

INTERFERENCE COMPETITION STRUCTURES HABITAT USE IN A LOCAL ASSEMBLAGE OF CORAL REEF SURGEONFISHES¹

D. ROSS ROBERTSON

Smithsonian Tropical Research Institute, APO Miami 34002-0011 USA

AND

STEVEN D. GAINES

Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 USA

Abstract. We examined use of food and habitat in relation to pairwise interference interactions among all 13 species of a surgeonfish assemblage that lived in a 0.225-ha section of the outer edge of the barrier reef at Aldabra, Indian Ocean. Eleven species defended feeding territories intraspecifically and, in most cases, interspecifically. Surgeonfish species pairs fell into two classes: (1) noninteractors ($n = 38$ pairs) rarely interacted agonistically, and individuals of the two species peacefully shared feeding areas; (2) interactors ($n = 27$ pairs) typically interacted agonistically whenever they met, and, except under special circumstances, did not share feeding areas. Dominance relations between interactors usually were highly asymmetrical, and in only one pair was there no evidence of a dominant/subordinate relationship. Between interactors diet overlap was higher and large-scale habitat overlap was lower than between noninteractors. In addition, within pairs of interactors with high large-scale habitat overlap, we found small-scale habitat segregation. Interactors did not differ from noninteractors in the extent of similarity in body size between the species in a pair. Reciprocal removal experiments performed with one trophic subset of the assemblage showed that agonistically subordinate species readily took over vacant habitat previously occupied by agonistically dominant species, but that the reverse rarely occurred. These data support the hypothesis that interference competition for food plays a part in structuring the assemblage, by determining many spatial distribution patterns, and promotes habitat partitioning among food competitors. Our data indicate that the presence or absence of such competition may affect 60–80% of habitat-use relationships in that assemblage.

Key words: *Acanthuridae; community structure; coral reef; feeding territoriality; habitat partitioning; herbivory; Indian Ocean; interference competition; spatial distributions.*

INTRODUCTION

There has been vigorous debate over the past decade on the relative importance of various processes that may influence the abundances and spatial distributions of reef fishes and the structure of their species-rich assemblages (Smith and Tyler 1972, Clarke 1977, Sale 1977, 1979, 1980, 1981, Gladfelter and Gladfelter 1978, Brock et al. 1979, Bohnsack and Talbot 1980, Gladfelter et al. 1980, Robertson and Lassig 1980, Anderson et al. 1981, Ogden and Ebersole 1981, Sale and Williams 1982, Bohnsack 1983, Doherty 1983, Gladfelter and Johnson 1983, Shulman et al. 1983, Williams 1983, Williams and Hatcher 1983, Kaufman and Ebersole 1984, Sale et al. 1984, Ebersole 1985, Warner and Chesson 1985). This discussion constitutes part of a general ongoing controversy over the relative importance of deterministic and stochastic processes in structuring marine, freshwater, and terrestrial communities (papers in Strong et al. 1984, review by Branch 1984, and see Wiens and Rotenberry 1981, Gilpin and Dia-

mond 1982, Grossman et al. 1982, Toft et al. 1982, Herbold 1984, Shorrocks et al. 1984, Simberloff and Connor 1984, Yant et al. 1984).

The portion of this debate that relates specifically to reef fishes has arisen for two main reasons. First, the results of studies of the composition and dynamics of reef fish assemblages have not produced concordant opinions on the degree to which those assemblages are stable and predictable (Sale and Dybdahl 1975, 1978, Talbot et al. 1978, Brock et al. 1979, Williams 1980, Ogden and Ebersole 1981, Sale 1981, 1982, Bohnsack 1983, Shulman et al. 1983, Sweatman 1983, Sale et al. 1984). Some of the observed instability and unpredictability evidently is due (Doherty 1981, 1983, Victor 1983) to variability in juvenile recruitment (Russell et al. 1977, Williams and Sale 1981, Shulman et al. 1983, Williams 1983, Eckert 1984). Second, it has been claimed that, within guilds (*sensu* Root 1967) of reef fishes, the levels of interspecific overlap in use of food and habitat on the local scale are greater than one would expect if resource partitioning was the primary factor maintaining species-richness and enabling potential or actual competitors to coexist on that scale (Sale and Dybdahl 1975, 1978, Sale 1977, 1978, Talbot

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et al. 1978, but see Jones 1968, Chave 1978, Gladfelter and Johnson 1983, Sale et al. 1980, Sale and Williams 1982).

Here we consider cause and effect relations between patterns of resource use and agonistic interactions in one family of herbivorous fishes, the surgeonfishes (Acanthuridae), at one local site at Aldabra Atoll (western Indian Ocean). We examined local-scale resource use to overcome spatial scale limitations (Sale and Williams 1982) that occur in other studies (e.g., Jones 1968, Chave 1978, Anderson et al. 1981, Russ 1984a, b). We chose to work on surgeonfishes because they generally are abundant on coral reefs and comprise major proportions of the numbers and biomass of herbivorous reef fishes (>50% of each measure at the Aldabra site, Robertson et al. 1979; see also Randall 1963, Brock et al. 1979, Bouchon-Navaro and Harmelin-Vivien 1981, Williams and Hatcher 1983, Russ 1984a, b). Our study area, the reef crest of an oceanic barrier reef, is representative of other areas in which surgeonfish assemblages are species-rich and surgeonfish population densities are high (see Williams and Hatcher 1983 and Russ 1984a, b).

Initial observations in our study area indicated that (1) many surgeonfishes defended feeding territories, and did so selectively against other surgeonfishes, (2) interspecific dominance relations often were asymmetrical, and (3) some species spatial distributions were nonrandom. These observations stimulated the formulation of the hypothesis that agonistic interactions occur among food competitors and that interference competition for food has a substantial effect on many habitat-use relationships and reduces interspecific overlap in habitat usage among competitors.

To demonstrate that interspecific differences in resource usage in an assemblage are due to competition one has minimally to show that such differences are greater than would be expected by chance (Sale 1974a, 1984, Schoener 1974, Strong et al. 1979, Connell 1980, Toft et al. 1982, Gladfelter and Johnson 1983). The two previous studies that examined whether such is the case in reef fish assemblages compared observed levels of difference to supposed "competition-free" levels. In both cases (Sale and Williams 1982, Gladfelter and Johnson 1983) the derivation of the "competition-free" values involved rearrangements of the data (see Sale 1974a). Procedures such as this involve dubious assumptions (May 1984), in this case that niche breadth and shape do not respond to competition. We took a different approach and examined four predictions that derive from our hypothesis: species that interact agonistically (1) should have more similar diets and (2) should show less overlap in their habitat distributions than species that do not so interact; (3) if usage of resources is size dependent (Smith and Tyler 1972, Schoener 1974) then interactors should be more similar in size than noninteractors are and (4) agonistically dominant interactors should prevent subor-

dinate species from using the dominants' habitat, and this effect should be nonreciprocal.

