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Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama

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Abstract Resource use by five sympatric species of parrotfish was quantified in the San Blas Archipelago of the Republic of Panama from March to August 1987. Detailed observations of parrotfishes on patch reefs and surrounding seagrass beds showed that they partition resources with respect to habitat, food and size, but not time. Although parrotfishes shared resources, the proportions of each resource used differed significantly among species. *Scarus iserti* (Bloch) scraped filamentous microalgae that grew from eroded coral pavement on lower slopes of patch reefs and in “halos,” the area of sparse vegetation surrounding reefs. *Sparisoma viride* (Bonnaterre) foraged on upper slopes of patch reefs where they mostly took bites from dead coral and associated algae. *S. aurofrenatum* (Cuvier and Valenciennes) had the broadest diet, which consisted mostly of seagrasses and macro- and microalgae that were attached to dead coral on lower reef slopes and in halos. Although *S. chrysopterygum* (Bloch and Schneider) commonly occurred on patch reefs, it primarily foraged in seagrass beds that surround them. *S. rubripinne* (Cuvier and Valenciennes) was distributed most widely, ranging from seagrass beds to reef crests, where it took bites from seagrasses, dead coral and macroalgae. Juveniles of all species occurred on lower slopes or in halos where they scraped filamentous microalgae from coral pavement. As they matured, parrotfishes moved into other habitats

changing access to different types of food. All of these parrotfishes fed throughout the daytime, and resource use did not differ between morning and afternoon.

Introduction

How so many species of fishes coexist on coral reefs remains a major ecological question. Niche diversification through competition initially was favored as an explanation, but strong evidence that competition limited distributions and abundances of reef fishes was difficult to obtain. Meanwhile, facilitation, disturbance, predation and recruitment also have been proposed as processes that structure reef fish communities (see Ebeling and Hixon 1991; Sale 1991 for reviews). Although multiple forces likely structure these communities, compelling evidence for any model remains elusive. A variety of predictions must be satisfied to demonstrate that any of these processes regulate community structure (see Ebeling and Hixon 1991 for review), and such demonstrations likely would derive from a substantial knowledge of complex communities. Detailed observational studies provide the basis for much of this understanding.

Careful observations of resource use formed the foundation for competition theory and continue to be important to its evaluation even though the merits of simplifying experimental manipulations have become recognized widely (Wiens 1977; Connell 1980, 1983; Alley 1982; Schoener 1982; Sale 1991). A major tenet of competition theory is that animals coexist by partitioning space, food or time. Fine partitioning of resources is apparent for some coral reef fishes but many other reef fishes do not appear to be particularly specialized (Sale and Dybdahl 1975; Clarke 1977; Sale 1977; Talbot et al. 1978; Ross 1986). One such group is parrotfishes.

Parrotfishes are large, abundant, conspicuous members of coral reef fish communities that forage over reefs during the daytime (Robblee and Zieman 1984; Lewis

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and Wainwright 1985). Scarids (79 species) comprise one of the two most speciose families of primarily herbivorous reef fishes (Choat 1991). With beak-like terminal jaws, parrotfishes feed nonselectively by taking bites from multispecific algal turfs or by scraping dead coral for endolithic microalgae. They also feed selectively by taking deliberate bites of seagrasses, macroalgae and live coral (Hiatt and Strasburg 1960; Litterer et al. 1989; Bellwood and Choat 1990; Choat 1991; Bruggemann et al. 1994). Strong, well-developed pharyngeal mills grind the ingested matter (Frydl and Stearn 1978; Lobel and Ogden 1981; Bruggemann et al. 1994). Laterally compressed fusiform bodies, and well-developed pectoral and pelvic fins permit slow swimming and precise control of body orientation during episodes of continuous, rapid grazing over small areas of the reef (Choat 1991). Parrotfishes are protogynous hermaphrodites and often have dichromatic life history phases, termed initial (generally female) and terminal (always male) phases, which are readily distinguished in the field (Barlow 1975; Choat and Robertson 1975). Caribbean scarids spawn every afternoon throughout the year, although spawning activity increases during summer (Colin 1978; Robertson and Warner 1978). Many parrotfishes retire to holes in the reef to sleep at night (Winn and Bardach 1959).

Although 13 species of scarids occur in the Caribbean (Randall 1968), only five species of parrotfishes are abundant on patch reefs along the Caribbean coast of Panama. Preliminary observations indicated that *Scarus iserti* was the most abundant parrotfish followed by four species in the genus *Sparisoma*: *S. viride*, *S. aurofrenatum*, *S. chrysopterum*, and *S. rubripinne*. Several other species were uncommon on these reefs, including *Scarus taeniopterus*, *Sc. guacamaia*, *Sc. coeruleus*, *Sc. coelestinus* and *Sc. vetula* (also see Weinstein and Heck 1979). In addition, the small parrotfishes, *S. radians* and *S. atomarium*, occurred in seagrass beds adjacent to reefs, while *Cryptotomus roseus* were found in seagrass beds farther from patch reefs.

Preliminary observations on patch reefs in the San Blas Archipelago revealed little evidence of resource partitioning in this assemblage of parrotfishes, and evidence from other functional groups of parrotfishes has been mixed (Choat 1969; Roughgarden 1974; Russ 1984; Lewis and Wainwright 1985). Therefore, a detailed evaluation of resource use by parrotfishes would augment the body of knowledge needed to evaluate the importance of competition in reef fish communities and provide new information on the ecology of this important group.

Despite considerable interest in resource partitioning by reef fishes, few investigators simultaneously have examined resource use along all three major niche dimensions: space, food and time (see Ross 1986 for review). In addition, ontogenetic shifts in resource use may occur. The purpose of the present study was to determine spatial, temporal and developmental patterns of habitat and food use by the five most common

parrotfishes that occur on patch reefs along the Caribbean coast of Panama.

Materials and methods

The present study was conducted in the San Blas Archipelago, off the Caribbean coast of the Republic of Panama, on 17 patch reefs within a 3 km² area near the Smithsonian Tropical Research Institute's field station from 30 March to 9 August 1987 (see Robertson 1987 for location of study site). These patch reefs are sheltered from waves by a barrier reef and experience high sedimentation and occasional low salinities from discharge by several large rivers (Ogden and Buckman 1973). Patch reefs generally occur in less than 10 m of water shoreward of a barrier reef and are comprised primarily of finger coral (*Porites porites*), staghorn coral (*Acropora cervicornis*), elkhorn coral (*Acropora sternalis*), fluted coral (*Agaricia agaricites*) and brain coral (*Monastrea* spp.). Mixed seagrasses (*Thalassia testudinum* and *Syringodium filiforme*), silty sand, gorgonians and scattered coral heads surround reefs.

