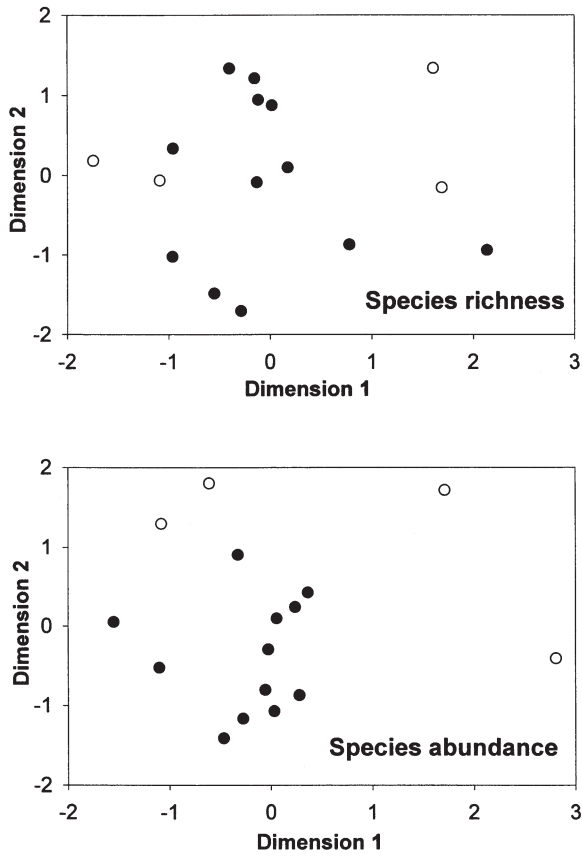


Fig. 1. Similarity plots from MDS analyses on number of species (presence-absence) and abundance of each species (standardized as local abundance to maximum abundance). Pairwise distances between points indicate proportions of Bray-Curtis similarities; sites close together share more species and abundances of fish species than sites farther apart. (●) Small patch reefs; (○) large patch reefs (3 times the mean size of small reefs)

in 2 groups (Fig. 1). The abundance of most species was higher on large reefs than on small reefs. The MDS plots accounted for 64% of the variance in the number of species and 69% of the variance in fish abundance.

Three large reefs had more species than any single corresponding small reef in reef groups, whereas the 4th large reef had fewer species than 2 of its small reefs (Appendix 1). In all 4 reef groups, species richness on the combined small reefs was similar to that on a large reef (Fig. 2). For example, the rarefaction curve for reef group 2 showed that the 3 small reefs collectively had 44 species per 500 fish, and the single large reef had 38 species for the same number of fish. Because there was a substantial overlap in standard deviations in all 4 reef groups, species richness did not differ significantly within any reef group. The PIE indicated that species evenness was also not significantly different between

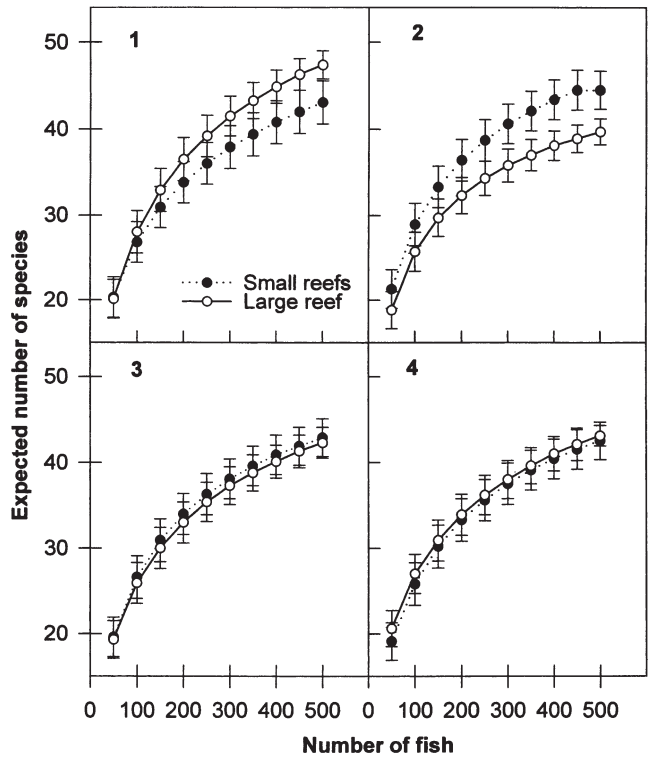


Fig. 2. Rarefaction curves for fish species richness on 4 reef groups, each containing 1 large reef and 3 small reefs of equal total area, at Glover's Reef, Belize; bars are ± 1 SD. No extrapolations were made for the number of fish greater than the minimum abundance on reefs

