THE RAFFLES BULLETIN OF ZOOLOGY 2007 Supplement No. **14**: 245-254
Date of Publication: 31 Jan.2007

PATTERNS OF MICROHABITAT USE BY FISHES IN THE PATCH-FORMING CORAL *PORITES RUS*

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ABSTRACT. **–** There is increasing evidence that some of the spatial variation in characteristics of local assemblages of reef fish can be explained by variation in the measurable features of the habitat. In lagoons at Moorea, French Polynesia, the coral, *Porites rus* forms large, structurally complex patch reefs with surface branches and numerous holes and interior cavities. We conducted visual surveys of the fishes associated with a set of 66 *P. rus* patch reefs and recorded the microhabitat (branch, crevice, interior cavity, water column, etc.) where each fish occurred. In total, 119 species of fish from 25 families were observed in 17 pre-specified microhabitats. The families displayed a range of patterns of occurrence among the microhabitats with some (e.g., Gobiidae, Scorpaenidae) restricted to only a few types, while others (e.g., Apogonidae, Labridae) occurred in a variety of microhabitat types. Similarly, some microhabitats were numerically dominated by individuals within a single family (e.g., Apogonidae in crevices) and other microhabitats (e.g., branches, cavities) were occupied by individuals from numerous families. Knowledge of patterns of microhabitat use can provide useful predictive insight into likely alterations in the composition and structure of coral associated fishes resulting from changes in coral structure that can occur via growth, mortality and/ or damage.

KEY WORDS. **–** Microhabitat, patch reef, species diversity, coral reef fishes, community assemblage.

INTRODUCTION

Assemblages of reef fish can vary greatly in composition, species richness and abundance over very small spatial scales and an understanding of the mechanisms underlying this spatial variation has been a focal point of ecological studies in marine systems. Numerous studies have explored relationships between abundance of fish and the quality or quantity of their habitats, with mixed results. The strongest positive associations have been found for species with narrow habitat requirements sampled at very small spatial scales (Syms, 1995; Munday, 2000; Holbrook et al., 2002a, 2002b). The effect of various structural aspects of habitat on fish assemblages has also been examined and in some cases, the degree of structural complexity has been a good predictor of abundance or diversity of fish (Gladfelter & Gladfelter, 1978; Gladfelter et al., 1980; Roberts & Ormond, 1987; Hixon & Beets, 1993; Ormond et al., 1996; Freidlander & Parrish, 1998; Jones & Syms, 1998; Holbrook et al., 2002a; Nanami & Nishihira, 2004). It has been argued that shelter habitats such as crevices, holes and branched coral provide critical refuge space for fish and thus positively affect the fish assemblage. Several experimental studies have verified the importance of this functional aspect of habitat structure (Beukers & Jones, 1998; Nemeth, 1998; Gratwicke & Speight, 2005; Juncker et al., 2005).

Coral reefs are subjected to a variety of natural and human-induced disturbances, some of which can greatly impact the abundance of key foundational species, as well as the structural characteristics of the reef. Different species of coral and types of physical habitat structure vary in their vulnerability to environmental perturbations, potentially resulting in a differential loss of certain microhabitats following disturbance to the reef. Clearly, knowledge of the effects of habitat features on fish assemblages could provide valuable insight into the potential consequences of temporal variation in reef habitats that can result from environmental disturbances.

Previously, we explored relationships between habitat structure and assemblages of reef-associated fishes on patch reefs comprised of the coral, *Porites rus* in lagoons of Moorea, French Polynesia (Holbrook et al., 2002a, 2002b). Variation in potential shelter space (e.g., amount of live surface area, number of holes and quantity of interior cavity space) in the patch reefs accounted for over half of the spatial variation in species richness and total abundance of fish among the patch reefs (Holbrook et al., 2002a). Furthermore, abundance of fish at the family level varied among reefs that had different combinations of key shelter microhabitats (Holbrook et al., 2002b). Here, we investigate variation in use of a set of 17 defined microhabitats within *P. rus* patch reefs by 25 families of fish. We present the observed patterns of microhabitat use and explore potential causes underlying the observed variation in these patterns.

MATERIALS AND METHODS

Fieldwork was conducted in lagoons on the North side of Moorea, French Polynesia (17°30'S 149°50'W) (for a general description of lagoons, see Galzin & Pointier, 1985). A barrier reef surrounds the island and encloses lagoons ranging from 0.8 to 1.3 km in width and about 5 to 7 m mean water depth. The lagoon bottom is a mosaic of patch reefs, coral rubble and sand. Over 600 marine fish species were reported by Randall (1985) from the Society Islands in French Polynesia and Galzin (1987) noted 280 species on a single transect that stretched from the fringing reef to the reef slope on the North side of Moorea. A total of 100 species have been observed in close association with patch reefs formed by the coral, *Porites rus* that were situated in the lagoon on the North shore of the island (Holbrook et al., 2002a).