Feeding habits of parrotfishes were studied while snorkeling or SCUBA diving on the 17 reefs from dawn to dusk when these diurnal parrotfishes were active. A total of 198 individuals [36 *Scarus iserti* (Bloch), 47 *Sparisoma viride* (Bonnaterre), 41 *S. aurofrenatum* (Cuvier and Valenciennes), 38 *S. chrysopterum* (Bloch and Schneider), 36 *S. rubripinne* (Cuvier and Valenciennes)] that were at least 2-cm long were followed for 5 min each. The number of bites taken from algae and other items, estimated total length, phase (initial or terminal) and time of day were recorded for each fish followed. Foods consisted of four macroalgae (*Udotea* spp., *Penicillus* spp., *Halimeda* spp., *Dictyota* spp.), two seagrasses (*Thalassia testudinum*, *Syringodium filiforme*), a thin layer of flocculant matter covering smooth eroded coral, which was termed coral "pavement", "algal turf", which grew on dead coral, and sand. Multispecific algal turf consists of macroalgae as well as filamentous, crustose and unicellular algae with representatives from five divisions (Cyanophyta, Chlorophyta, Chrysophyta, Phaeophyta and Rhodophyta; Carpenter 1986; Bruggemann et al. 1994). Algal turfs form a single category, because the plant species are interspersed and parrotfishes are nonselective at this level (Bruggemann et al. 1994). Bites frequently were taken from seagrasses, coral pavement, dead coral, *Halimeda* spp. and *Dictyota* spp. Foods that were eaten infrequently (*Udotea* spp., *Penicillus* spp., live coral, sponges) and bites of sand were combined into a single category called "other."

The availability of these six food types was quantified by recording the occurrence of plants, macroinvertebrates or substrates on two of the reefs, "Smithsonianup-1" and "Porvenir-20," which were approximately 80 and 25 m in diameter, respectively. Potential foods were recorded at 20-cm intervals along 20-m long haphazardly placed transects. A total of 15 transects were followed in five zones: crest, upper slope, lower slope, halo and adjacent seagrass bed. The crest was defined as the reef flat that was awash at low tide. The upper slope extended 3 m below the reef crest, and the lower slope extended 3 m above the bottom. The halo was the 3-m zone of sparse vegetation that surrounded the reef, and the seagrass zone extended 3 m into seagrass beds surrounding the halo.

Parrotfishes on Smithsonianup-1 and Porvenir-20 reefs were censused visually within each of the five zones between dawn and dusk (06:30 to 19:00 hrs) using a technique developed by Brock (1954), reviewed by Sale (1980) and modified by Lewis and Wainwright (1985). Parrotfishes within 1.5 m of a 20-m transect line were counted; each fish was categorized by species, phase, estimated total length (see Table 1 for size classes of each species) and time of day. Brock (1982) tested the reliability of this technique and found excellent agreement between the number of parrotfishes that were censused visually and the number that were removed after rotenone was applied to a patch reef. Lengths of fishes were validated periodically by comparing the estimated length of fish to background landmarks

Table 1 *Scarus iserti* and *Sparisoma* spp. Size classes based on total lengths (cm) of five species of parrotfishes observed on 17 patch reefs in the San Blas Archipelago, Panama

Species	Small	Medium	Large
<i>Sc. iserti</i>	3–9	10–14	>14
<i>S. viride</i>	3–17	18–32	>32
<i>S. aurofrenatum</i>	5–13	14–22	>22
<i>S. chrysopteryum</i>	4–15	16–27	>27
<i>S. rubripinne</i>	5–17	18–30	>30

that were later measured. Estimated lengths and measured distances of landmarks were generally within 2 cm for small fish and 3 cm for large fish. Fishes were censused along transects in the five zones of the two reefs a total of 105 times. Transects were removed and replaced haphazardly.

Behavioral interactions of parrotfishes were observed for indications of competitive behaviors. The participants were identified, their lengths were estimated, displays, postures and color changes were described and durations of encounters were noted.

Niche overlap indices, each with their particular biases, were not calculated for the many variables that were included in this multidimensional study of resource use. Instead, the Scheirer–Ray–Hare extension of the Kruskal–Wallis test was used to determine similarities in resource use by the five species with respect to habitat, diet, time, fish length and phase. This nonparametric test was used in lieu of a multiway analysis of variance (Sokal and Rohlf 1995). Nonsignificant interaction terms were removed to increase the degrees of freedom, and data were reanalyzed. All data were graphed in three dimensions to best portray multidimensional patterns of resource use, but this precluded the inclusion of error bars.

A two-way test was used to determine the similarity of feeding by the five species of parrotfishes among the five zones. A four-way test was used to determine whether or not the diet of each species shifted ontogenetically, temporally and with respect to phase. Hourly feeding rates of parrotfishes were determined to ensure that peak feeding rates did not occur near noon, before data were divided into mornings and afternoons. Distributions of potential foods among the five zones were tested using a two-way test.

A three-way test was used to identify differences in abundance of parrotfishes among the five zones of reefs during mornings and afternoons. Distributions of phases and sizes of parrotfishes were analyzed separately in two-way tests. Individuals could be scored as occurring among zones of the reef, but could not be counted again as belonging to particular size classes and phases within zones. Therefore, statistical interactions in multiway tests that would indicate whether or not adults migrated to different areas of reefs to spawn during afternoons were precluded.

Results

Dietary patterns of resource use

All five parrotfishes ate each of the six types of foods, but the proportions of foods eaten differed significantly

Fig. 1 *Scarus iserti* and *Sparisoma* spp. **A** Mean number of bites of six food items taken by five species of parrotfishes during 5-min observation periods on 17 patch reefs. 198 individuals (36 *Sc. iserti*, 47 *S. viride*, 41 *S. aurofrenatum*, 38 *S. chrysopteryum*, 36 *S. rubripinne*) at least 2-cm long censused. **B** Distribution of foods (mean percentage) among five zones of two of the patch reefs. Foods and substrates identified under 15 transect lines every 20 cm. A total of 15 transects censused. **C** Mean number of five parrotfishes per 20 × 3 m transects in five zones of two patch reefs. A total of 105 transects censused

among species (Fig. 1; Table 2). *Scarus iserti* ate microalgae associated with coral pavement, *Sparisoma viride* primarily took bites from dead coral and *S. chrysopteryum* mostly ate seagrasses. Both *S. aurofrenatum* and *S. rubripinne* mostly consumed seagrasses and dead