METHODS

We considered 13 surgeonfishes that were resident in a 0.225-ha section of the outer edge of the barrier reef at Aldabra: *Acanthurus lineatus*, *A. leucosternon*, *A. nigrofuscus*, *A. triostegus*, *A. nigricaudus* (= *A. gahhm* of Robertson et al. 1979), *A. tennenti*, *Zebbrasoma scopas*, *Z. veliferum*, *Naso lituratus*, *N. unicornis*, *N. brevivirostris*, *Ctenochaetus striatus*, and *C. strigosus*. A few individuals of one other species, *A. dussumieri*, were intermittently and briefly present in the study area; they were not considered to be residents.

The study area was a 25 × 90 m belt-transect that ran parallel to the depth gradient across the subtidal-intertidal interface of the reef. Observations and experiments were made from July 1975 to January 1976.

Analysis of stomach contents

During the last 2 mo of the study we speared specimens between 1100 and 1700, dissected them within 1.5 h of capture, and preserved their stomach contents in 5% buffered solution of formalin in seawater. Each sample (or an aliquot of a large sample) was spread out on a glass slide with an etched grid superimposed on it. All objects under ≈150 randomly chosen intersection points of this grid were identified using a dissecting microscope. Algae were identified to species.

Habitat distribution

Large-scale distributions.—The study transect spanned four physiognomic zones: (1) an intertidal reef flat, and, in descending order in the subtidal, (2) a flat rock pavement, (3) a regularly formed groove-and-spur formation, and (4) an irregularly structured, shallow (<7 m depth) reef slope (for details see Robertson et al. 1979, Robertson 1983). The numbers of adults and juveniles of each species observed feeding in each 5 × 5 m portion of that transect were counted at the beginning of the study.

Segregated use of overlap habitat.—Preliminary observations suggested that pairwise overlap in species diets and habitat distributions were highest within each of two sets of species that were common on the subtidal reef slope (three microalgivores: *A. leucosternon*, *Z. scopas*, and *A. nigrofuscus*; four detritivores: both *Ctenochaetus* species and *A. nigricaudus* and *A. tennenti*), and we examined whether these species pairs partitioned shared habitat on a fine scale. First we mapped the reef-slope part of the main transect and determined the proportions represented by (a) patches of high rock that rose above the basal level of the substratum and (b) areas of low rock, rubble, and sand between the high-substrate patches. We then counted the numbers of individuals of each species whose territories were centered on (i.e., comprised at least two-thirds of) each substratum type, and determined whether

those distributions were nonrandom with respect to substratum type. This was done for all three microalgivores and the two *Ctenochaetus* species, since their feeding areas were sufficiently small (<40 m²) for us to determine their positions relative to patches of each substratum type. The feeding areas of *A. nigricaudus* and *A. tennenti* were much larger (≥200 m²) and incorporated multiple patches of both substrata; therefore we compared their use of these substrata by relating the proportions of their feeding bites on each to the availability of each.

Second, two of the microalgivores, *Z. scopas* and juvenile (not adult) *A. nigrofuscus*, shared feeding territories (see Results: Interspecific Defense and Sharing), and we examined the relative amounts of their feeding activity in 10 types of microhabitat in their shared feeding areas. The definitions of these microhabitats took into account the nature of the substratum (rock, rubble, or sand), its height, its degree of surface curvature (approximately flat, depressions, or crevices of three size classes), and its inclination (approximately horizontal, approximately vertical). We recorded the number of bites taken from each microhabitat by individuals of each species that we observed for 10 min; we used these data to calculate proportional use of microhabitats. Although estimation of the extent of fine-scale habitat partitioning in this way is problematical (the biologist and the animal may well distinguish microhabitats differently), the errors involved probably are conservative.

Computation of overlap in resource use

To assess the degree of overlap in use of food and habitat among all species we used Czekanowski's Quantitative Similarity Index (C_z ; see Bloom 1981):

$$C_z = \frac{2 \sum_{j=1}^s \min(X_{ij}, X_{kj})}{\sum_{j=1}^s (X_{ij} + X_{kj})},$$

where X_{ij} = abundance of the j^{th} item (food type or fish species) in the i^{th} diet or habitat sample, X_{kj} = abundance of the same item in the k^{th} diet or habitat, and s = number of items over all diets or habitats. Values of C_z can range from 0.00 (no overlap) to 1.00 (complete overlap).

To calculate a dietary C_z (C_zD) for each species pair, we used the mean proportion of the stomach contents of each fish species represented by each dietary item. To calculate a habitat C_z (C_zH) for each species pair, we used the proportion of the population of each species that was present in each section of the main transect. For species with small (<40 m²) feeding territories (*A. lineatus*, *A. leucosternon*, *A. nigrofuscus*, *A. triostegus*, *Z. scopas*, *C. striatus*, and *C. strigosus*) the sections used were 5 m (long) × 25 m (wide). Four species (*Z. veliferum*, *N. lituratus*, *A. nigricaudus*, and *A. tennenti*)

had feeding areas that covered ≥200 m². When calculating C_zH values involving these four species the sections we used were the four physiognomic zones (see Methods: Habitat Distributions) in the main transect. The remaining two species, *N. unicornis* and *N. brevisrostris*, were nonterritorial and roamed over very large areas (on the order of hectares) when feeding. We calculated C_zH values for species-pairs involving those two species as follows. We recorded the number of bites taken on the substratum in each of the four physiognomic zones of the main transect during a 30-min period by a series of randomly selected individuals of these two species. We calculated proportionate use of each zone by each species from these numbers of bites, and calculated C_zH values using those proportions and the proportions of the populations of other species that lived in each zone. As a measure of the similarity in size within a species pair we used the ratio of the maximum masses of individuals of each species that we collected at Aldabra. We recognize the limitation of these data since the local populations of most species included a range of sizes of individuals.