In this study, we surveyed the fishes observed in close association with a collection of 66 patch reefs formed by *Porites rus* (Poritidae; Veron, 1986, 2000) from six sites between Opunohu Bay and Point Aroa during July and August of 2002 (for a description of sites, see Holbrook et al., 2002a). At each site, all of the *P. rus* patch reefs (up to a maximum of 10) within a 50 m × 75 m area were sampled. Two divers using SCUBA first approached each patch reef from opposite sides to minimize the chances of fishes associated with the exterior surfaces of the patch reefs escaping unnoticed. Both divers remained approximately 3 m away from a reef until all fishes associated with eight arbitrarily defined exterior microhabitats (water column immediately above the patch reef; on the top, side and bottom of the patch reef; in branches on the top, side and bottom; the sand/reef interface) had been counted. Following the completion of these counts, divers then approached each reef and used handheld flashlights to identify and enumerate all fishes within an additional nine arbitrarily defined interior microhabitats [in a hole at the top, side and bottom of the patch reef; in a crevice; in the water column of an interior cavity; on the floor of an interior cavity; under a ledge; in a damselfish turf garden; associated with another species of coral (*Pocillopora* spp., *Montipora* spp., *Porites lobata*) attached to the patch reef]. Holes were defined as indentations in the coral surface less than 10 cm in diameter and up to 25 cm deep; crevices were shallow fissures. Interior cavities were defined as large interior spaces greater than 10 cm in diameter and more than 25 cm deep. Holes and crevices were shallower than cavities and as a result had higher light levels.

Individual fish that were initially observed to be associated with exterior microhabitats were not included in counts of individuals associated with interior microhabitats if those individuals were judged to have altered their microhabitat use in response to the presence of the divers. As patch reefs differed in size and therefore total volume, the time spent by both divers in surveying each patch reef varied with the overall size of the individual reef (range: 5 - 35 minutes). Hence, the total time spent on each reef was approximately constant on a per patch reef volume basis. All counts were made over two consecutive days during daylight hours between 0800 and 1600 hours. Daily counts were averaged across the two days for each species to yield a mean count for each species/microhabitat combination observed on an individual *P. rus* patch reef. These data were then summed over all individual patch reefs at a site and used to calculate the proportion of the individuals of each species and family that occurred in the defined microhabitats, as well as the number of different microhabitats used by each family within a given site. A family was considered to use a microhabitat if at least 5% of the total observed individuals within that family occurred there. All analyses that we present here were performed on the proportion of individuals or species within a family utilizing each microhabitat averaged across the six sampling sites.

To explore relationships among the families of fish and the range of microhabitats used, we first regressed the total number of different microhabitats used by each family against the total number of species in that family observed during our surveys. Our second analysis considered only families represented by 20 or more individuals to provide greater confidence in the pattern of estimated microhabitat use. The number of different microhabitats used by a family was regressed against the number of individuals in the surveys. All regression analyses were performed using SAS statistical analysis software (SAS version 9.1, SAS Institute Inc., USA)

We used nonmetric, multidimensional scaling (NMS) techniques to explore patterns of microhabitat use among families and to look for redundancies within our a priori categorizations of microhabitat types. First developed by Shepard (1962a, 1962b) and later refined by Kruskal (1964), NMS provides several advantages over other commonly used ordination techniques such as Principal Components Analysis (PCA) or Canonical correspondence analysis (CCA) by avoiding assumptions requiring linearity or monotonicity in the community variables (Clarke, 1993). For all ordination analyses, we first transformed the proportion of each microhabitat occupied by a family or the proportion of all individuals utilizing each microhabitat type within each family using an arcsine squareroot transformation. Families with an average of less than 5 individuals observed (when summed across all microhabitat types and locations) were dropped from our analyses so as not to create false associations based on rarity (McCune & Grace, 2002). Nonmetric, multidimensional scaling was performed on the resulting transformed data in either family or microhabitat space using the Bray-Curtis measure of dissimilarity (Bray & Curtis, 1957) and the methods of Kruskal (1964) and

Table 1. Percentage occurrence within each microhabitat type for each family.