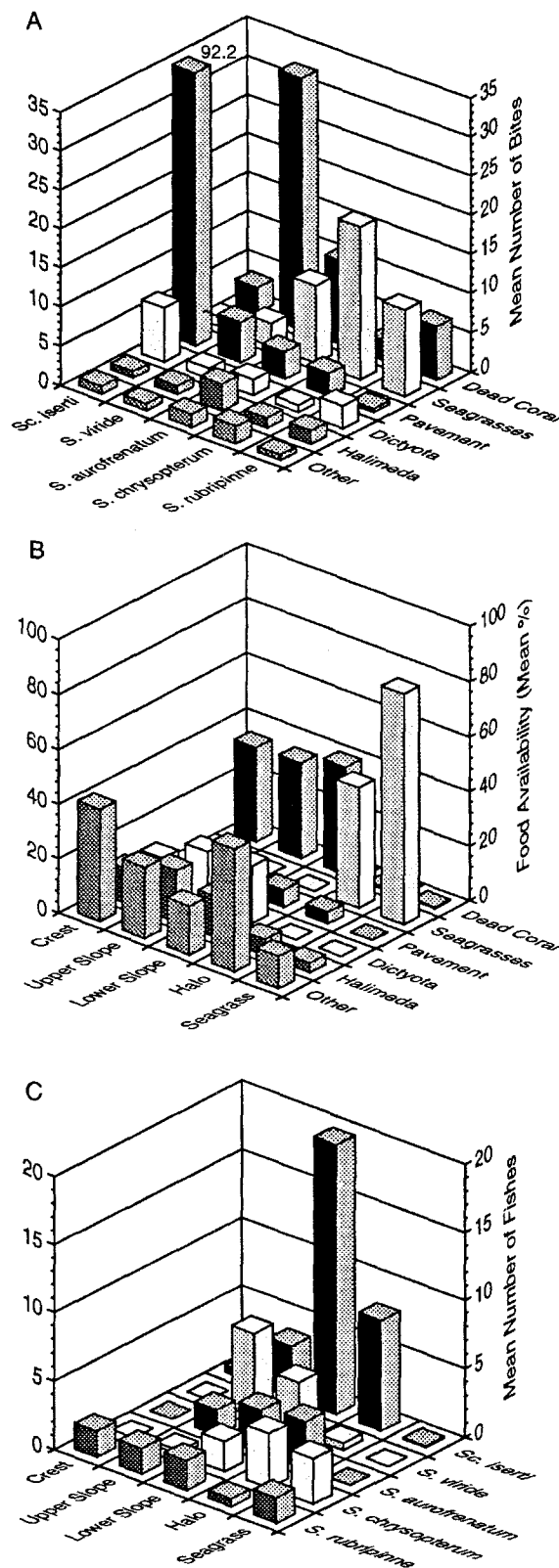


Table 2 *Scarus iserti* and *Sparisoma* spp. Scheirer-Ray-Hare tests. Number of bites of six food types (*Food*) taken by five species of parrotfishes (*Species*) during 5-min observation periods conducted on 17 patch reefs. 198 individuals (36 *Sc. iserti*, 47 *S. viride*, 41 *S. aurofrenatum*, 38 *S. chrysopterus*, and 36 *S. rubripinne*) at least 2-cm long censused. Abundances of food types (*Food*) available to parrotfishes that occur in five zones (*Zone*) of two patch reefs. A total of 15 transects censused. Abundances of five parrotfishes (*Species*) during mornings and afternoons (*Time*) in five zones (*Zone*). A total of 105 transects censused. *ns* indicates $p > 0.05$

Test Source	df	SS	H	p
Number of bites				
Food	5	16725235	144.92	<0.001
Species	4	17679898	153.20	<0.001
Food × Species	20	18721920	12.97	<0.001
Error	1152	83168206		
Food availability				
Food	5	2172.10	3.36	ns
Zone	4	10866.16	16.82	<0.010
Food × Zone	20	37811.62	58.54	<0.001
Error	60	6641.08		
Number of fishes				
Zone	4	1642651	72.78	<0.001
Species	4	391313	17.34	<0.010
Time	1	33121	1.47	ns
Zone × Species	16	3110748	137.82	<0.001
Error	499	6649516		

coral, but *S. aurofrenatum* did not forage in seagrass beds as did *S. rubripinne*. Furthermore, *S. aurofrenatum* had a more diverse diet than *S. rubripinne*; *S. aurofrenatum* took more bites from coral pavement, *Halimeda* spp., *Udotea* spp., *Sargassum* spp., crabs, urchins and sponges. Although *S. aurofrenatum* is more omnivorous than the other four species, many parrotfishes prefer sponges to algae when available (S.T. McAfee unpublished data; J. Wulff personal communication).

Nonsignificant ontogenetic shifts in diet were evident for four parrotfishes (Figs. 2, 3; Table 3). Juveniles of all five species took bites from pavement in halos and on lower slopes, and all mature fishes, except *Scarus iserti*, switched to other foods. Shifts in diet corresponded to shifts in habitat (see subsection "Spatial patterns of resource use"); parrotfishes generally ate the commonest foods wherever they occurred.

Food availability

These patch reefs were surrounded by expansive beds of *Thalassia testudinum* and *Syringodium filiforme*, and small amounts of green algae (*Udotea* spp. and *Halimeda* spp.) were interspersed among seagrasses (Fig. 1; Table 2). Seagrasses were less dense immediately next to patch reefs, presumably due to grazing by urchins and herbivorous fishes (Randall 1965; Ogden et al. 1973). Consequently more sand, coral pavement, *Hali-*