Agonistic relations

To define the nature of agonistic relations between the members of a species pair, we observed individuals of each and recorded: (1) whether they defended feeding areas, and if so against which species, (2) which other species defended their feeding areas against them, and (3) which species they did not interact agonistically with, even when in close proximity in overlapping feeding areas. Using these data we assigned each species pair to either of two classes: interactors, which typically interacted agonistically when they met, or noninteractors, which rarely interacted even when feeding in close proximity (within 1 m) of one another and whose feeding areas/territories overlapped.

Experimental manipulations of habitat use

To support the hypothesis that differences in habitat distributions of two species are due to interference competition it is necessary to show not only that one species defends its territories against the other and that the two do not have overlapping feeding territories, but also that the subordinate species would occupy habitat used by the dominant species if it were not prevented from doing so. Consequently, we removed (by spearing) territory owners of both members of all interacting species pairs in one trophic group, the microalgivores (species listed in Results: Dietary Overlap). Territories chosen were located in areas where several species commonly occurred, in overlap habitat and at the interface of habitat distributions.

RESULTS

Dietary overlap

The 13 species fall into three major feeding groups. (a) Microalgivores: *A. lineatus*, *A. leucosternon*, *A. ni-*

TABLE 1. Stomach contents of five species of microalgivores (food types representing $\geq 1\%$ of items in stomach).

Food type	<i>Acanthurus lineatus</i>	<i>Acanthurus leucosternon</i>	<i>Acanthurus nigrofuscus</i>	<i>Acanthurus triostegus</i>	<i>Zebrasoma scopas</i>
	Percent of stomach contents of each species (mean \pm SE)				
Algae					
<i>Polysiphonia</i> sp. a	17.1 \pm 5.4	19.0 \pm 3.2	22.0 \pm 1.5	4.5 \pm 0.7	6.0 \pm 1.6
<i>Laurencia</i> sp. a	13.1 \pm 2.8	18.2 \pm 2.7	1.1 \pm 0.5	13.0 \pm 3.4	1.5 \pm 0.9
Unidentified a	12.7 \pm 1.7	2.7 \pm 0.8
<i>Lyngbia</i> sp.	11.4 \pm 2.1	11.8 \pm 1.5	...	18.5 \pm 2.8	12.4 \pm 1.3
<i>Champia</i> sp.	10.3 \pm 1.5	11.8 \pm 2.2	6.2 \pm 1.8	7.3 \pm 1.3	10.1 \pm 2.7
<i>Colpomenia sinuosa</i>	8.7 \pm 2.0	3.5 \pm 1.4	...
<i>Gelidiaceae</i> sp.	6.3 \pm 1.4	13.5 \pm 1.5
<i>Ceramium</i> sp. a	6.0 \pm 1.1	3.5 \pm 0.8	17.7 \pm 1.7	7.4 \pm 1.2	8.1 \pm 1.2
<i>Centrocerus clavulatom</i>	5.5 \pm 1.1	7.2 \pm 2.0	1.2 \pm 0.6
<i>Cladophora</i> sp.	3.1 \pm 1.2	2.1 \pm 0.7	2.3 \pm 1.2
<i>Ceramium</i> sp. b	1.8 \pm 0.9	...	5.5 \pm 0.8	1.9 \pm 0.5	2.7 \pm 1.6
<i>Polysiphonia</i> sp. c	1.1 \pm 0.8
Unidentified b	1.1 \pm 0.6	1.0 \pm 0.3
<i>Jania</i> spp.	...	2.8 \pm 0.7
<i>Polysiphonia</i> sp. b	...	2.2 \pm 0.8	11.9 \pm 1.4
<i>Ceramium</i> sp. c	...	1.0 \pm 0.8	2.6 \pm 0.5
<i>Enteromorpha</i> sp.	9.4 \pm 2.0	5.1 \pm 1.3	...
<i>Herposiphonia</i> sp.	8.4 \pm 1.5	5.7 \pm 0.9	...
<i>Polysiphonia</i> sp. d	5.3 \pm 1.0	...	18.2 \pm 2.7
Unidentified c	4.3 \pm 1.5
<i>Chondria</i> sp.	3.5 \pm 1.2	...	2.7 \pm 1.6
Unidentified	1.0 \pm 0.4
<i>Gelidium</i> sp.	13.1 \pm 2.6	3.5 \pm 0.8
<i>Ulva</i> spp.	9.5 \pm 3.1	...
<i>Gelidiella</i> sp.	3.6 \pm 1.0	21.6 \pm 2.0
Unidentified e	4.4 \pm 2.5	...
Diatom c	1.0 \pm 0.7	...
<i>Erythrotricha</i> sp.	5.1 \pm 1.2
Copepods	3.9 \pm 1.5
No. stomachs	15	15	20	30	15

grosfuscus, *A. triostegus*, and *Z. scopas* ate microalgae and small fleshy branched algae, principally rhodophytes. In specific instances, significant quantities of chlorophytes and cyanophytes were eaten (Table 1). (b) Macroalgivores: *Z. veliferum*, *N. brevirostris*, *N. lituratus*, and *N. unicornis* ate mostly larger macroalgae but also included smaller algae in their diets. The former two species concentrated on a fleshy green alga and the latter two on leathery brown algae. Brown algae

were infrequently eaten by fishes other than *Naso lituratus* and *N. unicornis* (Table 2). (c) Detritivores: The remaining four fishes, *A. tennentii*, *A. nigricaudus*, *C. striatus*, and *C. strigosus*, consumed almost nothing but sediment and detritus (Table 3).

C_zD values (Table 4) were highest among the detritivores (range: 0.97–1.00), intermediate among the microalgivores ($\bar{X} = 0.41$, range: 0.32–0.75), and low to moderate among the macroalgivores ($\bar{X} = 0.25$, range:

TABLE 2. Stomach contents of four species of macroalgivores (food types representing $\geq 1\%$ of items in stomach).

Food type	<i>Naso lituratus</i>	<i>Naso unicornis</i>	<i>Naso brevirostris</i>	<i>Zebrasoma veliferum</i>
	Percent of stomach contents of each species (mean \pm SE)			
Algae				
<i>Turbinaria ornata</i>	57.5 \pm 4.2	70.0 \pm 3.8
<i>Padina</i> sp.	29.7 \pm 4.1
<i>Champia</i> sp.	10.8 \pm 2.3	23.8 \pm 4.7	...	1.5 \pm 1.1
<i>Ulva</i> sp.	...	6.0 \pm 2.6	86.9 \pm 45.0	51.1 \pm 12.5
<i>Enteromorpha</i> sp.	10.0 \pm 3.0	...
<i>Chondria</i> sp.	1.5 \pm 0.7	3.1 \pm 1.0
<i>Lyngbia</i> sp.	26.4 \pm 8.0
<i>Colpomenia sinuosa</i>	8.3 \pm 3.8
Unidentified e	2.1 \pm 1.9
<i>Polysiphonia</i> sp. a	1.5 \pm 0.6
<i>Cladophora</i> sp.	1.3 \pm 0.5
No. stomachs	15	8	12	15

TABLE 3. Stomach contents of four species of detritivores (food types representing $\geq 1\%$ of items in stomach).