Family (Number of Species)	Mean No. of Fish Observed	Percentage Occurrence (Number of Species)							
		Water Column	Top	Side	Bottom	Branches Top	Branches Side	Branches Bottom	Sand/Coral Interface
Acanthuridae (13)	931.0	3.2 (7)	12.9 (8)	22.7 (10)	10.7 (9)	3.4 (4)	3.8 (7)	0.9 (3)	1.7 (5)
Apogonidae (9)	4,121.5	0.5 (3)	11.2 (3)	20.2 (4)	8.5 (5)	0.4 (2)	5.0 (5)	4.8 (6)	5.3 (4)
Balistidae (4)	65.5	7.6 (3)	20.6 (4)	14.5 (3)	3.1 (2)	-	-	-	0.8 (1)
Blennidae (1)	1.0	50.0 (1)	50.0 (1)	-	-	-	-	-	-
Chaetodontidae (10)	147.0	-	17.7 (9)	26.2 (9)	6.1 (3)	8.2 (2)	10.9 (3)	2.7 (2)	4.4 (2)
Cirrhitidae (1)	7.5	-	20.0 (1)	13.3 (1)	-	26.7 (1)	26.7 (1)	-	-
Caesionidae (1)	1.0	-	-	-	100.0 (1)	-	-	-	-
Gobiidae (3)	202.0	-	-	-	0.5 (1)	-	-	-	90.1 (3)
Holocentridae (12)	605.5	3.3 (2)	5.4 (8)	17.4 (5)	4.3 (3)	4.0 (7)	10.7 (6)	0.2 (2)	0.1 (1)
Labridae (16)	590.5	7.1 (5)	25.2 (12)	16.7 (13)	7.4 (11)	6.2 (5)	7.9 (3)	1.9 (3)	15.7 (8)
Lethrinidae (2)	13.5	37.0 (2)	37.0 (1)	25.9 (2)	-	-	-	-	-
Lutjanidae (1)	2.5	-	-	-	60.0 (1)	-	-	-	40.0 (1)
Microdesmidae (1)	1.5	33.3 (1)	66.7 (1)	-	-	-	-	-	-
Mullidae (3)	26.5	1.9 (1)	24.5 (2)	20.8 (3)	17.0 (1)	-	1.9 (1)	-	20.8 (1)
Ostraciidae (2)	3.0	-	16.7 (1)	33.3 (1)	-	-	-	-	-
Pinguipedidae (1)	5.5	-	-	-	-	-	-	-	81.8 (1)
Pomacanthidae (4)	210.5	0.5 (1)	15.4 (4)	19.7 (4)	3.8 (3)	12.8 (4)	10.7 (2)	3.6 (3)	0.2 (1)
Pomacentridae (15)	8,247.5	29.6 (10)	13.2 (14)	15.0 (10)	0.9 (10)	15.1 (10)	21.0 (10)	1.7 (9)	0.2 (3)
Scaridae (3)	150.0	4.3 (2)	28.7 (3)	32.3 (3)	10.0 (2)	3.0 (1)	7.3 (2)	-	9.0 (20)
Scorpaenidae (3)	5.5	-	-	-	9.1 (1)	-	-	-	-
Serranidae (7)	108.0	30.6 (4)	12.0 (4)	4.2 (3)	3.7 (3)	10.6 (3)	10.2 (2)	-	0.5 (1)
Syngnathidae (1)	5.5	-	9.1 (1)	-	-	-	-	-	-
Synodontidae (2)	10.5	-	14.3 (2)	14.3 (2)	4.8 (1)	-	-	-	52.4 (2)
Tetradontidae (3)	20.0	-	5.0 (1)	45.0 (1)	10.0 (1)	-	5.0 (1)	-	7.5 (1)
Zanclidae (1)	2.0	25.0 (1)	50.0 (1)	25.0 (1)	-	-	-	-	-

Mather (1976) as implemented in the NMS procedure of the software package PC Ord version 4.34 (MJM Software, USA) (for a thorough description of the implementation, see McCune & Grace, 2002). To determine the appropriate dimensionality for use in each ordination, we first performed 40 ordinations using the data obtained from our surveys and random starting configurations in models varying in dimensionality from 1 to 6. The best model solution for each dimensionality was identified as the model that out of 40 runs produced a stable solution (standard deviation in stress values over last 15 iterations < 0.0001) and possessed the lowest stress value. We determined the final model dimensionality by comparing the stress values of the best solutions for models of dimensions 1 through 6 with results obtained from a randomization test employing 50 Monte Carlo runs for each dimension. Beginning with a 1-dimensional solution, we considered additional dimensions useful if they reduced the final stress value in the ordination of our survey data by 5 or more (on a scale of 100) and had a final stress value that was lower than those obtained in 95% of the randomized runs. The final ordination was then obtained by specifying the appropriate number of dimensions and re-running the analysis using the best and most stable solution for that dimensionality as the starting configuration.

RESULTS

A total of 119 species of fish from 25 families was observed during the sampling of the 66 patch reefs (Table 1). The number of individuals from each family ranged widely (1 to 8,247; total number in survey = 15,484.5), as did the number of species (range 1 to 16). Fewer than five total individuals were observed in six families (Blennidae, Caesionidae, Lutjanidae, Microdesmidae, Ostraciidae and Zanclidae) and these families were not used in the ordination analyses.

Families showed variable patterns of microhabitat occurrence (Fig. 1), with the number of different microhabitats used by individuals in a family ranging from 1 to 16. Not surprisingly, several families (e.g., Gobiidae, Scorpaenidae) were restricted to only a few microhabitat types, while others (e.g., Apogonidae, Balistidae, Holocentridae, Labridae) occurred in a large variety of microhabitats. One potential mechanism

Table 1. (continued)