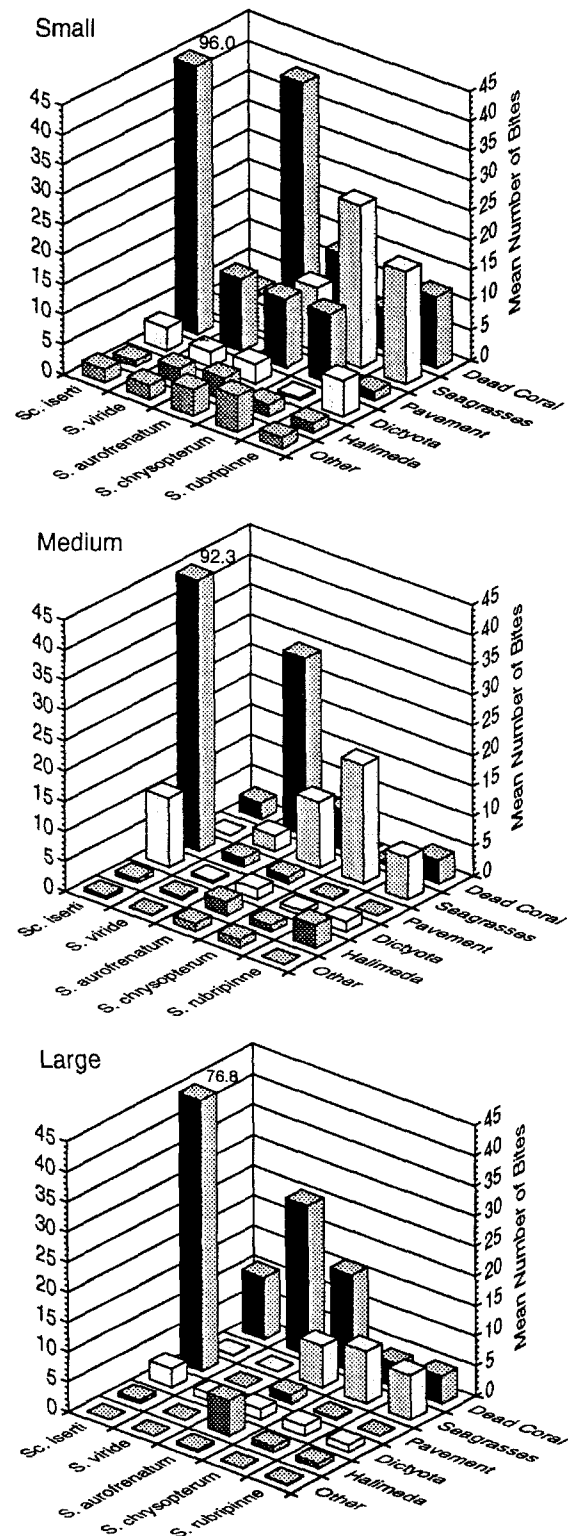


Fig. 2 *Scarus iserti* and *Sparisoma* spp. Mean number of bites of six food items taken by three size classes of five species of parrotfishes during 5-min observation periods on 17 patch reefs. See Fig. 1 for numbers of parrotfishes censused

meda spp., *Penicillus* spp. and *Udotea* spp. occurred in halos. Lower slopes, upper slopes and crests of patch reefs were comprised mostly of dead coral and associated multispecific algal turf, lesser amounts of

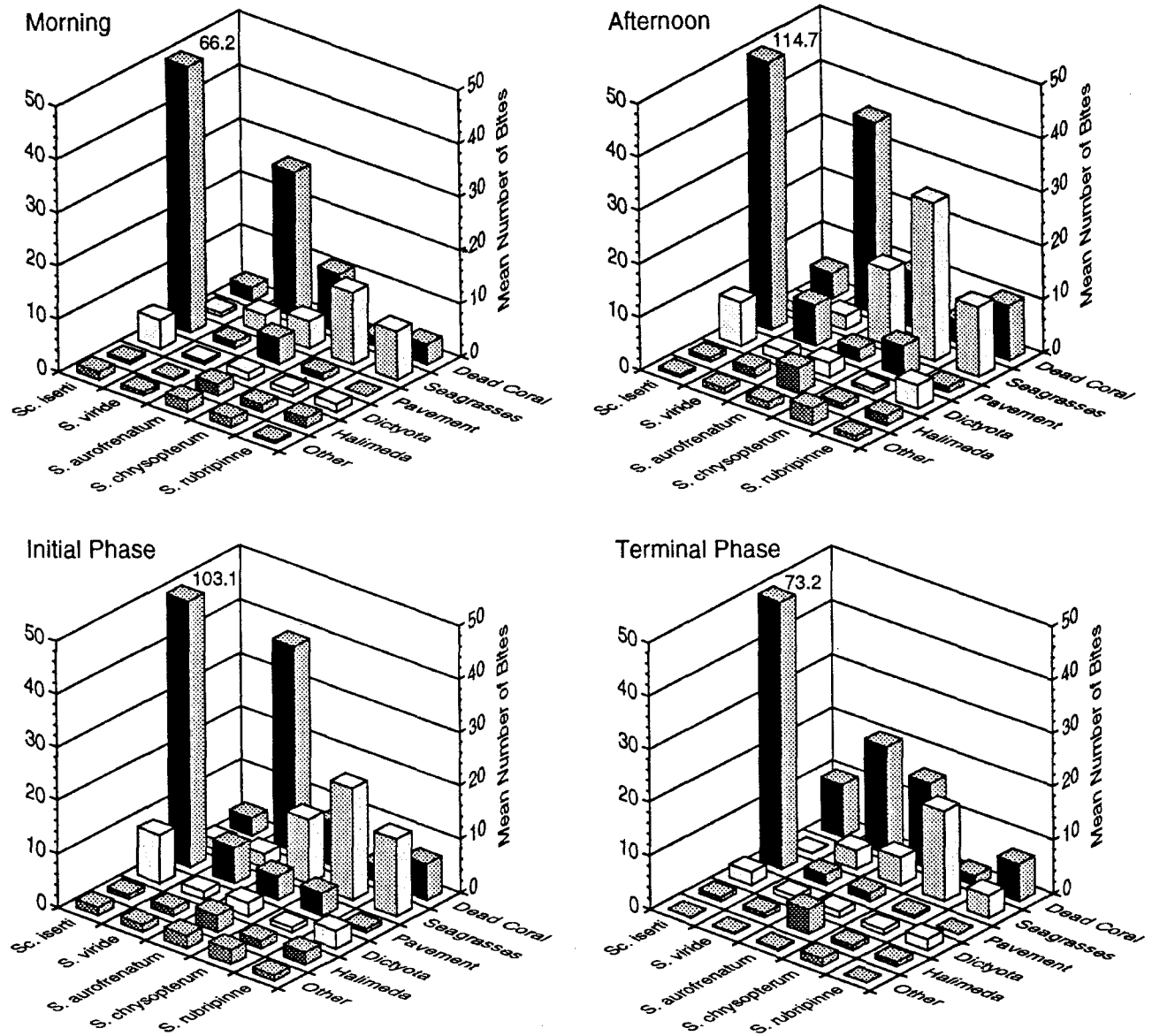


Fig. 3 *Scarus iserti* and *Sparisoma* spp. Mean number of bites of six food types taken by five species of parrotfishes during 5-min observation periods mornings and afternoons on 17 patch reefs (upper diagrams). Mean number of bites of food types taken by initial and terminal phase parrotfishes during 5-min observation periods on patch reefs (lower diagrams). See Fig. 1 for numbers of parrotfishes censused

Halimeda spp. and *Dictyota* spp. (which also grew on dead coral), and live coral. In addition, a small amount of coral pavement extended from the halo onto lower slopes of reefs.

Spatial patterns of resource use

Each of the five species of parrotfish had a unique pattern of distribution among zones despite overlap in habitat use (Fig. 1; Table 2). All parrotfish species oc-

curred in halos and on lower and upper slopes of reefs, but the extent to which zones were used by each species differed. Seagrass beds and reef crests were used less often than the other three zones by most parrotfishes.