Food type	<i>Acanthurus nigricaudus</i>	<i>Acanthurus tennentii</i>	<i>Ctenochaetus striatus</i>	<i>Ctenochaetus strigosus</i>
	Percent of stomach contents of each species (mean \pm SE)			
Detritus and sediment	97.9 \pm 0.4	93.1 \pm 2.2	99.7 \pm 0.2	99.7 \pm 0.2
Algae				
<i>Gelidiella</i> sp.	...	2.1 \pm 1.0
<i>Jania</i> sp.	...	2.4 \pm 1.0
No. stomachs	15	15	15	15

0.00–0.69). Though the C_2D values in Table 4 indicate almost complete diet overlap between the two genera of detritivores, in reality overlap probably is lower, since sediment in the stomachs of the two *Acanthurus* species was considerably coarser than that in the stomachs of both *Ctenochaetus* species (see also Randall 1955, Jones 1968).

Overlap in habitat usage

C_2H values based on the distributions of the 13 species throughout the main study area ranged from 0.00 to 1.00 (Table 4). For some species pairs these distributions produced overestimated habitat overlap: reduced C_2H values resulted when recalculations were based on the distributions of seven species in an area that included the main study transect plus a 10 m wide extension of one section that was run down to the lower limit of coral growth and inshore to an island beach. In four of the eleven cases in which both members of a species pair belonged to the same major feeding group and the C_2H value was >0.50 when calculations were based only on the main study area, the recalculated values were lower: *A. leucosternon*/*Z. scopas*, 0.50 vs. 0.69; *A. leucosternon*/*A. nigrofuscus*, 0.51 vs. 0.83; *A.*

nigrofuscus/*Z. scopas*, 0.25 vs. 0.66; and *C. striatus*/*C. strigosus*, 0.45 vs. 0.73. No additional data were obtained relating to the remaining seven species pairs.

The highest C_2H values among members of the same trophic group were among the three microalgivores *A. leucosternon*, *Z. scopas*, and (juvenile) *A. nigrofuscus*, and among the four detritivores (Table 4). The three microalgivores did not use feeding microhabitats in their overlap habitat in the same way. A disproportionately large number of adults of *A. leucosternon* had their feeding areas on patches of high rock substrate, while the feeding areas of *Z. scopas* and *A. nigrofuscus* were distributed randomly with respect to high and low substrata (Table 5). Further, space-sharing *Z. scopas* and juvenile *A. nigrofuscus* differed in the relative amounts of feeding they did in different microhabitats (Table 6).

The two *Ctenochaetus* species were, by far, the most abundant of the detritivores (Table 7). Although *C. strigosus* was common in a habitat not used by *C. striatus* (a habitat found immediately adjacent to the main transect), on the transect *C. striatus* was only found in the part it shared with *C. strigosus*. However, these two species' distributions differed along the main-

TABLE 4. Czekanowski Similarity Indices for overlap in the diets (C_2D) and overlap in the habitat-distributions (C_2H) of Aldabran surgeonfishes.*

	C_2D													
	Microalgivores					Macroalgivores				Detritivores				
	<i>Aln</i>	<i>Ale</i>	<i>Zs</i>	<i>Anf</i>	<i>Atr</i>	<i>Zv</i>	<i>Nl</i>	<i>Nu</i>	<i>Nb</i>	<i>Cst</i>	<i>Csg</i>	<i>Anc</i>	<i>Atn</i>	
<i>Aln</i>	...	0.75	0.38	0.32	0.48	0.25	0.11	0.10	0.00	0.00	0.00	0.00	0.00	
<i>Ale</i>	0.13	...	0.35	0.35	0.41	0.17	0.11	0.12	0.00	0.00	0.00	0.00	0.00	
<i>Zs</i>	0.03	0.69	...	0.33	0.43	0.19	0.08	0.08	0.02	0.00	0.00	0.00	0.02	
<i>Anf</i>	0.09	0.14†	0.07†	...	0.32	0.08	0.06	0.06	0.11	0.00	0.00	0.00	0.00	
<i>Atr</i>	0.11	0.02	0.02	0.13	...	0.39	0.07	0.13	0.15	0.00	0.00	0.00	0.02	
<i>Zv</i>	0.17	0.96	0.86	0.89	0.02	...	0.02	0.08	0.54	0.00	0.00	0.00	0.00	
<i>Nl</i>	0.16	0.88	0.78	0.90	0.23	0.75	...	0.69	0.00	0.00	0.00	0.00	0.00	
<i>Nu</i>	0.04	0.01	0.01	0.11	0.92	0.01	0.15	...	0.06	0.00	0.00	0.00	0.00	
<i>Nb</i>	0.06	0.02	0.02	0.11	0.92	0.02	0.27	0.99	...	0.00	0.00	0.00	0.00	
<i>Cst</i>	0.36	0.67	0.61	0.66	0.10	0.77	0.77	0.02	0.04	...	1.00	0.99	0.97	
<i>Csg</i>	0.20	0.81	0.68	0.73	0.03	0.94	0.83	0.02	0.04	0.73	...	0.99	0.97	
<i>Anc</i>	0.00	0.87	0.97	0.84	0.02	0.83	0.75	0.01	0.02	0.64	0.79	...	0.95	
<i>Atn</i>	0.00	0.87	0.97	0.84	0.02	0.83	0.75	0.01	0.02	0.64	0.79	1.00	...	

* Species abbreviations: *Aln*, *A. lineatus*; *Ale*, *A. leucosternon*; *Zs*, *Z. scopas*; *Anf*, *A. nigrofuscus*; *Atr*, *A. triostegus*; *Zv*, *Z. veliferum*; *Nl*, *N. lituratus*; *Nu*, *N. unicornis*; *Nb*, *N. brevirostris*; *Cst*, *C. striatus*; *Csg*, *C. strigosus*; *Anc*, *A. nigricaudus*; *Atn*, *A. tennentii*.