Family (Number of Species)	Percentage Occurrence (Number of Species)								
	Ledge	Crevice	Hole Top	Hole Side	Hole Bottom	Floor of Cavity	H_20 Column of Cavity	Damselfish Turf	Associated Coral
Acanthuridae (13)	2.9 (7)	-	0.1 (1)	0.4 (3)	27.3 (5)	-	10.2 (8)	-	0.1 (1)
Apogonidae (9)	19.8 (8)	7.3 (3)	0.1 (4)	3.5 (6)	1.0 (6)	-	9.7 (8)	2.5 (3)	0.1 (1)
Balistidae (4)	3.1 (1)	0.8 (1)	9.2 (2)	18.3 (1)	10.7 (2)	1.5 (1)	9.9 (1)	-	-
Blennidae (1)	-	-	-	-	-	-	-	-	-
Chaetodontidae (10)	8.5 (5)	1.0 (2)	0.3 (1)	2.7 (3)	-	-	9.9 (6)	-	1.4 (2)
Cirrhitidae (1)	-	-	-	-	-	-	-	-	13.3 (1)
Caesionidae (1)	-	-	-	-	-	-	-	-	-
Gobiidae (3)	9.4 (2)	-	-	-	-	-	-	-	-
Holocentridae (12)	10.6 (7)	0.3 (3)	6.8 (8)	18.9 (11)	0.9 (4)	-	16.8 (11)	-	-
Labridae (16)	4.6 (8)	0.2 (2)	0.2 (2)	1.2 (6)	-	-	2.0 (9)	3.6 (2)	0.2 (1)
Lethrinidae (2)	-	-	-	-	-	-	-	-	-
Lutjanidae (1)	-	-	-	-	-	-	-	-	-
Microdesmidae (1)	-	-	-	-	-	-	-	-	-
Mullidae (3)	3.8 (1)	-	-	-	-	-	3.8 (1)	5.7 (1)	-
Ostraciidae (2)	16.7 (1)	-	-	16.7 (1)	-	-	-	16.7 (1)	-
Pinguipedidae (1)	18.2 (1)	-	-	-	-	-	-	-	-
Pomacanthidae (4)	7.8 (3)	0.5 (1)	3.1 (3)	17.8 (3)	1.4 (1)	-	2.4 (2)	0.2 (1)	-
Pomacentridae (15)	0.4 (7)	0.1 (2)	0.1 (4)	0.6 (2)	0.0 (1)	0.1 (1)	0.0 (1)	1.4 (4)	0.5 (4)
Scaridae (3)	1.3 (2)	-	-	-	-	-	3.7 (2)	0.3 (1)	-
Scorpaenidae (3)	81.8 (3)	-	-	-	9.1 (1)	-	-	-	-
Serranidae (7)	6.9 (4)	0.5 (1)	0.9 (2)	3.7 (2)	1.8 (1)	10.6 (5)	2.8 (3)	0.9 (1)	-
Syngnathidae (1)	-	-	-	-	-	-	-	90.9 (1)	-
Synodontidae (2)	4.8 (1)	-	-	-	-	4.8 (1)	-	4.8 (1)	-
Tetradontidae (3)	25.0 (2)	-	-	-	-	-	2.5 (1)	-	-
Zanclidae (1)	-	-	-	-	-	-	-	-	-

underlying these differences in microhabitat occurrence is variation among the families in species richness. When data from all 25 families observed during our surveys were considered, there was a significant positive relationship ($F_{1,23} = 38.49$, $P < 0.0001$) between the number of observed species within a family and the number of different microhabitats used by those families (Fig. 2A). This relationship was particularly marked for families containing less than 10 species observed in association with *P. rus*. Interestingly, the pattern of microhabitat use did not appear to be related to the number of individuals within each family enumerated during the survey. For the 13 families with at least 20 observed individuals, there was no significant relationship ($F_{1,11} = 0.01$, $P = 0.9244$) between the number of microhabitats used and the number of individuals in the family (Fig. 2B).

There was substantial variation among the microhabitats in the number and composition of families they contained. Several microhabitats (other species of live coral associated with *P. rus*, floors of interior cavities) hosted only a few families (4 to 6), while others (under ledges, the sand-coral interface) were used by as many as 16 of the 25 families observed in our surveys (Fig. 3). Further, there was a wide range of variation in the degree of numerical dominance by a family within a given microhabitat. For example, although 16 families occurred under ledges, one family (Apogonidae) accounted for more than 75% of the total individuals seen. Similarly, pomacentrids comprised 82% of the fish that were enumerated on associated colonies of *Pocillopora* spp. and on *Porites lobata*.

The survey data also illustrated that the location of a microhabitat on a patch reef can influence which families predominate. For example, holes located on the top of the *P. rus* colony were dominated by Holocentridae, while holes at the bottom near the substrate contained mostly Acanthuridae (Fig. 3). Similarly, Pomacentridae dominated in the branches located on the top and sides of the coral (comprising 88% and 81% of all individuals enumerated in these habitats, respectively), but were much less common in branches near the bottom (38%), where individuals of the Family Apogonidae were the most abundant (53%) (Table 1).