Three species of parrotfishes primarily occurred on reef slopes and in halos. *Scarus iserti* was most abundant on lower reef slopes but also was common in halos (Fig. 1). *Sparisoma viride* was most abundant on upper reef slopes, and *S. aurofrenatum* was most common in halos and on lower slopes. *S. chrysopteron* primarily occurred in seagrass beds and halos but also was common on lower slopes. *S. rubripinne* is the only parrotfish that was common in all five zones, but it was present in lower abundance. Thus despite overlapping distributions, highly significant differences in habitat use by parrotfishes were evident.

Highly significant ontogenetic shifts in habitat use were evident for four species (Fig. 4; Table 4). Juvenile fishes at least 2-cm long primarily occurred around

Table 3 *Scarus iserti* and *Sparisoma* spp. Four-way Scheirer-Ray-Hare tests of number of bites of six foods (*Food*) taken by small, medium and large (*Size*) and initial and terminal phase (*Phase*) parrotfishes during mornings and afternoons (*Time*) on 17 patch reefs. *ns* indicates $p > 0.05$. See Table 1 for numbers of parrotfishes censused

Species Source	<i>df</i>	SS	H	<i>p</i>
<i>Sc. iserti</i>				
Food	5	4974261	90.8413	<0.001
Size	2	2435	0.0445	ns
Phase	1	54	0.0010	ns
Time	1	24	0.0004	ns
Error	206	6796132		
<i>S. viride</i>				
Food	5	13415173	115.6547	<0.001
Size	2	2048766	14.6990	<0.050
Phase	1	147441	1.0578	ns
Time	1	216947	1.5565	ns
Error	206	20632928		
<i>S. aurofrenatum</i>				
Food	5	2527456	46.7970	<0.001
Size	2	225742	4.1797	ns
Phase	1	1701	0.0315	ns
Time	1	69600	1.2887	ns
Error	206	10407688		
<i>S. chrysopterum</i>				
Food	5	3359736	61.8385	<0.001
Size	2	541914	6.6096	<0.050
Phase	1	46681	0.5694	ns
Time	1	60	0.0007	ns
Size × Time	2	528054	6.4406	<0.050
Error	206	18592326		
<i>S. rubripinne</i>				
Food	5	6465529	46.1342	<0.001
Size	2	1471752	9.0753	<0.050
Phase	1	230	0.0014	ns
Time	1	831461	5.1270	<0.050
Error	206	23135740		

halos or lower reef slopes and moved into other zones as they grew. *Scarus iserti* moved from halos and lower slopes to lower and upper slopes as they matured. *Sparisoma viride* shifted from lower slopes to upper slopes, and *S. aurofrenatum* moved from halos and lower slopes to upper slopes. *S. chrysopterum* shifted from halos to seagrass beds as they developed. *S. rubripinne* typically moved from lower slopes to all zones, but the apparent ontogenetic shift in habitat use was not significant because few fishes occurred in transects.

The distributions of initial and terminal phase parrotfishes often differed (Fig. 5; Table 5) because terminal phase parrotfishes were associated with preferred spawning sites. Terminal phase *Scarus iserti* spawned on upper and lower slopes, but initial phase fish primarily occurred on lower slopes and in halos. *Sparisoma viride* and *S. aurofrenatum* spawned with females on upper reef slopes. However, most initial phase *S. aurofrenatum* occurred in halos and on lower slopes, whereas

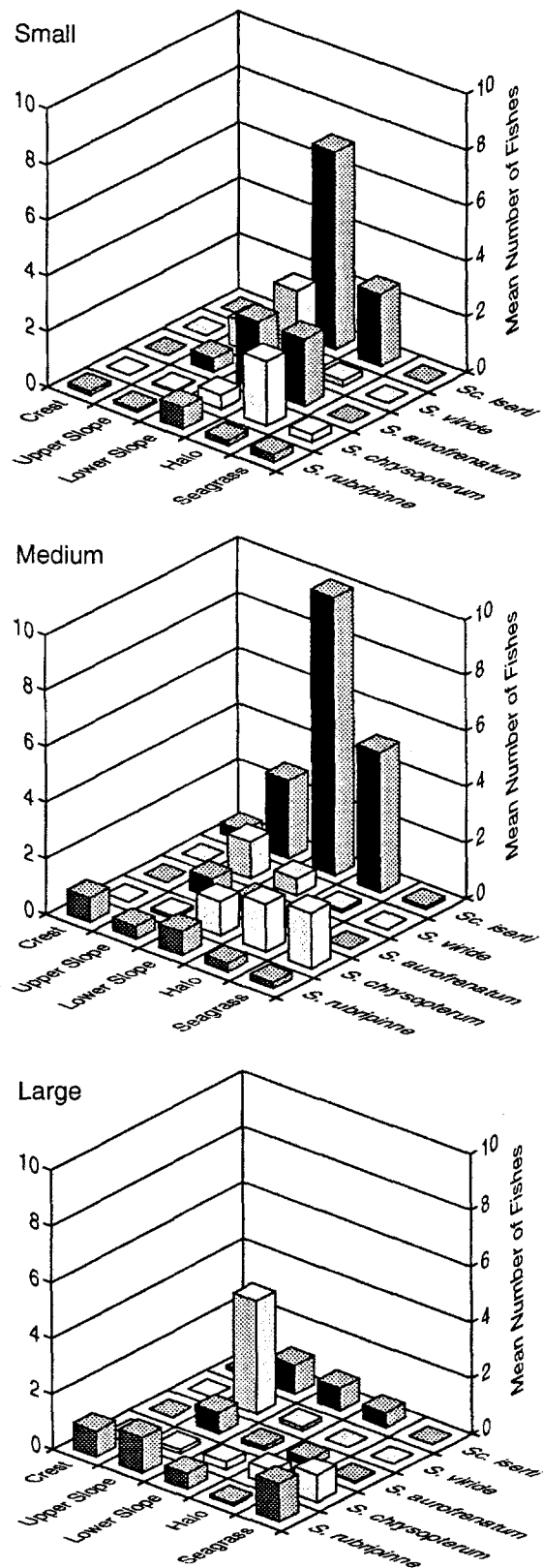


Fig. 4 *Scarus iserti* and *Sparisoma* spp. Mean number of three size classes of five parrotfishes per 20×3 m transect in five zones of two patch reefs. A total of 105 transects censused

Table 4 *Scarus iserti* and *Sparisoma* spp. Two-way Scheirer-Ray-Hare tests of abundances of three sizes (*Size*) of parrotfishes in five zones (*Zone*) on two patch reefs. A total of 105 transects censused. *ns* indicates $p > 0.05$

