

Comparative resource use by juvenile parrotfishes in the Florida Keys

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ABSTRACT: Many parrotfishes (Scaridae) co-occur in mixed-species aggregations as juveniles, but diverge in resource use and social structure as adults. Focal observations of 3 juvenile parrotfishes (*Scarus coeruleus*, *Sparisoma aurofrenatum*, *Sparisoma viride*) were conducted on inshore patch reefs in the Florida Keys to examine feeding rates, food type, habitat use, and aggressive interactions. All species overlapped extensively in their use of space and food. Home ranges physically overlapped, and the proportion of microhabitats present within home ranges was similar for all species. Home range size increased with body size for *S. coeruleus* and *S. aurofrenatum*. Diets of all species were extremely similar. All fed selectively from the available foods and fed primarily (>50% total bites) on the calcareous macroalga *Halimeda opuntia* despite its potentially high energetic costs of procurement, low food value, and predicted avoidance. Focal individuals interacted aggressively with conspecifics, other juvenile parrotfishes, damselfishes, and occasionally grunts and wrasses. *S. aurofrenatum* and *S. viride* were most aggressive toward conspecifics. Aggressive interactions with adult parrotfishes were rare. Both *Sparisoma* spp. were chased more often by damselfishes than any other species. These findings support the growing body of evidence that herbivorous fish do not feed randomly from all potential foods. The aggressive interactions observed among juvenile parrotfishes are likely affecting their use of resources and may act as a precursor to subsequent territoriality as adults.

KEY WORDS: Foraging behavior · Habitat use · Aggression · Scaridae · Coral-reef fish · Herbivory

INTRODUCTION

The coexistence of so many ecologically similar, closely related fishes on coral reefs continues to be a topic of considerable debate in marine ecology. Detailed observation of resource use among these fishes is an essential precursor to designing the manipulative experiments necessary to quantify the relative importance of the processes that may structure reef fish communities such as competition, predation, disturbance, and recruitment (reviewed by Ebeling & Hixon 1991). Reef fishes commonly undergo ontogenetic changes in resource use including diet (Bellwood 1988, Harmelin-Vivien 1989) and habitat use (Shulman

& Ogden 1987, Harmelin-Vivien 1989, Lirman 1994, Green 1996). However, there are currently no quantitative data available on how food and space requirements change during the life history of any reef fish (Robertson 1998). The intention of this study was to examine resource use in 3 species of juvenile parrotfishes (Scaridae) that co-occur in mixed-species aggregations as juveniles, but diverge significantly in resource use and social structure as adults.

Parrotfishes are a major component of the diverse assemblage of herbivorous fishes on coral reefs (reviewed by Hixon 1997) and possess the unique ability to remove all functional groups of algae (Steneck & Dethier 1994). Although often considered to be a homogeneous group of grazing herbivores (Ogden 1976, Hay et al. 1983, Lewis 1985, 1986, Carpenter 1990), recent studies have shown considerable diversity among adult parrotfishes in terms of morphology, ecology, behavior, and habitat utilization (Bellwood &

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Choat 1990, Bellwood 1994, Bruggemann et al. 1994a). However, data on the resource requirements of juveniles are conspicuously lacking, presumably because of difficulties in identification of individual species from congeners (Bellwood 1988).

Despite the well-documented inter- and intraspecific variation in social and mating patterns among adult parrotfishes at a range of spatial scales (Ogden & Buckman 1973, Dubin 1981, van Rooij et al. 1996b), the potential for social interactions among juvenile parrotfishes remains unexplored. Although sexually immature, and therefore lacking the complex mating strategies of adults, juveniles are likely to be involved in aggressive interactions with potential food competitors such as confamilials or territorial damselfish (Pomacentridae). Active territorial defense by pomacentrids suggests that they compete with juvenile parrotfishes for access to food within algal mats defended by the damselfish (Low 1971, Ebersole 1977, Itzkowitz 1990). However, all previous studies of parrotfish social interactions have reported zero or low frequencies of aggressive interactions involving juveniles (Dubin 1981, McAfee & Morgan 1996, van Rooij et al. 1996a).

Aggregations of juvenile parrotfishes are common on inshore patch reefs in the Florida Keys and typically contain *Scarus iserti*, *Sparisoma aurofrenatum*, and *Sparisoma viride*, and occasionally *Scarus coeruleus* and *Sparisoma atomarium*. The blue parrotfish *S. coeruleus* is among the least studied of the 12 common Caribbean scarids. Adults of this species are thought to be specialized sand-suckers, foraging directly from the sandy halos that surround patch reefs (Longley & Hildebrand 1941). When mature, individuals form large roving groups with home ranges encompassing numerous patch reefs and may reach up to 120 cm in length (Böhlke & Chaplin 1993). *S. aurofrenatum*, the redband parrotfish, is abundant in the Florida Keys, where terminal phase (TP) males are permanently territorial and defend a harem of females (Muñoz 1996). Its adult diet consists primarily of benthic turf algae in the Virgin Islands (Randall 1967) and mainly the calcareous macroalga *Halimeda opuntia* in the Florida Keys (Muñoz 1996). The stoplight parrotfish *S. viride* has a variable social structure throughout its geographic range, and all phases are common in the Florida Keys. Its feeding behavior is well-studied in Bonaire, where all phases fed primarily on endolithic algae and associated algal turfs (Bruggemann et al. 1994a,b, van Rooij et al. 1996a,c).