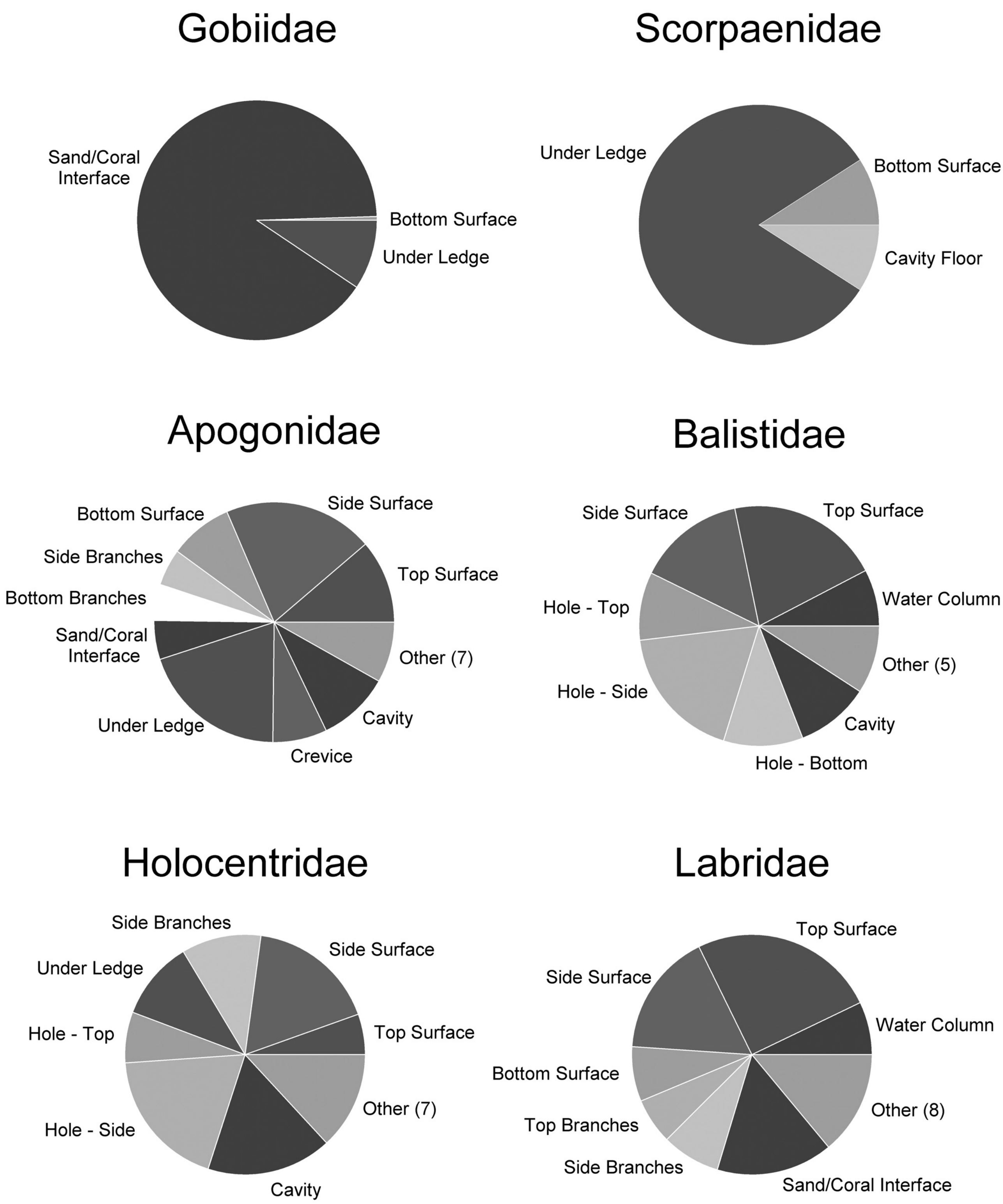

Fig. 1. *Porites rus* microhabitat use by selected families. Microhabitat types that make up less than 5% of the total have been combined into the category "Other". Numbers in parentheses refer to the number of combined microhabitat types.

The results of the ordination analyses indicate the presence of strong structure within the assemblage of families observed using the microhabitats contained within colonies of *P. rus*. A three-dimensional solution proved to be the most appropriate model ordinating the average percentages of each family within microhabitat space (mean stress of original data with dimensionality of 3 = 9.194, result of Monte Carlo randomization test for three-dimensional solution P = 0.0196, final ordination stress = 8.47 after 70 iterations utilizing a stability criterion of 0.00001) and the three axes together contained 87% of the information present in the original data space. Bi-plots using these three ordination axes (Fig. 4A) show good separation between the 19 families used in the ordination and suggest that, in aggregate, each family used a unique combination of the microhabitat types available within *P. rus*.

The ordination of microhabitats also indicated the presence of structure within the survey data based on the assemblage of families using each microhabitat type. In this case, a two-dimensional solution proved to be the most appropriate model describing microhabitat use within family space (mean stress of original data with dimensionality of 2 = 13.186, result of Monte Carlo randomization test for two-dimensional solution P = 0.0196, final ordination stress = 9.75 after 143 iterations utilizing a stability criterion of 0.00001) and together, the two axes represented 90% of the information contained in the original data space. Further, these results suggest that only two pairs of our arbitrarily defined microhabitats [the top (T) and side (S) of the patch reef and the top branches (BT) and side branches (BS)] consisted of redundant classifications as indicated by overlapping microhabitats in Figure 4B.