several small (mean \pm SE: 0.928 ± 0.002) and single large reefs (mean \pm SE: 0.922 ± 0.008) (Fig. 3). The large values of the PIE metric suggested that a large random component was associated with these commu-

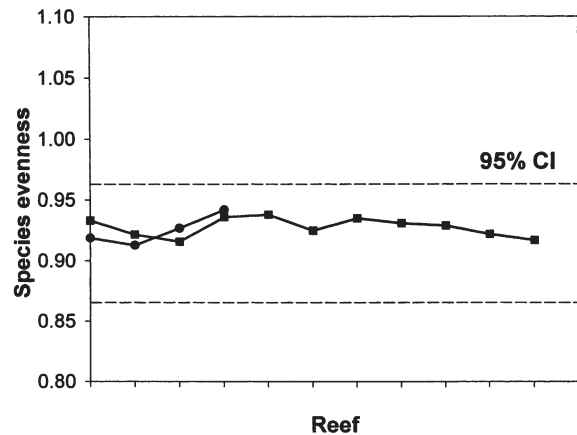


Fig. 3. Probability of an interspecific encounter (PIE) as a measure of species evenness on 4 large reefs (●) and 12 small reefs (■). The 95% confidence intervals were similar for both reefs and are shown as a single set of lines

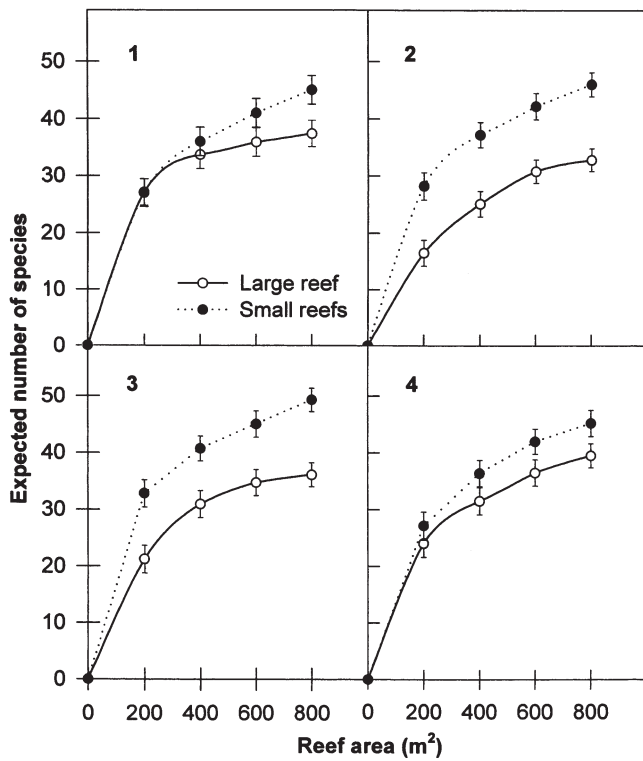


Fig. 4. Rarefaction curves for fish species density on 4 reef groups, each containing 1 large reef and 3 small reefs of equal total area, at Glover's Reef, Belize; bars are ± 1 SD. No extrapolations are made for reef sizes greater than the maximum size of small reefs

nities (Hurlbert 1971). This indicates that, although more fishes were found on a single large reef than on a single small reef, species evenness was similar on a single large reef and groups of 3 small reefs. Furthermore, the rarefaction curves for species density indicated that more species were expected in equal-sized plots of reef habitat on small reefs than on large reefs, and the differences were substantial in at least 2 of the 4 reef groups (Fig. 4). For example, a small patch in reef group 2 was expected to have 43 species on a 600 m² area, compared to 30 species on the same area of a large reef.