† C_2H values based on adult *A. nigrofuscus* only; values based on adult + juvenile *A. nigrofuscus* are: *Ale/Anf*, 0.83; *Zs/Anf*, 0.66.

TABLE 5. Use of two reef slope substrata by seven surgeonfishes.

Proportion of habitat occupied by each substratum type	Proportion of fish with feeding areas centered on each substratum type†					Proportion‡ of bites taken from each substratum type by	
	<i>Acanthurus leucosternon</i>	<i>Zebra-soma scopas</i>	<i>Acanthurus nigrofuscus</i>	<i>Ctenochaetus strigosus</i>	<i>Ctenochaetus striatus</i>	<i>Acanthurus nigricaudus</i>	<i>Acanthurus tennentii</i>
High rock patches = 0.20	0.81 ***	0.15 NS	0.20 NS	0.40 ***	0.26 NS	0.02 ± 0.01 ***	0.09 ± 0.2 ***
Low rock and rubble = 0.80	0.19	0.85	0.80	0.60	0.74	0.98 ± 0.01	0.91 ± 0.2
No. individuals	69	34	110	179	106	14§	7

† Results of χ^2 comparisons of the two substratum types are indicated for each species: *** $P < .001$; NS, $P > .05$.
 ‡ Mean ± standard error. *A. nigricaudus* samples homogeneous ($P < .001$), *A. tennentii* samples heterogeneous ($P < .001$), as determined by heterogeneity χ^2 (Sokal and Rohlf 1981:721).
 § 36 observation periods.
 || 26 observation periods.

study-area transect (i.e., in overlap habitat) (Table 7, chi square = 50.3, $P < .001$); proportionately more *C. strigosus*, but not *C. striatus*, had their feeding areas situated on patches of high substrate than would be expected by chance (Table 5). The two detritivorous *Acanthurus* species fed to a disproportionately high degree on low substratum (Table 5). Although we did not collect data to make direct comparisons of the feeding activities of the *Ctenochaetus* and *Acanthurus* in a variety of microhabitats, our qualitative observations indicate that both *Acanthurus* species fed mainly in small patches of sandy substratum interspersed between the *Ctenochaetus* territories. Jones (1968) noted a similar difference in the feeding activities of detritivorous *Acanthurus* species and *Ctenochaetus* species.

TABLE 6. Use of 10 feeding microhabitats by two interacting surgeonfishes sharing territories in overlap habitat.

Microhabitat	Proportion of bites taken from each microhabitat by each species ($\bar{X} \pm SD$)†	
	<i>Z. scopas</i>	<i>A. nigrofuscus</i> ‡
Low substratum		
Rubble/sand	0.04 ± 0.10	0.03 ± 0.09
Horizontal rock	0.20 ± 0.12	0.51 ± 0.17
Vertical rock	0.29 ± 0.11	0.28 ± 0.13
Shallow crevice	0.15 ± 0.08	<0.01 ± 0.01
Deep crevice	0.06 ± 0.07	<0.01 ± 0.01
High substratum		
Horizontal rock	0.04 ± 0.05	0.06 ± 0.09
Vertical rock	0.10 ± 0.08	0.09 ± 0.13
Shallow crevice	0.03 ± 0.03	0
Deep crevice	0.02 ± 0.02	0
Cave	0.04 ± 0.04	0
Number of observation periods/number of individuals observed	37/35	110/80

† Species differences were significant: chi-square (using summed proportions for all individuals) = 42.6, $P < .001$.
 ‡ Juveniles only.

Interspecific defense and sharing of feeding territories

Individuals of 38 noninteracting pairs (Table 8) often completely overlapped feeding areas (i.e., they cohabited) even when both species were intraspecifically territorial and also interspecifically territorial towards "third-party" species. Agonistic interactions between noninteracting cohabitants were infrequent and too weak to result in the displacement of either species from the cohabited area. Members of the 27 interacting species pairs (Table 8) interacted agonistically whenever they came into contact, and rarely cohabited. Except in special circumstances (see next paragraph), any sharing of feeding space by interactors was transient and one species dominated and evicted the subordinate, at most within several minutes of the subordinate's entry into the dominant's feeding area.

Interactors exhibited four types of agonistic/space-use relationships (Table 8). (a) Three pairs of mutually territorial species defended their feeding areas against each other, and heterospecific neighbors rarely tolerated significant areal overlap of their feeding areas. (b) In 14 species pairs, one species strongly dominated the other, and was completely intolerant of the subordinate and evicted it from the dominant's territories. The subordinate rarely was aggressive towards the dominant (e.g., *A. nigrofuscus* dominated *A. triostegus*; Table 8). (c) In two cases one species dominated the other, but, although the dominant was intolerant of the subordinate, their feeding territories overlapped because the subordinate was able to avoid eviction: juveniles (but not adults) of *A. nigrofuscus* were able to hide in small shelters and remain in the territories of two larger dominants, *A. leucosternon* and *Z. scopas*. Although *Z. scopas* and *A. nigrofuscus* frequently attacked each other, *Z. scopas* invariably won fights in which both species were aggressive ($n = 56$). (d) In eight species pairs, one species dominated and could evict the other from the dominant's feeding territories but tolerated short bouts of feeding by the subordinate. In this man-

TABLE 7. Large-scale distributions of Aldabran surgeonfishes* in different zones of the main study transect.

Transect		Microalgivores					Macroalgivores				Detritivores					
Zone†	Section	<i>Aln</i>	<i>Ale</i>	<i>Anf</i>	<i>Atr</i>	<i>Zs</i>	<i>Zv</i>	<i>Nl</i>	<i>Nu</i>	<i>Nb</i>	<i>Anc</i>	<i>Atn</i>	<i>Cst</i>	<i>Csg</i>		
Proportion of population of each species in each transect section or zone																
I	1	0	0	0.01	0.17	0	0	0.25	0.98	0.96	0	0	0	0		
	2	0	0	0.04	0.17	0	0				0	0	0	0	0	0
	3	0	0	0.02	0.17	0	0				0	0	0	0	0	0
	4	0.01	0	0.02	0.21	0	0				0	0	0	0	0	0
	5	0.02	0	0.02	0.19	0	0				0	0	0	0	0	0
II	1	0.21	0	0	0.08	0	0	0.01	0.02	0	0	0.10	0.01			
	2	0.29	0	0	0	0	0			0	0	0	0.07	0.01		
	3	0.24	0	0	0	0	0			0	0	0	0.07	0.04		
III	1	0.17	0.03	0.02	0	0	0.17	0	0	0	0	0.06	0.08			
	2	0.06	0.10	0.04	0	0.03		0	0	0	0	0.06	0.07			
IV	1	0	0.06	0.10	<0.01	0.11	0.83	0.75	0.01	0.02	1.0	1.0	0.06	0.09		
	2	0	0.11	0.12	<0.01	0.03							0.09	0.08		
	3	0	0.14	0.14	0.01	0.11							0.06	0.13		
	4	0	0.15	0.14	0	0.11							0.11	0.05		
	5	0	0.09	0.11	0	0.18							0.12	0.09		
	6	0	0.08	0.08	0	0.24							0.12	0.12		
	7	0	0.15	0.08	0	0.18							0.05	0.13		
	8	0	0.09	0.07	0	0.03							0.04	0.10		
No. fish		84	79	167	174	38	6	8	‡	‡	7	2	154	204		