The goal of this research was to examine resource use and related social behaviors in juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* on inshore patch reefs in the Florida Keys, specifically addressing the following questions: (1) What are the differences in foraging behavior and habitat use

among the 3 species? (2) Are these fishes feeding selectively from among the available food items, and, if so, are there interspecific differences in selectivity? (3) Is there evidence of aggressive interactions among these juvenile parrotfishes, and are these species the recipients of aggression from herbivores more frequently than non-herbivores?

MATERIALS AND METHODS

Study sites. This study was conducted on the inshore patch reefs of Coral Gardens in Hawk Channel adjacent to Lower Matecumbe Key in the upper-middle Florida Keys, USA (80° 44' W, 24° 51' N) from April to November 1996. The average depth at this site is approximately 5 m, and the numerous patch reefs range in size from 10 to 2000 m². The study area consisted of 3 moderate-sized (~1000 m²) adjacent patch reefs surrounded by halos of sand and *Thalassia testudinum* seagrass beds. Dominant scleractinian corals on these reefs include *Diploria* spp., *Montastrea annularis*, *M. cavernosa*, and *Siderastrea* spp., and the dominant macroalga is *Halimeda opuntia*.

Supplemental observations of juvenile *Sparisoma viride* were made on the patch reefs of Little Africa near Loggerhead Key in the Dry Tortugas National Park (82° 56' W, 24° 38' N) in October of 1996. This area is shallower than Coral Gardens, with a mean depth of approximately 2.5 m. Thickets of dead *Acropora cervicornis* are dominant at this site, and live coral cover (mostly *Montastrea annularis* and *Porites asteroides*) is minimal. *Halimeda opuntia* is the dominant macroalga. Scarids were less abundant at this site; only 3 of the 5 species of juveniles common at Coral Gardens were present (*Scarus iserti*, *Sparisoma aurofrenatum*, *S. viride*).

Field observations. All behavioral observations were conducted using SCUBA between 10:00 and 16:00 h, and were made only when horizontal visibility was at least 3 m. Twelve focal individuals each of *Sparisoma aurofrenatum* and *Sparisoma viride*, and 7 individuals of *Scarus coeruleus* were observed. (*S. coeruleus* was less abundant at Coral Gardens than the other 2 species.) The identities of focal individuals were determined by relative size and characteristic markings. Time of day was recorded for all observations, and total length (TL) of each fish was determined to the nearest 5 mm. Lengths of focal fishes were repeatedly verified by comparing length estimates to a variety of background landmarks. Size ranges of focal individuals were similar for all 3 species and ranged from 40 to 100 mm for *S. aurofrenatum* (mean TL \pm SD, 65 \pm 17), 40 to 90 mm for *S. viride* (60 \pm 15), and 40 to 95 mm for *S. coeruleus* (59 \pm 20).

Foraging and social behavior. After a 5 min habituation period, focal individuals were followed at a distance of ~1 m for 15 min to record all occurrences of feeding. Each bite, the substrate from which it was taken, and the number of bites per foraging bout were recorded. A foraging bout was defined as a series of bites taken from the same location where the only observable movement of the fish is that required to reapply the jaws to the substrate. Substrate categories included 2 upright foliose macroalgae (>15 mm frond height), *Halimeda opuntia* and *Dictyota* spp.; large algal turfs (≥ 10 mm frond height) referred to as 'turf'; sedimented algal turf that consisted of sedimented sparse algal turfs (<10 mm frond height); turtle grass *Thalassia testudinum*; and sand. Both large and sparse algal turfs were multispecific assemblages containing crustose, filamentous, and unicellular algae of all major divisions. An 'other' category encompassed all substrates from which few bites were taken, including crustose coralline algae, sponges, and coprophagy.

During each 15 min focal observation period, we also recorded the occurrence of all social interactions involving the focal individual. The frequency per minute of all overt aggressive and agonistic behaviors (including chases, mouth to mouth displays, dorsal fin raising, and caudal or pelvic fin flaring) was tallied on slates. Participants in these encounters were identified to species, and the color phase was recorded for all scarids.

Habitat use. After completing collection of feeding and social interaction data, we continued to follow the focal individual to determine the size of its home range. Home ranges for these fishes were defined as the area through which the fish ranged habitually, and were measured for a period of at least 60 min, or until no further increase in area occurred. We dropped weights with attached fluorescent surveyor's tape at every point where the fish changed direction, and weights were repositioned as necessary until the individual no longer strayed beyond the boundary created by the markers, suggesting that the entire home range of the individual had been mapped. Each side of the resultant polygon was then measured to the nearest centimeter with a tape measure, and a compass heading determined for each edge. We redrew each home range using Designer Version 3.1 (Micrografix 1992) and measured its area in square meters using Sigma-Scan/Image Version 1.2 (Jandel Scientific 1994). Home range data were collected for all 7 *Scarus coeruleus* focal individuals, and 10 each of *Sparisoma aurofrenatum* and *Sparisoma viride*.