Species Source	df	SS	H	p
<i>Sc. iserti</i>				
Zone	4	8066631	35.115	<0.001
Size	2	5068135	22.062	<0.001
Zone × Size	8	5221037	22.728	<0.010
Error	300	53776007		
<i>S. viride</i>				
Zone	4	14327828	73.973	<0.001
Size	2	1372205	7.085	<0.050
Zone × Size	8	5975853	30.853	<0.001
Error	300	39143040		
<i>S. aurofrenatum</i>				
Zone	4	3241888	16.385	<0.001
Size	2	1750490	8.847	<0.050
Zone × Size	8	4025605	20.346	<0.050
Error	300	53107985		
<i>S. chrysopteron</i>				
Zone	4	4067150	21.092	<0.001
Size	2	638538	3.311	ns
Zone × Size	8	3207695	16.635	<0.050
Error	300	52635627		
<i>S. rubripinne</i>				
Zone	4	6293012	33.756	<0.001
Size	2	583315	3.129	ns
Zone × Size	8	1837335	9.855	ns
Error	300	49824618		

initial phase *S. viride* co-occurred with terminal phase fish. *S. chrysopteron* typically spawned over grassbeds where adults were most abundant, and initial phase fish occurred mostly in halos and secondarily in seagrass beds and on lower slopes. Initial and terminal phase *S. rubripinne* frequented all zones; however, most terminal phase fishes occurred on upper slopes, except during afternoons, when they swam off reefs to spawn over seagrass beds.

Temporal patterns of resource use

Food and habitat use generally did not change significantly during the day (Figs. 3, 5; Tables 2, 3). Although parrotfishes tended to eat more in the afternoon than in the morning, temporal changes in the composition of diets were not found for any species (Fig. 3; Table 3).

Behavioral interactions

Only four competitive, nonsexual interactions between parrotfishes were seen during the hundreds of hours that they were observed. Three of the four encounters involved *Sparisoma viride*, and the other occurred be-

tween *Scarus iserti* and *S. coeruleus*. In these cases, fishes engaged in erect fin posturing, color changes, and chasing. Parrotfishes also were observed acting aggressively toward nonscarids on two occasions, when *S. aurofrenatum* pursued black-ear wrasses (*Halichoeres poeyi*), apparently to steal food.

Discussion

Parrotfishes showed significant differences in resource use with respect to habitat, food and size, but not time. Parrotfishes that used similar spatial resources used different food resources. Adult *Scarus iserti*, *Sparisoma viride* and *S. aurofrenatum* frequented upper reef slopes but ate different foods (Table 6). *Sc. iserti* scraped microalgae from pavement, *S. viride* took bites from dead coral and *S. aurofrenatum* ate a wide variety of foods, including seagrasses, various macroalgae and microalgae growing from dead coral and pavement, crabs, urchins and sponges. Adult *S. chrysopteron* foraged on seagrasses in seagrass beds, and *S. rubripinne* ranged over all five zones taking bites from dead coral, seagrasses and macroalgae. Thus, each species had a unique pattern of resource use, although none of the parrotfishes exclusively used a particular habitat or food. This type of resource use may be common among reef fishes, many of which do not show obvious differences in resource use (Sale and Dybdahl 1975; Clarke 1977; Sale 1977; Talbot et al. 1978; Ross 1986). However, whether or not reef fish assemblages showing this type of resource use are maintained by partitioning resources is equivocal. Although parrotfishes that used similar resources in one niche dimension used different resources in another dimension, as predicted by competition theory, the overlap in resource use is not consistent with competitive exclusion through niche separation.

Aggressive, nonsexual encounters among parrotfishes were rare, which suggests that competition among these species was minimal. Either competition may not be important in structuring this parrotfish assemblage, or the abundance of algae on patch reefs reduced competitive interactions among parrotfishes. The decimation of the herbivorous sea urchin (*Diadema antillarum*) by a waterborne disease throughout the Caribbean in 1983 (Lessios 1988a) led to measurable increases in the abundance of filamentous and frondose algae (Littler and Littler 1984; Hay and Taylor 1985). This increase in algal abundance has been correlated with increases in abundances of parrotfishes and other herbivorous reef fishes in the San Blas islands and elsewhere in the Caribbean (Hay and Taylor 1985; Carpenter 1990; Robertson 1991). Reduced urchin densities also corresponded to invasion of shallow reef habitats by herbivorous fishes that previously had been found deeper on reefs (Carpenter 1988; Morrison 1988),