* Species abbreviations as in Table 4.

† I = intertidal reefcrest, II = subtidal rock pavement, III = subtidal groove and spur, IV = subtidal reef slope.

‡ For method of calculation, see Methods: Computation of Overlap in Resource Use.

ner *Z. veliferum* was dominated but partly tolerated by both *A. leucosternon* and *Z. scopas*. The amount of feeding by the subordinate species in the dominant's territory varied among species pairs.

Reciprocal removal experiments

The result of the removal experiments bear on agonistic relations and priority of access to feeding space in two ways. First, which species took over which types of vacant space? All species took over vacated conspecific sites. The patterns of intra- and interspecific take-overs of each species' territories were nonrandom (Table 9). Vacant *A. lineatus* territories were taken over by all microalgivores, but *A. lineatus* did not take over vacant areas of any other species. Vacant *A. leucosternon* areas were taken over by conspecifics, and by *A. nigrofuscus* and *A. triostegus*, while *A. leucosternon* only took over *A. lineatus* areas and, on one occasion, part of a *Z. scopas* territory. The other species that took over *Z. scopas* territories were *Z. scopas*, *A. nigrofuscus*, and *A. triostegus*. Vacant *A. nigrofuscus* territories were taken over only by conspecifics and *A. triostegus*, and those of *A. triostegus* were taken over only by conspecifics. Second, which species evicted which other species that had initially taken control of vacated space? We assumed that such an eviction had occurred when we saw a second occupant actively driving away and, in some instances, fighting with an individual of the species that had originally occupied the territory, when the latter individual attempted to reenter the territory. Our observations indicate that *A. lineatus*

evicted all four other species but was never evicted by heterospecifics. *A. leucosternon* evicted *Z. scopas*, *A. nigrofuscus*, and *A. triostegus*; *Z. scopas* evicted only *A. nigrofuscus* and *A. triostegus*; *A. nigrofuscus* evicted only *A. triostegus*; and *A. triostegus* did not evict any other species.

Dominance hierarchies

All species interacted agonistically with one or more heterospecifics, and 42% of species pairs interacted in this manner. Several interconnected linear dominance hierarchies existed, but there were no indications of nontransitive dominance networks (sensu Buss and Jackson 1979). The dominance relations detailed in Table 8 are based on the ratio of attacks by one species on the other and the ability of one species to aggressively control space suitable for feeding territories, as indicated by the pattern of takeovers and evictions from experimentally vacated territories (see Results: Reciprocal Removal Experiments). For example, *A. lineatus* dominated *A. nigrofuscus* because (a) 92% of intra-pair attacks by one species on the other were by *A. lineatus* on *A. nigrofuscus* (Table 8) and (b) *A. lineatus* evicted *A. nigrofuscus* that initially occupied vacated *A. lineatus* territories but the reverse did not occur (Table 9). Only 3 of 27 interacting species pairs, all involving mutually territorial species, showed dominance relations that were not strongly asymmetrical: *A. lineatus/A. leucosternon*, *A. leucosternon/Z. scopas*, and *C. striatus/C. strigosus* (Table 8). For two of these three there is evidence of partial asymmetry: (1) *A.*

TABLE 8. Agonistic dominance relations among the 13 surgeonfishes.* (Species referred to as *a* in footnotes are those listed across the top of the table, and species *b* those down the left margin.)

		Number of attacks involving territory owners of a species†												
		<i>Aln</i>	<i>Ale</i>	<i>Zs</i>	<i>Anf</i>	<i>Atr</i>	<i>Zv</i>	<i>Nl</i>	<i>Nu</i>	<i>Nb</i>	<i>Cst</i>	<i>Csg</i>	<i>Anc</i>	<i>Atn</i>
Nature of relationship‡	<i>Aln</i>		$\frac{46}{69}$	$\frac{-}{19}$	$\frac{14}{162}$	$\frac{-}{798}$	$\frac{-}{21}$	$\frac{-}{75}$	$\frac{-}{22}$	$\frac{-}{18}$	$\frac{6}{4}$	$\frac{2}{7}$	$\frac{-}{17}$	$\frac{-}{8}$
	<i>Ale</i>	†		$\frac{31}{77}$	$\frac{16}{237}$	$\frac{-}{578}$	$\frac{-}{84}$	$\frac{-}{4}$	-	-	$\frac{3}{2}$	$\frac{5}{4}$	$\frac{-}{37}$	$\frac{-}{66}$
	<i>Zs</i>	←	†		$\frac{97}{112}$	$\frac{2}{24}$	$\frac{2}{9}$	-	-	-	-	$\frac{-}{1}$	-	-
	<i>Anf</i>	←	←p	←p		$\frac{16}{245}$	$\frac{-}{3}$	-	-	-	$\frac{-}{3}$	-	$\frac{9}{9}$	$\frac{-}{13}$
	<i>Atr</i>	←	←	←	←		-	-	-	-	-	-	-	-
	<i>Zv</i>	←	←p	←p	0	ND		-	-	-	-	-	-	-
	<i>Nl</i>	←p	0	0	0	0	0		$\frac{-}{22}$	-	-	-	-	-
	<i>Nu</i>	←	0	ND	0	0	ND	←		-	-	-	-	-
	<i>Nb</i>	←	ND	ND	0	0	ND	0	0		-	-	-	-
	<i>Cst</i>	0	0	0	0	0	0	0	0	ND		$\frac{83}{86}$	$\frac{-}{14}$	$\frac{-}{19}$
	<i>Csg</i>	0	0	0	0	0	0	0	ND	ND	†		$\frac{-}{12}$	$\frac{-}{14}$
	<i>Anc</i>	←	←	0	0	0	0	0	ND	ND	←p	←p		$\frac{-}{15}$
	<i>Atn</i>	←	←	0	0	0	0	0	ND	ND	←p	←p	←p	

* Species abbreviations as in Table 4.