We determined the percentage cover of microhabitats (living coral; rubble; gorgonians; sponges; sand; macroalgae *Halimeda opuntia* and *Dictyota* spp.; large algal turfs; sparse sedimented algal turfs; and seagrass *Thalassia testudinum*) in each home range using mul-

tiple chain-link transects that were 2.0 m and 90 links in length (Porter 1972). Five to eight replicate transects were taken per home range, and relative abundances of microhabitats within each home range were determined from the mean of these replicates. Sample sizes were determined using a performance curve of the standard deviation of the percentage cover of each substrate type as a function of sample size, and varied to accommodate differences in home range sizes among individuals (Brower et al. 1989). Transect location was randomized within home ranges, and the number of links covering each microhabitat type was used to estimate its relative cover within that home range.

Statistical analyses. All analyses were performed with the SigmaStat Version 2.0 statistical software package (Jandel Scientific 1995). Data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variances using the Levene median test at $\alpha = 0.05$ before performing any parametric statistics. Data that did not meet the assumptions for parametric statistics after transformation were analyzed by nonparametric methods. Mann-Whitney tests were used to compare total bites, bites to particular substrata, home range size, and microhabitats available within home ranges for *Sparisoma viride* from the Dry Tortugas with those from Coral Gardens. Because none of these variables was significantly different between sites, data for *S. viride* from the 2 locations were pooled in all subsequent analyses.

One-way ANOVA was used in lieu of 2-way (1 repeated factor) ANOVA for among- and within-species comparisons of feeding and aggression variables because of violations of parametric assumptions. The only 2-way nonparametric ANOVA (Scheirer-Ray-Hare extension of the Kruskal-Wallis test) does not allow for a repeated measures factor, and Zar (1996) cautions strongly against its use. To ensure that there was no significant interaction between factors, 2-way (1 repeated factor) ANOVA was used to test log-transformed data that were normal, but heteroscedastic. Lacking interaction, within-species data were analyzed by separate 1-way nonparametric repeated measures ANOVA (Friedman's χ^2) and among-species comparisons were conducted using a parametric 1-way ANOVA or Kruskal-Wallis 1-way ANOVA (KW) on ranks when appropriate. These methods were employed for comparisons of the number of bites on each food item, microhabitat data, the relative frequency of feeding, intra-, and interspecific aggression, and focal individuals as aggressors or recipients of aggression. Kruskal-Wallis 1-way ANOVA was also used to compare home range size and rugosity among species. Student-Neuman-Keuls' (SNK) test or Dunn's multiple comparisons (DMC) tests (for cases of unequal sample

sizes) were used for multiple comparisons of all significant ANOVA effects ($p < 0.05$).

Linear least-squares regressions were used to examine the relationship between total bites or home range size (log-transformed) and fish size (TL) within each species. A χ^2 test was used to compare the frequency distribution of foods available within home ranges ('expected') to those fed upon ('observed') to test the selectivity of feeding within each species. The frequency of foods available was determined from chain-transect data. Coral, gorgonians, and rubble were excluded from the 'expected' frequencies because no individuals were observed feeding from them.

RESULTS

General behavior

Aggregations of juvenile parrotfishes were common on the patch reefs of Coral Gardens and were numerically dominated by *Scarus iserti*, followed by fewer numbers of *Sparisoma aurofrenatum* and *Sparisoma viride*, and an occasional *Scarus coeruleus* or *Sparisoma atomarium*. These groups typically included 10 or fewer individuals and were highly fluid, with fish joining and leaving as often as every 30 s. Identifiable individuals were seen repeatedly at the same locations over several weeks, and therefore exhibited some degree of day-to-day site attachment. All 3 species spent most of their time feeding (>90%) and often swam around the edges of their home ranges, maintaining a swimming position of no more than 1 m above the reef. Occasionally entire groups or individuals would make short forays off the reefs into the seagrass beds, feed on *Thalassia testudinum*, and then return to the reef.

Habitat use

Home ranges of all 3 species of juveniles overlapped extensively (Fig. 1). Mean home range size was not significantly different among the 3 species (KW, $H_2 = 4.8$, $p = 0.09$). Home ranges of *Scarus coeruleus* tended to be the largest ($35.8 \pm 18.3 \text{ m}^2$, $n = 7$), followed by those of *Sparisoma aurofrenatum* ($23.6 \pm 26.0 \text{ m}^2$, $n = 10$), and *Sparisoma viride* ($17.6 \pm 13.0 \text{ m}^2$, $n = 10$). Within species, home range size increased with body size (TL), and this trend was significant for *S. coeruleus* and *S. aurofrenatum* (Fig. 2). For these species the relationship between body size and home range size