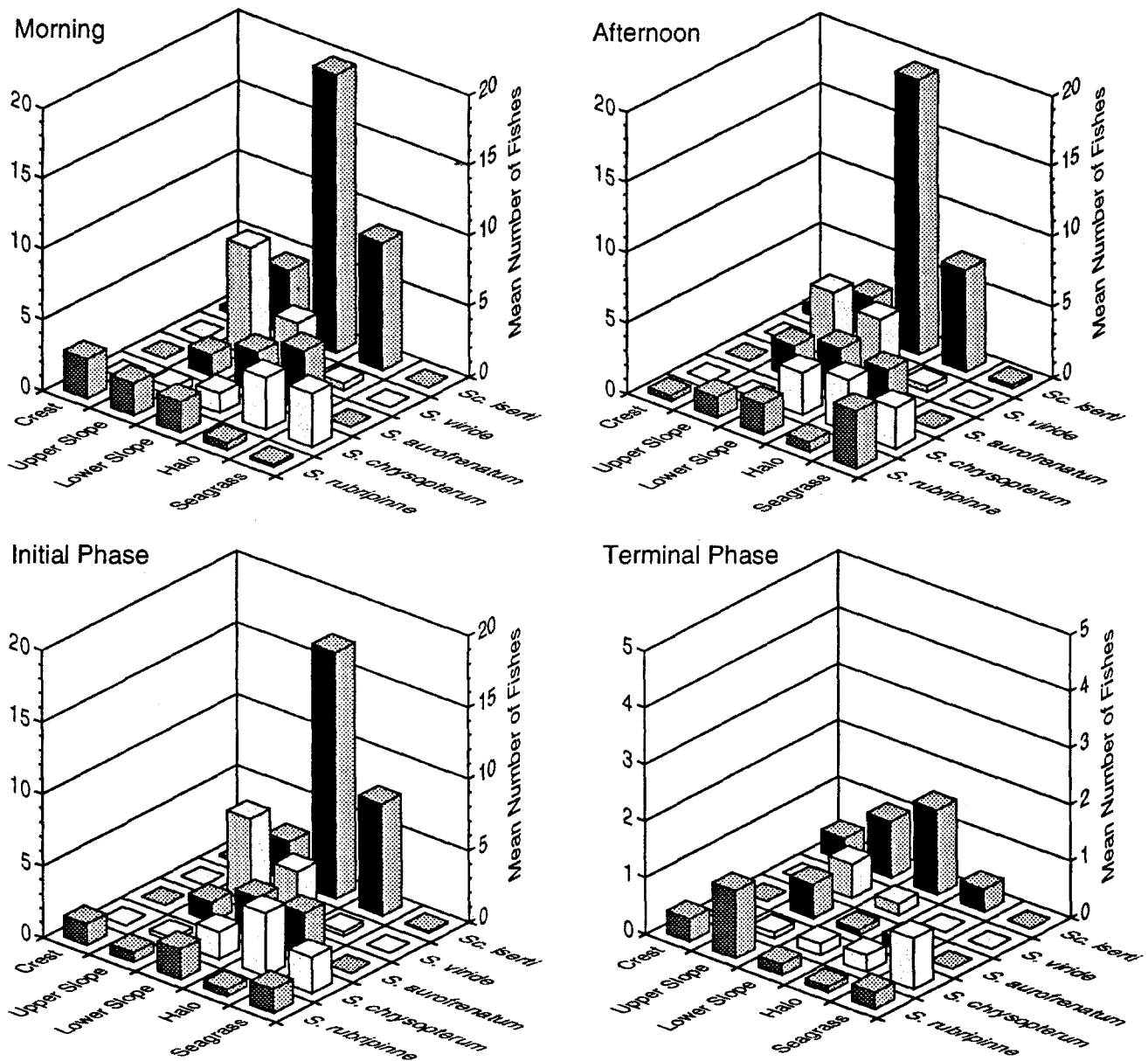


Fig. 5 *Scarus iserti* and *Sparisoma* spp. Mean number of five parrotfishes per 20×3 m transect in five zones of two patch reefs mornings and afternoons (upper diagrams). Abundances of initial and terminal phase parrotfishes in the five zones (lower diagrams). A total of 105 transects censused

suggesting that grazing by urchins also may affect habitat use and foraging behavior of parrotfishes. Despite two to three-fold increases in the numbers of parrotfishes and other herbivorous fishes, algae continued to increase, indicating that increased grazing by parrotfishes does not compensate for the decline of urchins (Carpenter 1990; Robertson 1991). When this study was conducted at San Blas in 1987, *D. antillarum* populations were still $<10\%$ of previous mean densities (3.5 m^{-2}) (Lessios et al. 1988b; Robertson 1991). As urchin populations continue to rebound and algae becomes less abundant on patch reefs in the San Blas Archipel-

ago, aggressive nonsexual interactions among parrotfishes may increase, population sizes may diminish, and habitat use and foraging behaviors may be expected to change if competition is important in structuring this assemblage of parrotfishes.

The abundance of algae raises another point concerning the foraging ecology of parrotfishes. *Halimeda* spp., *Dictyota* spp. and *Udotea* spp. produce secondary compounds that deter herbivory by reef fishes (Hay 1991). Although none of these macroalgae was a primary component of the diet of any of the five species of parrotfishes, they comprised a considerable portion of the diet of *Sparisoma rubripinne* and *S. aurofrenatum*, and commonly were eaten by the other three species. Therefore, secondary compounds of macroalgae may not strongly deter herbivory by these parrotfishes because they were commonly eaten despite the higher abundances of algal turf and seagrasses.

Schoener (1974) suggested that habitat dimensions are more important than food dimensions, which in turn are more important than temporal dimensions of resources for niche separation. However, coral reef fishes, temperate reef fishes and mobile marine inver-

tebrates apparently partition food resources, and space and time are of secondary and tertiary importance, respectively (Branch 1984; Ross 1986). In the present study, habitat use and diet were interrelated and could not be ranked. Although resources were not partitioned temporally, feeding rates of parrotfishes tended to increase in the afternoon. This may have resulted from high levels of photosynthate in productive turf and seagrass communities at this time (Polunin and Klumpp 1989).

Table 5 *Scarus iserti* and *Sparisoma* spp. Two-way Scheirer-Ray-Hare tests of abundances of initial and terminal phase (Phase) parrotfishes in five zones (Zone) on two patch reefs. A total of 105 transects were censused

Species Source	df	SS	H	p
<i>Sc. iserti</i>				
Zone	4	4830076	51.416	<0.001
Phase	1	895895	9.537	<0.001
Zone × Phase	4	1707009	18.171	<0.001
Error	200	12200804		
<i>S. viride</i>				
Zone	4	1641556	66.685	<0.001
Phase	1	5798320	18.685	<0.001
Zone × Phase	4	2042358	23.489	<0.001
Error	200	8690398		
<i>S. aurofrenatum</i>				
Zone	4	1831905	21.472	<0.001
Phase	1	1668538	19.557	<0.001
Zone × Phase	4	1785010	20.922	<0.001
Error	200	12545973		
<i>S. chrysopteron</i>				
Zone	4	1803130	23.094	<0.001
Phase	1	1218547	15.607	<0.001
Zone × Phase	4	2171603	27.813	<0.001
Error	200	11125294		
<i>S. rubripinne</i>				
Zone	4	1877761	21.638	<0.001
Phase	1	483546	5.572	<0.050
Zone × Phase	4	804761	9.274	0.050
Error	200	14970831		

Although typically overlooked in resource use studies, ontogenetic shifts in habitat and diet were observed for four parrotfish species. Adults of these species often occurred on the upper slope and in seagrass beds, whereas juvenile fishes primarily occurred in halos and on lower reef slopes where they apparently exploited diatoms and small protein-rich invertebrates living in algal mats (see Bellwood 1988; Bruggemann et al. 1994) and epiphytes on macroalgae and seagrasses. Ontogenetic changes (nonsignificant) in diet likely resulted from a mechanical limitation in jaw structure. Small parrotfishes (2 to 4 cm) could not bite through most macroalgae, seagrasses or coral exoskeletons. Ontogenetic shifts in the diets of *Scarus iserti* did not occur because these small parrotfishes consumed mostly diatoms and filamentous algae throughout their lifetimes.

In conclusion, the five sympatric species of parrotfishes shared resources, and few aggressive nonsexual encounters occurred in the vicinity of patch reefs. However, significant differences in space and food use were observed. Whether or not similar patterns of resource use by these species occur on barrier reefs remains to be examined. The observed interspecific differences in resource use may occur if this assemblage of parrotfishes was structured by competition, predation, larval recruitment or chance. Additional surveys and complementary

Table 6 *Scarus iserti* and *Sparisoma* spp. Summary of habitat and food use by five sympatric parrotfishes (small and large) in five zones (reef crest, upper reef slope, lower reef slope, halo and surrounding seagrass) of Caribbean patch reefs. Asterisks indicate zones where fishes predominated

Species	Habitat			Food	
	Overall	Small	Large	Small	Large
<i>Sc. iserti</i>	Upper Lower* Halo*	Lower Halo	Upper Lower	Pavement	Pavement
<i>S. viride</i>	Upper* Lower	Lower	Upper	Pavement Dead Coral	Dead Coral
<i>S. aurofrenatum</i>	Upper Lower* Halo*	Lower Halo	Upper	Pavement Dead Coral Seagrasses	Dead Coral Seagrasses <i>Halimeda</i> spp.
<i>S. chrysopteron</i>	Lower Halo* Seagrass*	Halo	Seagrass	Pavement	Seagrasses
<i>S. rubripinne</i>	Crest Upper Lower Halo Seagrass	Lower	Crest Upper Lower Halo Seagrass	Pavement Seagrasses Dead Coral	Seagrasses Dead Coral

experimental approaches will be needed to elucidate the relative importance of different structuring mechanisms.