† Indicated as $\frac{n_1}{n_2}$, where n_1 = number of attacks by *a* on *b*, n_2 = number of attacks by *b* on *a*. - = no attacks observed.

‡ For interacting species, b^a = *a* dominates and totally excludes *b* from *a*'s territories; $b^a p$ = *a* dominates *b* but does not totally exclude *b* and the two share feeding areas in part; $b^a \dagger$ = *a* and *b* are mutually territorial and mutually exclude each other. Noninteracting species pairs indicated by 0. ND = insufficient data to define dominance relations.

lineatus seemed to partly dominate *A. leucosternon* because *A. lineatus* evicted *A. leucosternon* that initially took over experimentally vacated *A. lineatus* feeding areas (Table 9) and (2) *A. leucosternon* attacked *Z. scopas* twice as frequently as the converse (Table 8) and, in one instance, evicted *Z. scopas* from part of an experimentally vacated *Z. scopas* feeding territory (Table 9). We have no evidence of an asymmetry in the *C. striatus*/*C. strigosus* interaction.

Interspecific interactions and overlap in resource use

In general, interactors had more similar diets and less overlap at large scales of habitat use than did noninteractors, but on average the two species of an interacting pair did not differ in size to any greater extent than the two members of a noninteracting pair (Table 10). There were a number of exceptions to these patterns in C_zD and C_zH values. First, the distributions

of C_zH values were bimodal among both interactors and noninteractors: values for 16 interactors ranged from 0.00 to 0.17 (\bar{X} = 0.09), and for all others from 0.69 to 1.00 (\bar{X} = 0.80); 12 values for noninteractors ranged from 0.00 to 0.36 (\bar{X} = 0.12), and for 26 others from 0.61 to 0.99 (\bar{X} = 0.82). Eight of the 11 interactors with high C_zH values segregated use of microhabitats in overlap habitat (see Results: Overlap in Habitat Usage). Another two had low diet overlap, and in only one case (*A. nigricaudus*/*A. tennentii*) was there high overlap in use of habitat, feeding microhabitats, and food. *A. tennentii* was the rarest resident surgeonfish in the main study area (Table 7) and was subordinate to five other species in that area (Table 8). Elsewhere on Aldabra, *A. tennentii* population density was much higher, and the five dominant species were much rarer, both absolutely and relatively (Table 11). In eight of the 12 noninteractors with low C_zH values one member of the pair was agonistically subordinate to a third

TABLE 9. Replacement following removal of territory holders of five microalgalivorous surgeonfishes.

Species removed	Number of territories manipulated	Number of vacant territories occupied* by				
		<i>A. lineatus</i>	<i>A. leucosternon</i>	<i>Z. scopas</i>	<i>A. nigrofuscus</i>	<i>A. triostegus</i>
<i>A. lineatus</i>	24	12 (0)*	9 (3)	0 (2)	4 (4)	13 (4)
<i>A. leucosternon</i>	9	0 (0)	9 (0)	0 (0)	3 (2)	4 (2)
<i>Z. scopas</i>	8	0 (0)	1 (0)	8 (0)	0 (2)	2 (4)
<i>A. nigrofuscus</i>	30	0 (0)	0 (0)	0 (0)	25 (0)	7 (0)
<i>A. triostegus</i>	21	0 (0)	0 (0)	0 (0)	0 (0)	18 (0)

* Occupied = defense of part or whole of a vacated feeding area by ≥ 1 individuals. Data are of the form $n1(n2)$, where $n1$ = number of territories occupied ≥ 5 d after removal; $n2$ = number of areas (other than those included in $n1$) occupied for ≤ 2 d after the removal and subsequently occupied by another species that apparently evicted the first occupant. The number of territories manipulated may be exceeded by the totals for occupations because the number of occupations included concurrent partial occupations by more than one species. Results of χ^2 tests of H_0 : The pattern of takeovers of a species' territories does not differ from that expected from the relative abundances of the five species in the study area (see Table 3): $P < .01$ for each of the five species.

species that showed high habitat overlap with the second member of the pair. Second, although C_zD values among noninteractors never exceeded 0.15, 7 of 27 interactors had C_zD values ≤ 0.15 .

DISCUSSION

Our data generally support the hypothesis that Aldabran surgeonfishes that interact agonistically are actively competing for food (although we did not show that they are food limited), and that interspecific interference competition is a major factor structuring large-scale habitat use, by reducing overlap among competitors. There is no evidence that competitive interactions are related to size-dependent usage of resources.

The hypothesis is further supported by the results of the removal experiments. These show that agonistically subordinate species readily use habitat occupied by a more dominant species, but that the reverse rarely occurs. There are several reasons why the patterns of takeovers observed in our experiments reflect asymmetries in dominance ability rather than chance. First, those patterns do not relate to the relative abundances of the species. Second, they do not derive from interspecific differences in readiness to relocate, since all species moved into at least one type of vacated territory. Third, all species were presented with opportunities to relocate; the experiments were performed in

habitat where many species lived. Further, all of the Aldabran microalgalivores frequently made excursions outside their territories (D. R. Robertson, *personal observation*), which enabled them to monitor their local environment and locate vacancies (cf. the behavior of territorial damselfishes; Bartels 1984). Fourth, interspecific evictions from newly vacated areas were non-reciprocal.

The general conclusion that can be drawn from our results is that interference interactions may have reduced large-scale habitat overlap among 16 of 27 interactors, and that high habitat overlap among 26 of 38 noninteractors reflects a lack of competitive interaction; i.e., the presence or absence of interference competition may affect 65% of large-scale habitat-use relationships. This conclusion is supported in 9 of the 10 cases we examined experimentally. Further, although we commonly observed exceptions to the tendency for interactors to show greater diet overlap and less large-scale habitat overlap than noninteractors, most of the exceptions are consistent with our hypothesis. First, 8 of the 11 interactors that had high large-scale habitat overlap exhibited small-scale habitat segregation (although we cannot say whether such differences in microhabitat usage were greater than among noninteractors). Among the remaining three exceptions, two had relatively low diet overlap. The single case in which there is no evidence of any segregated

TABLE 10. Differences in the similarity of diets, habitat distributions, and body sizes between interacting and noninteracting species pairs of surgeonfishes.