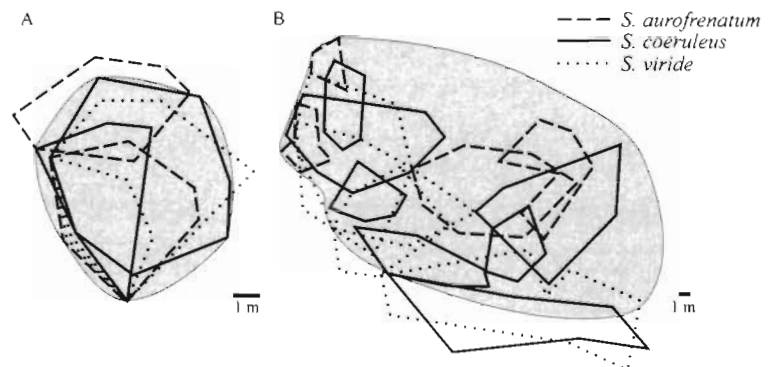


Fig. 1. Overlapping home ranges of individual juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* for all fishes observed on 2 patch reefs at Coral Gardens, Florida. Shaded areas indicate the extent of the patch reefs

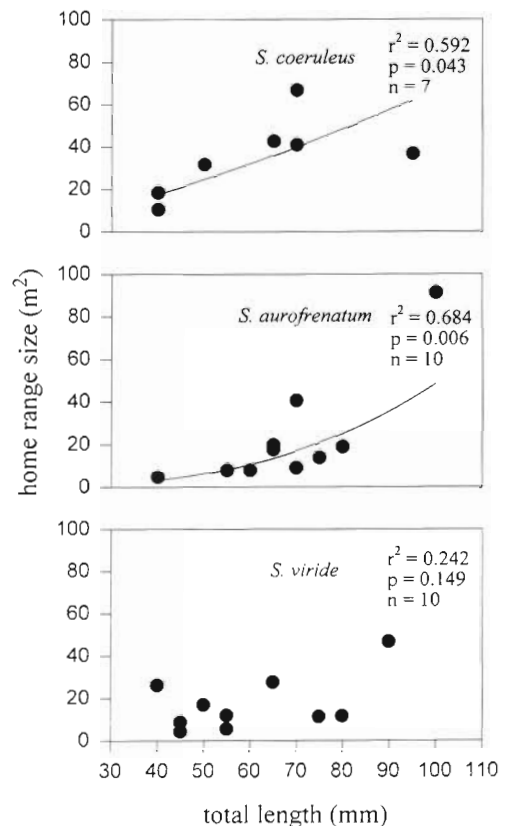


Fig. 2. Home range size (m^2) as a function of fish size (mm TL) for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*. For *S. coeruleus* and *S. aurofrenatum*, regression variables based on linear least-squares regression of log-transformed variables (*S. coeruleus*: $\log y = -1.044 + 1.435 \log x$; *S. aurofrenatum*: $\log y = -4.114 + 2.922 \log x$)

was best described by regression of log-transformed variables. Home range size did not increase significantly with body size in *Sparisoma viride*.

The relative percentage cover of microhabitats in the home ranges of each species was similar (Table 1). Home ranges of *Scarus coeruleus* contained similar amounts of *Halimeda opuntia*, sedimented algal turfs (SAT), hard coral, and sand. This was the only species that utilized substantial portions of the sandy halos that surround the patch reefs of Coral Gardens in its home ranges. Home ranges of *Sparisoma aurofrenatum* contained significantly more *H. opuntia* than any other microhabitat, followed by similar amounts of SAT and hard coral. Certain individuals of this species included portions of *Thalassia testudinum* beds in their home ranges. Home ranges of *Sparisoma viride* had similar cover of *H. opuntia* and SAT followed by hard coral cover. All individuals of this species limited their home ranges to portions of the patch reef itself. There were no differences among species in the percentage cover of any one microhabitat (ANOVA, $p > 0.05$).

Foraging

Total bites taken from all food types combined per 15 min observation period were not significantly different among the 3 species (ANOVA, $F_{2, 28} = 2.45$, $p = 0.11$), although the statistical power to detect differences was low, 0.27, implying that small sample size may have precluded rejection of the null hypothesis (Zar 1996). *Scarus coeruleus* took 116.0 ± 21.6 bites per 15 min (mean \pm SD, $n = 7$), *Sparisoma viride* took 103.1 ± 26.1 bites ($n = 12$), and *Sparisoma aurofrenatum* took 88.6 ± 29.5 bites ($n = 12$). The total number of bites per 15 min was not related to TL for any species (linear least-squares regression, $p > 0.05$). Therefore, feeding rate did not vary predictably over the size ranges observed.