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References

- Alley TR (1982) Competition theory, evolution and the concept of ecological niche. *Acta biotheor* 31: 165–179
- Barlow GW (1975) On the sociobiology of four Puerto Rican parrotfishes (Scaridae). *Mar Biol* 33: 281–293
- Bellwood DR (1988) Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *J Fish Biol* 33: 213–219
- Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Envir Biol Fish* 28: 189–214
- Branch GM (1984) Competition between marine organisms: ecological and evolutionary implications. *Oceanogr mar Biol A Rev* 22: 429–593
- Brock RE (1954) A method of estimating reef fish populations. *J Wildl Mgmt* 18: 297–308
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bull mar Sci* 32: 269–276
- Bruggemann JH, van Oppen MJH, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Mar Ecol Prog Ser* 106: 41–55
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56: 345–363
- Carpenter RC (1988) Mass mortality of a Caribbean sea urchin: immediate effects on community metabolism and other herbivores. *Proc natn Acad Sci USA* 85: 511–514
- Carpenter RC (1990) Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. *Mar Biol* 104: 79–86
- Choat JH (1969) Studies on the biology of labroid fishes (Labridae and Scaridae) at Heron Island, Great Barrier Reef. PhD dissertation, University of Queensland, Australia
- Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 120–155
- Choat JH, Robertson DR (1975) Protogynous hermaphroditism in fishes of the family Scaridae. In: Reinboth R (ed) *Intersexuality in the animal kingdom*. Springer-Verlag, Heidelberg
- Clarke RD (1977) Habitat distribution and species diversity of chaetodontid and pomacentrid fishes near Bimini, Bahamas. *Mar Biol* 40: 277–289
- Colin PL (1978) Daily and summer/winter variation in mass spawning of the striped parrotfish *Scarus croicensus*. *Fish Bull US* 76: 117–124
- Connell JH (1980) Diversity and coevolution of competitors, or the ghost of competition past. *Oikos* 35: 131–138
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122: 661–696
- Ebeling AW, Hixon MA (1991) Tropical and temperate reef fishes: comparison of community structures. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 509–563
- Frydl P, Stearn CW (1978) Rate of bioerosion by parrotfish in Barbados reef environments. *J sedim Petrol* 48: 1149–1158
- Hay ME (1991) Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, New York, pp 96–119
- Hay ME, Taylor PR (1985) Competition between herbivorous fishes and urchins on Caribbean reefs. *Oecologia* 65: 591–598
- Hiatt RW, Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol Monogr* 30: 65–127
- Johannes RE (1981) *Words of the lagoon: fishing and marine lore in the Palau District of Micronesia*. University of California, Berkeley
- Lessios HA (1988a) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *A Rev Ecol Syst* 19: 371–393
- Lessios HA (1988b) Population dynamics of *Diadema antillarum* (Echinodermata: Echinoidea) following mass mortality in Panama. *Mar Biol* 99: 515–526
- Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. *J exp mar Biol Ecol* 87: 215–228
- Littler MM, Littler DS (1984) Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky intertidal system. *J exp mar Biol Ecol* 74: 13–34
- Littler MM, Taylor PR, Littler DS (1989) Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80: 331–340
- Lobel PS, Ogden JC (1981) Foraging by the herbivorous parrotfish *Sparisoma radians*. *Mar Biol* 64: 173–184
- Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* 69: 1367–1382
- Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *Diadema antillarum philippi*: formation of halos around West Indian patch reefs. *Science*, NY 182: 715–717
- Ogden JC, Buckman DS (1973) Movements, foraging groups, and diurnal migration of the striped parrotfish, *Scarus croicensus* Block (Scaridae). *Ecology* 54: 589–596
- Polunin NVC, Klumpp DW (1989) Ecological correlates of foraging periodicity in herbivorous reef fishes of the Coral Sea. *J exp mar Biol Ecol* 126: 1–20
- Randall JE (1965) Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. *Ecology* 46: 255–260
- Randall JE (1968) Caribbean reef fishes. TFH, Hong Kong
- Robblee MB, Zieman JC (1984) Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bull mar Sci* 34: 335–345
- Robertson DR (1987) Responses of two coral reef toadfishes (Batrachoididae) to the demise of their primary prey, the sea urchin *Diadema antillarum*. *Copeia* 1987: 637–642
- Robertson DR (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Mar Biol* 111: 437–444
- Robertson DR, Warner RR (1978) Sexual patterns of the labroid fishes in the western Caribbean. II. The parrotfishes (Scaridae). *Smithson Contr Zool* 255: 1–26
- Roughgarden J (1974) Species packing and the competition function with illustrations from coral reef fish. *Theor Popul Biol* 5: 163–186
- Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 1986: 352–388
- Russ GR (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. II. Patterns of zonation of mid-shelf and outershelf reefs. *Mar Ecol Prog Ser* 20: 35–44
- Sale PF (1977) Maintenance of high diversity in coral reef fish communities. *Am Nat* 111: 337–359

- Sale PF (1980) The ecology of fishes on coral reefs. *Oceanogr mar Biol A Rev* 18: 367–421
- Sale PF (1991) Reef fish communities: open nonequilibrium systems. In: Sale PF (ed) *The ecology of fishes on coral reefs*, Academic Press, New York
- Sale PF, Dybdahl R (1975) Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* 56: 1343–1355
- Schoener TW (1974) Resource partitioning in ecological communities. *Science*, NY 185: 27–39
- Schoener TW (1982) The controversy over interspecific competition. *Am Scient* 70: 586–595
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman, New York
- Talbot FH, Russell BC, Anderson GRV (1978) Coral reef fish communities: unstable, high-diversity systems? *Ecol Monogr* 48: 425–440
- Weinstein MP, Heck KL Jr (1979) Ichthyofauna of seagrass meadows along the Caribbean coast of Panama and in the Gulf of Mexico: composition, structure and community ecology. *Mar Biol* 50: 97–107
- Wiens JA (1977) On competition and variable environments. *Am Scient* 65: 590–597
- Winn HE, Bardach JE (1959) Differential food selection by moray eels and a possible role of the mucous envelope of parrotfishes in reduction of predation. *Ecology* 40: 296–298