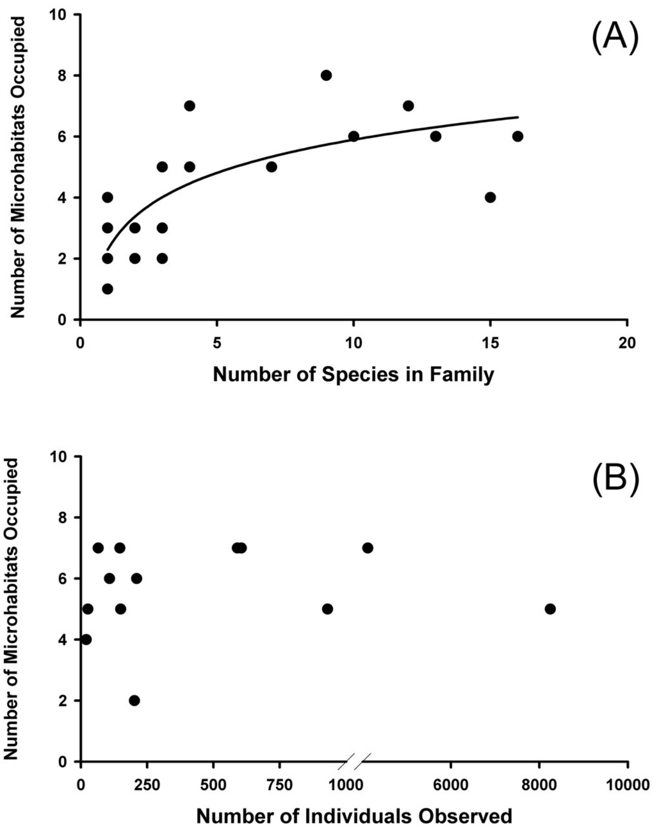

Fig. 2. (A) The relationship between the number of species observed within each of the 25 families and the number of microhabitats occupied by that family. (B) The relationship between the number of individuals observed within each family and the number of microhabitats occupied by that family. Families with less than 25 individuals were excluded from the analysis.

DISCUSSION

Understanding the factors underlying the distribution and abundance of coral reef fishes and the structure of their assemblages has been the focus of numerous studies in recent decades. Coral reef fish assemblages pose a particular challenge because they are typically extremely diverse and have relatively low abundance on a per species basis, even over very small spatial scales. (e.g., Sale & Dybdahl, 1975; Gladfelter et al., 1980). Despite this, there is increasing evidence that variation in habitat features of continuous as well as patch reefs can account for substantial variation in the spatial patterns of associated fish assemblages, particularly with respect to species richness and overall abundance (Munday, 2000; Syms & Jones, 2000; Holbrook et al., 2000, 2002a, 2002b; Jones et al., 2004).

While there is growing evidence that habitat features can influence local assemblages of coral reef fishes, less is known about how assemblage structure changes as particular microhabitat features vary temporally. Such knowledge is of great interest because coral reefs experience a variety of short-term (e.g., coral bleaching, storms, predator outbreaks) and long-term (e.g., climate variation) disturbances that affect both the distribution and abundance of corals and thus, the supply of microhabitats available to fish (Connell et al., 1997, 2004; Hughes & Connell, 1999). Several studies have explored responses of fish assemblages to natural disturbances that alter reef habitats (e.g., Galzin, 1987; Jones & Syms, 1998; Sano, 2000, 2001; Cheal et al., 2002; Adjeroud et al., 2002; Jones et al., 2004), revealing mixed responses. For example, following declines in overall cover of live coral, some groups appeared unaffected, others declined in abundance and some even increased in abundance (Jones & Syms, 1998; Jones et al., 2004). These results do not appear to be wholly dependent on whether the members of an affected group are obligate coralivores. They suggest that it may be important to separate the effects of a decline in live coral cover from other potential effects of disturbances, such as alteration of reef structural complexity and availability of other microhabitats that are not directly associated with living coral. Growing expectation that climate forcing may result in declines in diversity and abundance of corals underscores the need to predict possible effects of these losses on fish assemblages. Clearly, a more complete understanding of how fish use microhabitats created by or associated with live coral will be needed to accomplish this goal.

Species of the coral, *Porites* are one of the most important structure-producing components in lagoons at our study site. When they become large, patch reefs formed by *Porites* support a high diversity and abundance of fish (Holbrook et al., 2002a, 2002b). One reason for this is the structurally