Total bites taken from particular substrata were significantly different within each species (Fig. 3; Friedman's repeated measures ANOVA, *Scarus coeruleus*: $\chi^2_6 = 22.4$, $p = 0.001$; *Sparisoma aurofrenatum*: $\chi^2_6 = 6.0$, $p < 0.001$; *Sparisoma viride*: $\chi^2_6 = 62.4$, $p < 0.001$). All 3

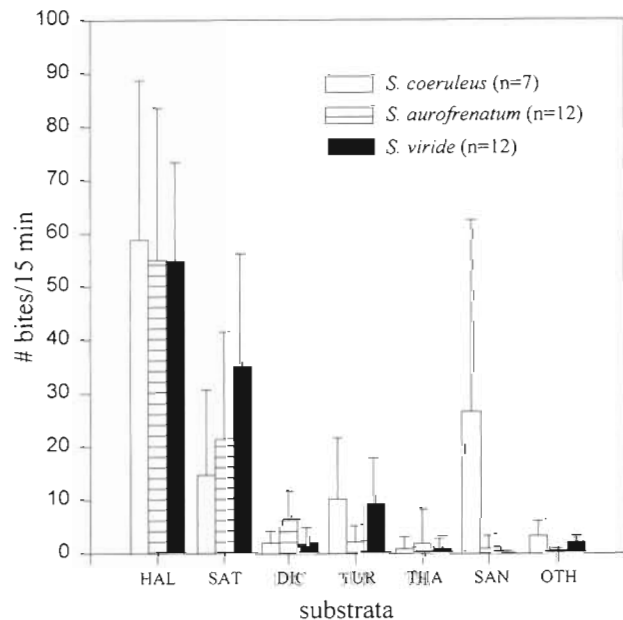


Fig. 3. Mean (\pm SD) number of bites per 15 min observation period on various substrata for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*. HAL: *Halimeda opuntia*; SAT: sedimented algal turf; DIC: *Dictyota* spp.; TUR: turf algae; THA: *Thalassia testudinum*; SAN: sand; OTH: other substrata including sponge, bare coralline algae, and coprophagy

species took significantly more bites from *Halimeda opuntia* than any other food type (SNK, $p < 0.05$). Bites from *H. opuntia* constituted at least half of all bites taken by each species (mean bites per 15 min \pm SD; *S. coeruleus*: 58.9 ± 31.9 , *S. aurofrenatum*: 55.0 ± 28.5 , *S. viride*: 54.7 ± 18.7). Visible bite scars remained on *H. opuntia* blades after feeding by these juveniles, indicating that they were feeding on the tissues of the macroalga itself rather than scraping only epiphytes. After *H. opuntia*, *S. coeruleus* fed equally from all substrata, with the exception of *Thalassia testudinum*, from which it took fewer bites than any other food. *S. aurofrenatum* took more bites from SAT than from *Dictyota* spp. followed by similar numbers of bites from

Table 1. Percent cover of microhabitats present in juvenile home ranges of each parrotfish species. χ^2 values from Friedman's nonparametric repeated measures ANOVA. Underlined means are not significantly different ($p > 0.05$, nonparametric Student-Neuman-Keuls). *** $p < 0.001$

| Species | Microhabitats | | | | | | | | | χ^2_7 |
|-------------------------------|-----------------------------------|-------------------------------|---------------|-------------|-------------------------|---------------|---------------------------------------|-----------------|-------|------------|
| | <i>Hali- meda opuntia</i> | Sed- imented algal turf | Hard coral | Sand | <i>Dictyota</i> spp. | Large turf | <i>Thalassia testudi- num</i> | Coral rubble | Other | |
| <i>Scarus coeruleus</i> | 29.1 | 25.3 | 14.4 | 22.6 | <u>1.2</u> | 3.0 | 2.1 | 0.0 | 2.3 | 35.72*** |
| <i>Sparisoma aurofrenatum</i> | 39.9 | <u>21.6</u> | 14.2 | <u>10.3</u> | 4.5 | 2.9 | 2.9 | 0.8 | 2.9 | 4.48*** |
| <i>Sparisoma viride</i> | <u>37.5</u> | <u>29.6</u> | 13.9 | 7.0 | 2.6 | 1.6 | 1.1 | 3.4 | 3.3 | 49.40*** |

Table 2. Relative abundances (%) of food types available in home ranges, and relative frequencies (%) of bites taken from each food type for each parrotfish species. The relative frequency of foods available was compared with the relative frequency of bites taken from each food type using χ^2

| Species | Food types | | | | | | | χ^2_6 | p |
|-------------------------------|-----------------------------------|-------------------------------|------|-------------------------|---------------|---|-------|------------|--------|
| | <i>Hali- meda opuntia</i> | Sed- imented algal turf | Sand | <i>Dictyota</i> spp. | Large turf | <i>Thalassia</i> <i>testudi- num</i> | Other | | |
| <i>Scarus coeruleus</i> | | | | | | | | | |
| Available | 34.1 | 29.7 | 26.5 | 1.4 | 3.5 | 2.5 | 2.3 | 27.40 | <0.001 |
| Eaten | 50.5 | 12.6 | 23.0 | 1.7 | 8.7 | 0.7 | 2.8 | | |
| <i>Sparisoma aurofrenatum</i> | | | | | | | | | |
| Available | 47.5 | 25.7 | 12.3 | 5.4 | 3.5 | 3.5 | 2.3 | 17.74 | <0.01 |
| Eaten | 62.5 | 24.4 | 1.1 | 7.1 | 2.5 | 2.1 | 0.3 | | |
| <i>Sparisoma viride</i> | | | | | | | | | |
| Available | 47.5 | 36.1 | 8.5 | 3.2 | 2.0 | 1.3 | 3.2 | 33.32 | <0.001 |
| Eaten | 52.2 | 33.8 | 0.2 | 2.4 | 8.8 | 0.6 | 2.0 | | |