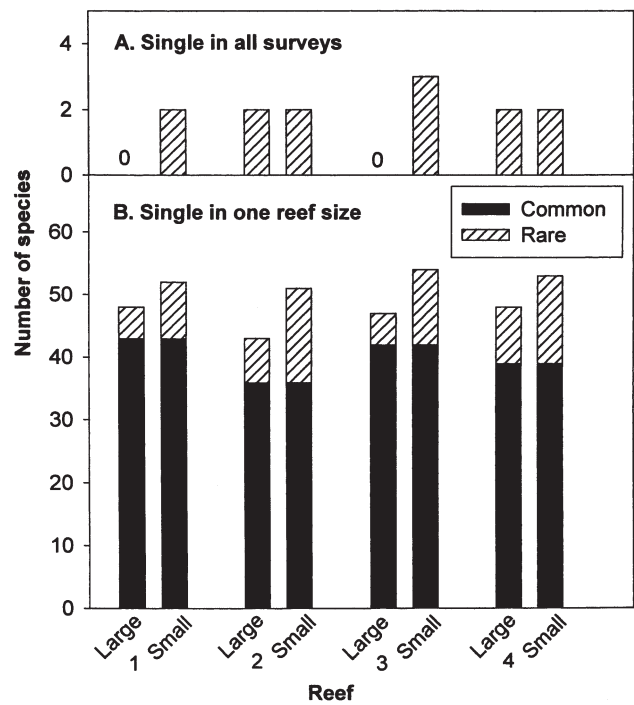


Fig. 5. (A) The numbers of numerically rare fish species observed on only 1 reef during all surveys. None of the fish on the large reefs in reef group 1 and 3 qualified as rare. (B) The numbers of rare species observed on 1 reef size (large or small) in any reef group. The numbers of species common to both large and small reefs are shown for reference

Of the 85 species censused, 25 species including both residents and transients were common to all reefs. In the analysis for nested subset patterns in the whole community, none of the reef groups showed a significant degree of nestedness among the remaining 61 species when ordered by either reef area, reef isolation, or species richness (Table 2). None of the reef groups had more than a 25% difference in the observed-to-expected nested patterns.

Among all 16 reefs, 9 species were found only on a small reef and 4 species were found only on a large reef (Fig. 5). Abundances of all these species were low

Table 2. Analysis of nestedness for groups of reefs sorted by area, isolation, and species richness. Percent of perfect nestedness is calculated as: %PN = 100[(R-D)/R], where: D = observed number of departures from nestedness; R = estimated number of departures for 1000 randomly ordered matrices; and P = proportion of random runs with fewer departures than the actual matrix (see Lomolino 1996). Shown are %PN(P)

	Reef group			
	1	2	3	4
Area-ordered	19.82 (0.14)	7.61 (0.24)	18.63 (0.08)	23.42 (0.09)
Isolation-ordered	10.21 (0.39)	3.01 (0.73)	3.14 (0.34)	8.83 (0.40)
Species richness-ordered	19.45 (0.14)	9.93 (0.96)	18.12 (0.10)	22.71 (0.10)

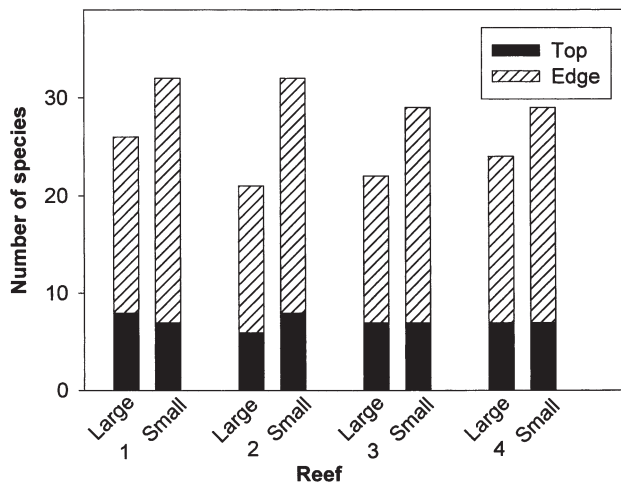


Fig. 6. The spatial distribution of fish species on top and edge habitats of large and small reefs in 4 reef groups. The number of top-dwelling species was not significantly different between large and small reefs, or among reef groups. The number of edge-dwelling species was significantly greater on small reefs