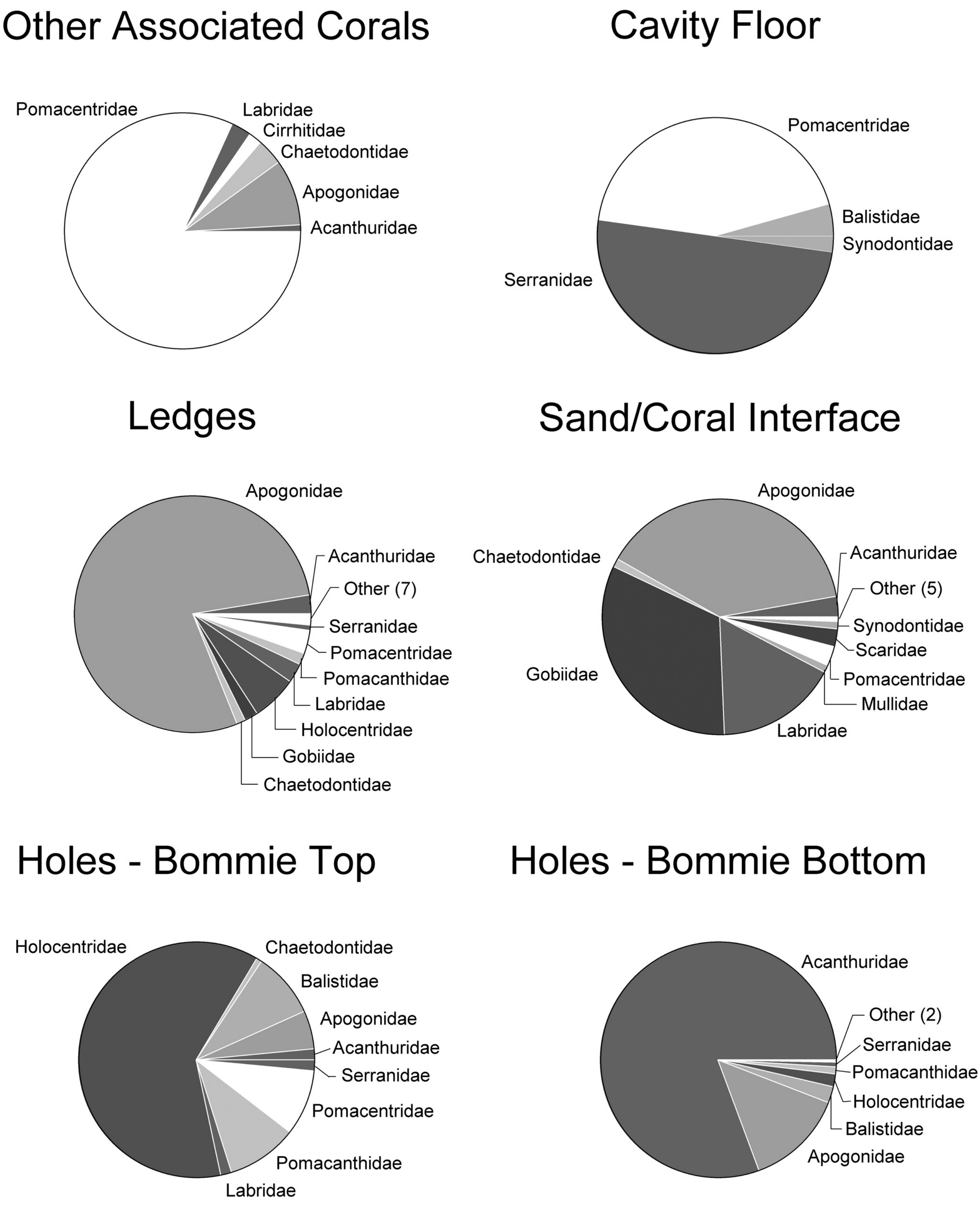

Fig. 3. The use of selected *Porites rus* microhabitats by the 25 families. Families that make up less than 5% of the total have been combined into the category "Other". Numbers in parentheses refer to the number of combined families.