Variable	Overlap index value ($\bar{X} \pm SE$)		Difference between interactors and noninteractors† (\bar{X} and CI‡)
	Interactors	Noninteractors	
Dietary similarity (C_zD)	0.43 \pm 0.07	0.03 \pm 0.01	+0.40 \pm 0.23*
Habitat use similarity (C_zH)	0.38 \pm 0.07	0.60 \pm 0.06	-0.22 \pm 0.20*
Size similarity	0.60 \pm 0.05	0.49 \pm 0.04	+0.11 \pm 0.13 NS

† Difference tested by Hotelling's multivariate T^2 (Morrison 1976:128): $F_{(3,9)} = 48.1$, $P < .001$. (Since each species was used as a replicate and any two species share one C_z value for each variable, significance was tested using one less degree of freedom per group.) Differences for each variable tested by separate Mann-Whitney U tests. Diet similarity: $Z = 4.93$, $P < .01$; habitat similarity: $Z = 2.22$, $P < .05$; size similarity: $Z = 1.27$, $P > .05$.

‡ Bonferroni simultaneous 95% confidence interval, * $P < .05$, NS $P > .05$.

TABLE 11. Abundances of detritivorous surgeonfishes at two sites at Aldabra.

Species	Number of individuals per hectare	
	Main study area	Dune D'Messe
<i>A. tennentii</i>	16	220
<i>A. nigricaudus</i>	55	5
<i>C. striatus</i>	1200	0
<i>C. strigosus</i>	1600	0
Area sampled (ha)	0.125	1

resource use involved one species (*A. tennentii*) that appeared to be virtually excluded from the study area. Second, 11 of the 13 species interacted with more than one species, and at least six were agonistically subordinate to two or more species. In 8 of the 12 exceptions to high habitat overlap among noninteractors, one member of the species pair interacted with a third species that had high habitat overlap with the second member of the noninteractor pair. Consequently, reduced habitat overlap in each of those eight cases may be due, indirectly, to an interference interaction. Third, interactors with zero diet overlap probably have a potential for greater diet overlap, which, due to the interaction(s), is not realized. For example, none of the detritivores had any diet overlap with the microalgivore *A. lineatus*, but only the *Ctenochaetus* did not interact with *A. lineatus*. While the *Ctenochaetus* species apparently are incapable of feeding as microalgivores do, by biting off attached algae (Randall 1955), the detritivorous *Acanthurus* can feed as microalgivores (D. R. Robertson, *personal observation*). Thus the apparent exceptions to expectations regarding habitat-use patterns are consistent with the hypothesis in 16 of 23 cases, and the presence or absence of interference competition may affect 60–80% of habitat-use relationships in one way or another.

While maintaining that interference competition is a major force influencing habitat-use relationships, we do not assert that it is the sole factor in any particular case nor that it is equally important in all cases. There is evidence that subordinate interactors' habitat preferences do not always overlap completely with those of dominants. For example, the precise form of takeover of vacated *A. lineatus* territories by *A. leucosternon* varied according to the physiognomy of the substratum (Robertson et al. 1979).

Previous studies of the structure and dynamics of reef fish assemblages have ranged from examinations of a broad range of species (e.g., Sale and Dybdahl 1978, Talbot et al. 1978) to studies focused on restricted ecological groups, e.g., nocturnal carnivores (Chave 1978, Gladfelter and Johnson 1983), diurnal planktivores (Williams 1980), benthic-feeding corallivores/carnivores (Anderson et al. 1981), or herbivores (Jones 1968, Sale 1974b, Sale et al. 1980, Doherty 1982, 1983,

Russ 1984a, b, Ebersole 1985). Apart from Jones' (1968) and Russ's (1984a, b) studies, work on the herbivores has been concentrated on the territorial species of the Pomacentridae. Among the studies of specific groups of reef fishes, only those of Gladfelter and Johnson (1983) and Ebersole (1985) indicate that competition can enhance resource partitioning in reef fish communities. Although the former study did not specifically examine proximate factors that produced partitioning, it did indicate that ongoing competition may not have had a strong effect, since the two most abundant and widely distributed species in the assemblage studied apparently competed for food but partitioned food and habitat less than did other species. Ebersole's (1985) work on territorial, herbivorous damselfishes has shown that interference interactions sometimes influence habitat-use relations in a predictable manner, although Doherty (1982, 1983) found that such is not always the case. Other work (Sale 1979, and references therein) on habitat use in the same guild on which Doherty worked (but at a different time, site, and habitat) has indicated that small-scale habitat partitioning is weak, that competitive interactions between members of this group sometimes are strong, but that agonistic dominance relations are sufficiently symmetrical for interference interactions to have no predictable effect on use of space.

Our results present a picture that differs substantially from that presented by studies of territorial damselfishes other than that of Ebersole (1985). Many species in the Aldabran surgeonfish assemblage interact agonistically (probably due to food competition), dominance relations among most species are distinctly asymmetrical, and interference competition has a substantial effect in patterning large-scale, and possibly small-scale, habitat use. However, it does not necessarily follow that the form and causes of the structure we observed are fixed characteristics of surgeonfish assemblages in general. Indeed, *personal observation* (D. R. Robertson) indicates that there can be substantial variation in agonistic and habitat-use relationships within a species-pair: at Palau (West Pacific) and Lizard Island (Australia) as well as Aldabra, all *A. lineatus* adults observed had cohabitant *C. striatus* living peacefully in their territories; at Moorea and Bora Bora (South Pacific), such cohabitation was exceptional (and apparently habitat specific) and most *A. lineatus* defended their territories against and did not cohabit with *C. striatus*.

We recognize that our study is limited in several significant ways. We considered only one family and one ecological group at one local site at one point in time. We examined only habitat-use relationships, and we can say nothing about effects of interference competition on abundance relationships in the assemblage or the temporal stability and persistence of any assemblage characteristics. We do not think that our results and conclusions preclude a significant role for a range

of other intrinsic or extrinsic processes, e.g., recruitment variation (cf. Doherty 1981, 1983, Victor 1983) or predation, in the assemblage we studied. There is now sufficient evidence that a variety of processes can and do affect the structure of reef fish assemblages, and we agree with others (Smith 1978, Brock et al. 1979, Ogden and Ebersole 1981, Shulman et al. 1983) that the potential for a synthesis must now be explored.

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