turf, *T. testudinum*, sand, and other substrata. *S. viride* took more bites from SAT than turf, less from other substrata, and the fewest bites from *Dictyota* spp., *T. testudinum*, and sand. Among-species comparisons of the number of bites per 15 min on individual food items were not significant for major food items (Fig. 3; *H. opuntia* or SAT; KW, $p > 0.05$). However, differences were apparent for turf (KW, $H_2 = 8.8$, $p = 0.01$) and sand (KW, $H_2 = 10.5$, $p = 0.005$). Both *S. coeruleus* and *S. viride* took more bites from turf algae than *S. aurofrenatum* (DMC, $p < 0.05$). *S. coeruleus* fed more often from sand than either of the other species (DMC, $p < 0.05$).

The relative frequency of bites taken from different substrata was compared with the relative abundance of those substrata in the home ranges of each species. This comparison indicated that the diet of all 3 species was significantly different from that expected under random food selection (Table 2). *Scarus coeruleus* preferred *Halimeda opuntia* and large turf algae and avoided sedimented algal turf. *Sparisoma aurofrenatum* also selected *H. opuntia* and avoided bites to bare sand. *Sparisoma viride* took bites from *H. opuntia* approximately in proportion to its abundance, selected large turf algae, and avoided taking bites from sand. The proportion of bites taken from all other substrata were similar to their relative abundances in the environment.

Aggression

Focal individuals of all 3 species of juveniles were aggressive towards conspecifics, other juvenile parrotfishes, damselfishes, and occasionally towards grunts and wrasses (Table 3, Fig. 4). Aggression directed by juveniles at adult parrotfishes was never observed,

with the exception of interactions with initial phase (IP) *Scarus iserti*, a relatively small parrotfish with an average size of 7.5 cm TL (Robertson & Warner 1978). Adults of this species were not distinguished from juveniles. Among species, there were no significant differences in the amount of aggression directed towards herbivores (ANOVA, $F_{2, 28} = 0.64$, $p = 0.54$) or non-herbivores (KW, $H_2 = 4.6$, $p = 0.10$). For these comparisons, herbivores included all parrotfishes and damselfishes. Within species, both *Sparisoma aurofrenatum* and *Sparisoma viride* were more aggressive towards herbivores than non-herbivores (paired *t*-test, *S. aurofrenatum*: $t_{11} = 3.78$, $p = 0.003$; *S. viride*: $t_{11} = 3.29$, $p = 0.007$). Within the category of herbivorous fishes, *S. aurofrenatum* and *S. viride* were significantly more aggressive towards conspecifics than other parrotfishes or damselfishes (KW, *S. aurofrenatum*: $H_3 = 10.5$, $p = 0.015$; *S. viride*: $H_3 = 9.3$, $p = 0.025$; SNK, $p < 0.05$).

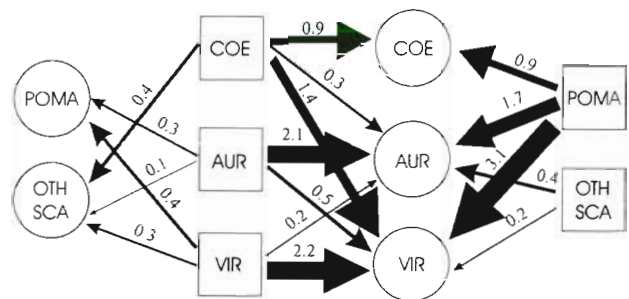


Fig. 4. Frequency of aggression observed between focal juvenile *Scarus coeruleus* (COE), *Sparisoma aurofrenatum* (AUR), and *Sparisoma viride* (VIR) and conspecifics, other scarids (OTH SCA), and pomacentrids (POMA). Circles represent individuals receiving aggression and squares represent the aggressors. Arrow widths are proportional to mean number of interactions per 15 min. Interactions between conspecifics are the sum of focal individuals as aggressors and recipients

Table 3. Amount of aggression directed by focal individuals towards other fishes (A) and that received by focal individuals from other fishes (B). Mean number of aggressive interactions (± 1 SD) per 15 min shown for families, and total numbers of observations shown for each species. – indicates no interactions observed. * $p < 0.05$ (Student Neuman Keuls: within species comparisons by family); † $p < 0.05$ (Dunn's Multiple Comparisons: among species comparison)