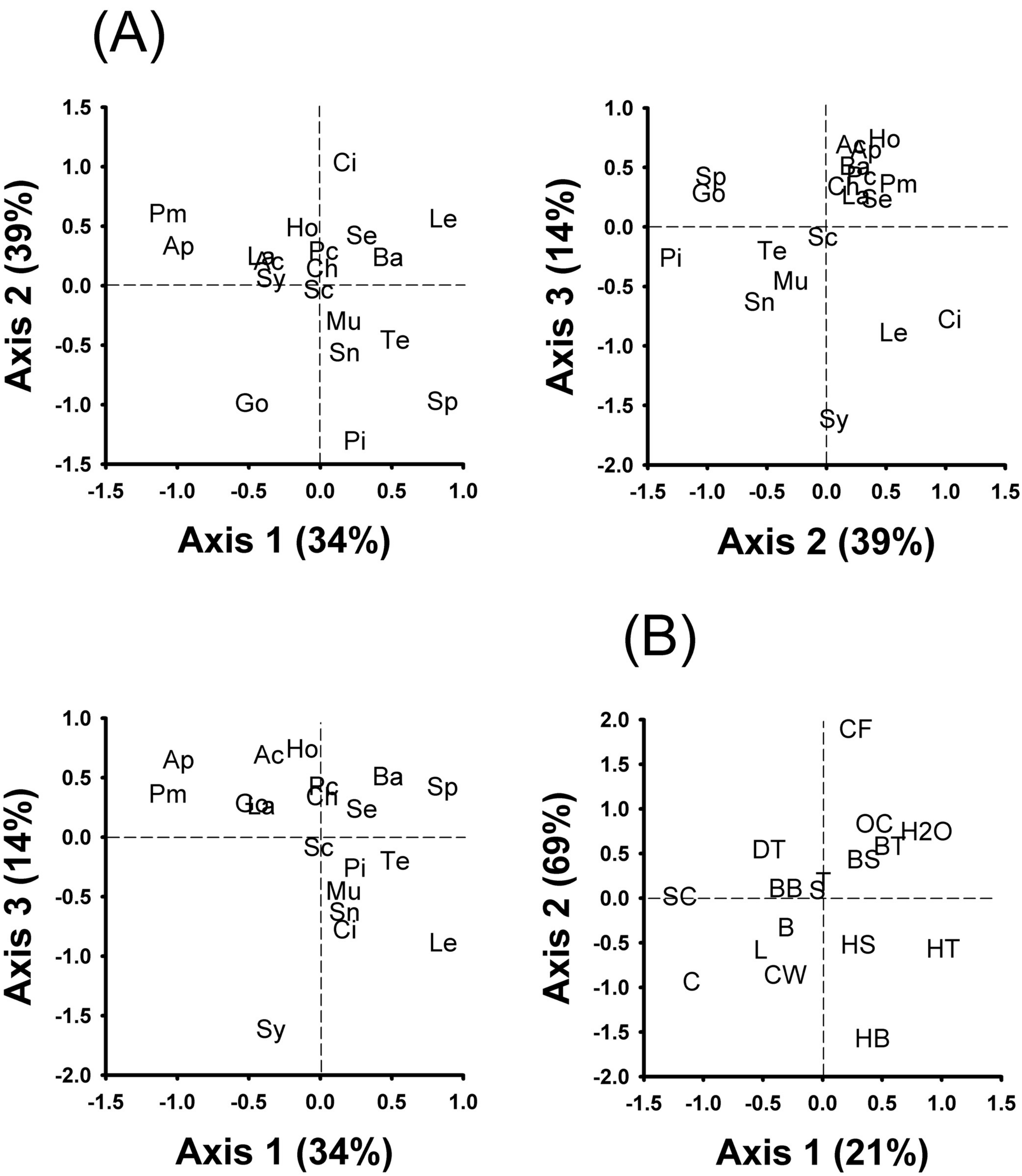

Fig. 4. (A) Plots of family positions along the three ordination axes obtained when families were ordinated in microhabitat space. Numbers in parentheses along each axis refer to the percentage variation in the original data space explained by each axis. Only families that had at least five individuals observed during the surveys were used. Ac = Acanthuridae; Ap = Apogonidae; Ba = Balistidae; Ch = Chaetodontidae; Ci = Cirrhitidae; Go = Gobiidae; Ho = Holocentridae; La = Labridae; Le = Lethrinidae; Mu = Mullidae; Pi = Pinguipedidae; Pc = Pomacanthidae; Pm = Pomacentridae; Sc = Scaridae; Sp = Scorpaenidae; Se = Serranidae; Sy = Syngnathidae; Sn = Synodontidae; Te = Tetradontidae. (B) Plots of microhabitat positions along the two ordination axes obtained when microhabitats were ordinated in family space. Numbers in parentheses along each axis refer to the percentage variation in the original data space explained by each axis. Only families that had at least five individuals observed during the surveys were used. H_2O = Water column; T = Top of bommie; S = Side of bommie; B = Bottom of bommie; BT = Branches at top of bommie; BS = Branches along side of bommie; BB = Branches along bottom of bommie; SC = Sand/coral interface; L = Ledge; C = Crevice; HT = Hole at top of bommie; HS = Hole along side of bommie; HB = Hole at bottom of bommie; CF = Cavity floor; CW = Cavity water column; DT = Damselfish turf; OC = Other associated coral species.

complex nature of patch reefs made of *P. rus*. They contain a rich variety of microhabitats that are occupied by a wide range of fish taxa. In fact, our results suggest that for the majority of families with species that were observed in association with *P. rus* patch reefs, the greater the number of microhabitats present on a reef, the greater the number of species from that family that were observed in the associated assemblage. When some of these microhabitats were absent, for example on patch reefs formed by *P. lobata*, both the abundance and species richness of fish are lower than on reefs formed by similarly sized *P. rus* (Holbrook et al., 2002b).

The results of this current study reveal that families of fish differ greatly in the range and types of microhabitats used on *P. rus* patch reefs. This information allows predictions to be made about the potential effects of environmental disturbance. Families with the smallest range of microhabitat use might be more vulnerable than those with broader microhabitat use, especially if those microhabitats are themselves more vulnerable to disturbances. For example, large proportions of both Pomacentridae and Cirrhitidae were observed in the branches and adjacent water column of *P. rus*. Coral branches are easily broken off during storms, resulting in the disappearance of that microhabitat. By contrast, some microhabitats, such as the interior cavity of the coral or the sand-coral interface, are much less likely to be lost, unless the disturbance is very extreme. Hence, taxa that use these might not decline in abundance, unless the disturbance is catastrophic. Such differential responses to the effects of a disturbance due to patterns of microhabitat use might help explain the mixed results of studies that have assessed responses of fish assemblages to temporal variation in coral cover. This is also consistent with the results of a six-year study on reefs in Kimbe Bay, Papua New Guinea by Jones et al. (2004). Their findings showed that as the branching corals died off, there were substantial declines in species of fish that occupied these corals, compared to fish that occupied other reef microhabitats.

ACKNOWLEDGMENTS

We thank K. Seydel and J. Lape for outstanding assistance in the field. N. Davies and S. Holloway who provided additional logistical help. We gratefully acknowledge the support of the National Science Foundation (Grants OCE 99-10677, OCE 04-17412), the W. M. Keck Foundation and the Gordon and Betty Moore Foundation. This is Contribution No. 124 of the UC Berkeley Gump Research Station.

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