(1 to 3 individuals) except for a group of 20 tomtate *Haemulon aurolineatum*. The number of rare species occurring on only 1 reef in a reef group was also significantly higher on small reefs (mean 12.5 species) than on large reefs (mean 6.5 species) in the 4 reef groups (Mann-Whitney test: $U = 0.50$, $p = 0.03$) (Fig. 5). Again, these rare species were also found in low abundances (1 to 6 individuals). In contrast, the number of common species among reef groups was not significantly different between large and small reefs.

For species exhibiting spatial segregation, 8 species primarily occupied reef tops and 42 species used reef edges (Appendix 1). Significantly more species occurred on reef edge habitats (mean \pm SE: 12.9 ± 0.43) than reef tops (7.9 ± 0.43) on all sizes of reefs (Kruskal-Wallis $H = 17.6$, $df = 2$, $p < 0.001$) (Fig. 6). The number of top-dwelling species (8) was similar on large and small reefs, but the number of edge-dwelling species was greater on small (40 species) than on large reefs (28 species). The distribution of more species on small reefs may be related to the combined larger perimeter:area ratios, and thus, more reef edge habitat on small reefs than that available on large reefs.

DISCUSSION

The size of a habitat patch is widely held to be the primary determinant of species diversity, but this general principle may mask a number of complex interactions between faunal communities and habitat patchiness, depending on the scale of observations (Wiens

1976, Cornell & Karlson 1997). While species diversity in fish communities was most often associated with habitat area, studies on the correlations between species diversity and other habitat characteristics are often conflicting (Sale 1980). In our study, we attempted to minimize the variability in physical structural attributes of coral reef patches so that associations between habitat patchiness and fish community diversity and structure could be explored. In the lagoon of the Glover's Reef atoll, large patch reefs have a higher abundance of fishes but the number of species on large reefs was variable. However, groups of 3 small reefs collectively had similar numbers of species than a corresponding large reef of equal total area in all 4 reef groups. The majority of species appeared to be resident obligate reef dwellers.

Similar to patterns in species richness, species evenness on groups of small reefs was equivalent to that on the large reefs. Several species were consistently abundant (e.g. wrasses, Labridae; damselfishes, Pomacentridae; parrotfishes, Scaridae; grunts, Haemulidae; and some snappers, Lutjanidae), whereas others were found in high density aggregations on only 1 or a few reefs (e.g. lane snapper *Lutjanus synagris*; tomtate *Haemulon aurolineatum*). The values from the randomization tests indicated that species evenness was defined by a large stochastic component. This pattern was in agreement with studies suggesting that diversity in many coral reef fish communities is similar to that expected by chance due to stochasticity in larval recruitment, assuming that habitat area and characteristics are relatively homogeneous (Sale 1977, Sale & Williams 1982, Caley & St. John 1996). When standardized by reef area, the density of species on small reefs was similar to or greater than species density on large reefs. These patterns suggest that fish diversity on groups of smaller reefs was consistently high and similar to diversity on a single large reef of equivalent area.

Nested subsets of species are attributed to differences in habitat area, habitat isolation, and gradients in species richness (Darlington 1957, Patterson & Atmar 1986, Lomolino 1996). Species-rich communities are expected to occupy larger, less-isolated habitat patches, whereas subsets of this fauna would occupy smaller, more-isolated habitat patches. Our results from Glover's Reef did not reveal any nested patterns in the reef fish communities on discrete patch reefs when the communities were ordered by species richness, reef size, or reef isolation. This indicated that the smaller reefs had statistically independent species assemblages at scales of $O(100\text{ m})$ to $O(1\text{ km})$. At a similar spatial scale, McLain & Pratt (1999) determined that nestedness was exhibited by some families of obligate reef fishes but not others on fringing reefs

near the US Virgin Islands. They suggested that nestedness can occur without differences in species' dispersal abilities or extinction vulnerability. However, Kadmon (1995) provided strong inference that those species lacking mechanisms for the widespread dispersal of their propagules are expected to exhibit nestedness in patchy landscapes, whereas nestedness is not expected for species with widely dispersing propagules. Furthermore, nested patterns are necessarily expressed at the scale at which all species are equally isolated (Atmar & Patterson 1993). Our study reefs (and those of McLain & Pratt 1999) were not isolated for a number of species for which adults are capable of interpatch dispersal, as well as for larvae of most fish species occupying coral reefs (Doherty & Williams 1988). The spatial scale at which nestedness is exhibited in coral reef fish communities may be larger than the local scale. The autecology of many coral reef fish species is not well known, and generalizations on dispersal abilities and extinction vulnerabilities must be viewed with caution.