| | Focal individuals | | |
|--|-------------------------|-------------------------------|-------------------------|
| | <i>Scarus coeruleus</i> | <i>Sparisoma aurofrenatum</i> | <i>Sparisoma viride</i> |
| A. Focal fishes as aggressors toward: | | | |
| Conspecifics | 0.7 \pm 1.3 | 1.6 \pm 1.6* | 1.1 \pm 1.2* |
| Scaridae | 0.4 \pm 0.5 | 0.3 \pm 0.6 | 0.4 \pm 0.5 |
| <i>Scarus coeruleus</i> | 5 | – | – |
| <i>S. iserti</i> | 3 | 1 | 3 |
| <i>Sparisoma aurofrenatum</i> | 2 | 19 | 2 |
| <i>S. viride</i> | 10 | 6 | 13 |
| Pomacentridae | – | 0.3 \pm 0.6 | 0.4 \pm 1.0 |
| <i>Stegastes fuscus</i> | – | 3 | 2 |
| <i>S. variabilis</i> | – | – | 3 |
| Other families | 0.3 \pm 0.5 | 0.3 \pm 0.5 | 0 |
| <i>Haemulon</i> spp. | – | 2 | – |
| <i>Halichoeres</i> spp. | 2 | 2 | – |
| Total | 1.4 \pm 1.6 | 2.4 \pm 2.0 | 1.9 \pm 2.0 |
| B. Focal fishes as recipients from: | | | |
| Conspecifics | 0.1 \pm 0.4 | 0.7 \pm 1.5 | 1.0 \pm 1.5 |
| Scaridae | 0.1 \pm 0.4 | 0.6 \pm 0.8 | 0.7 \pm 1.0 |
| <i>Scarus coeruleus</i> | 1 | 2 | 10 |
| <i>S. iserti</i> | – | 2 | 2 |
| <i>Sparisoma atomarium</i> | – | 1 | – |
| <i>S. aurofrenatum</i> | – | 8 | – |
| <i>S. viride</i> | – | 2 | 13 |
| Pomacentridae | 0.9 \pm 0.9 | 1.7 \pm 2.3 | 3.0 \pm 1.6* |
| <i>Stegastes fuscus</i> | 1 | 8 | 8 |
| <i>S. leucostictus</i> | 1 | 6 | 16 |
| <i>S. variabilis</i> | 4 | 6 | 11 |
| <i>S. partitus</i> | – | – | 2 |
| Other families | 0.3 \pm 0.5 | 0.3 \pm 0.9 | 0.4 \pm 0.7 |
| <i>Haemulon</i> spp. | 1 | – | 2 |
| <i>Halichoeres</i> spp. | – | 4 | 1 |
| Total | 1.3 \pm 0.5 | 3.3 \pm 3.1 | 5.1 \pm 2.9† |

Focal individuals were the recipients of aggression from conspecifics, other juvenile parrotfishes, damselfishes, grunts, and wrasses (Table 3, Fig. 4). Juvenile parrotfishes rarely received aggression from adult parrotfishes. Exceptions included 2 chases of juvenile *Sparisoma aurofrenatum* by IP conspecifics and chases or displays by IP *Scarus iserti*. Juvenile *Sparisoma viride* were the recipients of aggression more often than the other 2 species and were the recipients of aggression more often than they were aggressive towards other fishes (2-way ANOVA, species: $F_{2, 56} = 3.81$, $p = 0.03$; behavior: $F_{1, 56} = 4.48$, $p = 0.04$; species \times behavior: $F_{2, 56} = 2.68$, $p = 0.08$; DMC, $p < 0.05$). All 3

species received similar amounts of aggression from non-herbivores (KW, $H_2 = 0.7$, $p = 0.712$). Both *S. aurofrenatum* and *S. viride* received more aggression from herbivores than non-herbivores (paired t -test, *S. aurofrenatum*: $t_{11} = 2.54$, $p = 0.028$; *S. viride*: $t_{11} = 5.52$, $p < 0.001$). *Sparisoma viride* was the recipient of aggression from herbivores more frequently than either *S. coeruleus* or *S. aurofrenatum* (ANOVA, $F_{2, 28} = 4.60$, $p = 0.03$; SNK, $p < 0.05$). Within the category of herbivorous fishes, *S. viride* received significantly more aggression from damselfishes than either conspecifics or other parrotfishes (KW, $H_3 = 17.8$, $p < 0.001$).

DISCUSSION

Overlap in use of space

Use of space on the reef is clearly not partitioned among these 3 species of juvenile parrotfish in terms of physical overlap of home ranges or microhabitats present within home ranges. However, on a larger scale, subtle variations are apparent among species. *Scarus coeruleus* is the only species that includes substantial portions of the sandy halos that surround the patch reefs of Coral Gardens in its home ranges, and many *Sparisoma aurofrenatum* include portions of the *Thalassia testudium* beds adjacent to reefs in their home ranges. Juvenile *Sparisoma viride* never venture away from the reef proper, which may be related to an increased risk of predation over sand or seagrass. The juvenile coloration of this species (3 rows of white spots on a dark red background) is distinct from all other small parrotfishes on these reefs (pale, striped pattern) and is perhaps more likely to be conspicuous against a sandy background than to the reef proper.