While the number of common species on both large and small reefs was similar, patterns of numerically rare species were more complex. Species rarity can result from a number of factors that impact diversity patterns in different ways (Kunin & Gaston 1993). The most widespread pattern may be simply an artifact of sampling species that are rare in one area but are common in nearby unsampled habitats, termed 'diffusive rarity' (Schoener 1987). Truly rare species that influence alpha diversity are those specialists with low densities everywhere in their range, termed 'suffusive rarity' (Schoener 1987). For example, Novotný & Bassett (2000) found that 30% of terrestrial insects sampled intensively in a tropical rainforest occurred as single specimens. Rare fish species in the Glover's Reef lagoon were almost twice as abundant on the small reefs than on the large reefs. Of those that could be reliably classified as transient or resident, ca. 50% were large transient predators of which their true abundances are not known, including groupers (*Myceteroperca* spp.), hogfish *Lachnolaimus maximus*, triggerfish *Balistes vetula* and *Canthidermus sufflamen*, and nurse shark *Ginglomostoma cirratum*. Additionally, sergeant major *Abudefduf saxatilis* was rare in this habitat but occurs in great abundance in other parts of its geographic range (e.g. Florida Keys; C.A.A. pers. obs.). The remaining 50% consisted of small reef residents that represented suffusively rare species such as tobaccofish *Serranus tabacarius*, bandtail pufferfish *Sphoeroides spengleri*, sanddiver *Synodus intermedius*, glasseye snapper *Priacanthus cruentatus*, and spotted moray *Gymnothorax moringa*. Even when the potentially diffusively rare species are removed, the suffusively rare species were found in

numbers on the small reefs similar to or greater than on large reefs.

The spatial distribution of species within a patch may have significant impacts on community structure and diversity (MacArthur 1958). When classified by their observed spatial distribution on isolated coral reefs at Glover's Reef, 44% of fish species did not exhibit any spatial fidelity. These included wide-ranging predators such as barracuda *Sphyraena barracuda* and queen triggerfish *Balistes vetula*, as well as smaller reef obligates such as parrotfish *Sparisoma* spp. and wrasses *Thalassoma bifasciatum* and *Halichoeres garnoti*. Among spatially segregated species, significantly more species occupied reef edge habitats than the reef top. The top-dwelling species were dominated by the hamlets *Hypoplectrus* spp. and the territorial damselfishes *Stegastes* spp. (except for bicolor damselfish *Stegastes partitus*). Although a few edge-dwelling species were small reef residents (e.g. *Chromis cyanea*, *Gramma loreto*), most were large species that appear to use the reef primarily as shelter between transit. This simple spatial segregation may explain why rugosity of reef substratum is an unreliable predictor of diversity when only families of 'obligate' reef dwellers are considered. Reef-edge habitat, as indicated by the perimeter:area ratio, was twice as large on small reefs combined than on the large reefs, and this resulted in up to 30% more edge-habitat species on small reefs.

Despite the contention that the sloss concept has limited utility in ecology, analyses of this and related patterns have revealed important information on how communities are influenced by habitat patchiness (Cook 1995). These patterns of diversity are real but appear to be highly dependent on scale. Our comparisons of fish communities on single large and several small reefs indicated that species diversity was similar across patches of equivalent total area. Furthermore, at this spatial scale, fish species assemblages on small reef patches were not nested subsets of those on large reefs. The number of rare species and the greater extent of reef edge habitat on small reefs appear to contribute to this pattern of diversity. The full influences of habitat patchiness on coral reef fish community diversity and structure may not be fully understood until autecological data, particularly on larval and adult dispersal, become available.

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