Home range size may be influenced by numerous factors including the density of intra- or interspecific competitors, and the distribution and quality of food, shelter, and mating sites (Ebersole 1980, Hixon 1980b, Norman & Jones 1984, Tricas 1989, Grant 1993). Home range size increases with body size within juvenile size classes for *Scarus coeruleus* and *Sparisoma aurofrenatum*, and home ranges measured for juveniles in this study are considerably smaller than those recorded for conspecific adults. Therefore, juvenile parrotfishes may increase their use of space on the reef as they grow. As adults, *S. aurofrenatum* and *Sparisoma viride* often defend all-purpose territories used for feeding, shelter, and reproduction (Dubin 1981, Clavijo 1982, Bruggemann et al. 1994a,c, Muñoz 1996). However, as sexually immature juveniles, it is most likely not feasible for these small fishes to exclusively defend an area from all intruders. The mean home range size of juvenile *S. aurofrenatum* in this study (24 m²) is smaller

than that of IP conspecifics in Barbados (39 to 99 m²) (Dubin 1981). Territory sizes of TP *S. aurofrenatum* have been variable among sites. Clavijo (1982) estimated territory size to be 88 m² in Puerto Rico, Dubin (1981) reported a range from 141.8 to 215.2 m² in Barbados, and the mean territory size at Coral Gardens, Florida is 240 m² (Muñoz 1996). Home ranges of juvenile *S. viride* are also much smaller (mean = 17.6 m²) than adult territories in Bonaire which ranged from 300 to 500 m² (van Rooij et al. 1996b).

Dietary overlap and selectivity of feeding

There is little evidence for resource partitioning of food by these species. Spatial segregation of individual bites does not exist because all 3 species would often feed side by side from the same patch. Mixed-species foraging aggregations of these juveniles did not separate into individual species when feeding as seen among members of large *Scarus iserti* core-species schools in Panama (Ogden & Lobel 1978). The diets of all 3 juvenile parrotfishes consist primarily (>50%) of *Halimeda opuntia*. This calcareous green macroalga (Chlorophyta) is both chemically and structurally defended. The younger portions of *Halimeda* spp. contain the highest concentrations of secondary terpenoid compounds (Paul & Fenical 1983, Hay et al. 1988), which have been shown to deter grazing in the buck-tooth parrotfish *Sparisoma radians*, as well as numerous other parrotfishes and surgeonfishes (Lewis 1985, Hay 1991). The older portions are low in food value, heavily calcified, and thought to be highly resistant to herbivory (Littler & Littler 1980, Hay et al. 1988). Juveniles of all 3 species studied fed predominantly from older, structurally defended portions of *H. opuntia* and left visible bite scars. In addition, both *Scarus coeruleus* and *Sparisoma aurofrenatum* fed more often from *H. opuntia* than would be expected under random food selection.

The prevalence of *Halimeda opuntia* in the diet of *Scarus coeruleus* is particularly interesting because none of the 45 members of the genus *Scarus* has ever been known to consume upright foliose macroalgae or seagrasses (Randall 1967, Sano et al. 1984, Wolf 1985, Bellwood & Choat 1990, Bruggemann 1994, p. 179–190, Bruggemann et al. 1994c). Juvenile *S. coeruleus* also feed occasionally from the seagrass *Thalassia testudinum*. Adults of this species are thought to be specialized sand-suckers that forage directly from sandy bottoms (Longley & Hildebrand 1941). Adults of 4 *Scarus* spp. from the Great Barrier Reef also fed from bare sand (Bellwood & Choat 1990). Although all juvenile *S. coeruleus* in this study included patches of bare sand in their home ranges, they did not selectively take

bites from this substrate and instead fed from a variety of substrata including *H. opuntia*, multispecific algal turfs, and *T. testudinum*. This suggests a potential ontogenetic trend toward specialization in the diet of this species from a juvenile feeding on a variety of foods to a more specialized adult that feeds primarily from sand.

The diet of juvenile *Sparisoma aurofrenatum* is remarkably similar to that of conspecific adults at the same study site. Terminal phase *S. aurofrenatum* took an average of 54 bites per 15 min on *Halimeda opuntia* (Muñoz 1996), and the corresponding mean for juveniles was 55 bites. Overall feeding rate is only slightly higher for juveniles than adults (89 vs 75 total bites per 15 min). This species fed predominantly on seagrass in Barbados (Dubin 1981) and Panama (McAfee & Morgan 1996). The latter study found macroalgae such as *Halimeda* spp. to be more important in the diet of larger *S. aurofrenatum*, and cited mechanical limitations of the jaw as the probable cause of the ontogenetic shift. Juveniles in this study (4 to 10 cm TL) clearly demonstrated no such functional constraints, and diets are remarkably similar for adults and juveniles at this site in the Florida Keys.

The feeding habits of juvenile *Sparisoma viride* are similar to those of conspecifics studied elsewhere. Juveniles of this species feed from *Halimeda opuntia* as often as would be expected by chance and selectively from large algal turfs. All phases of *S. viride* primarily took bites from multispecific algal turfs in Panama (McAfee & Morgan 1996) and fed primarily on endolithic algae, and selectively fed from large turfs and macroalgae (Bruggemann et al. 1994a,b, van Rooij et al. 1996a,c). The combined cover of large algal turfs and macroalgae is considerably less in all zones on the fringing reefs in these studies (3.0 to 7.7 %), and macroalgae are dominated by Phaeophyta rather than Chlorophyta such as *Halimeda* spp. (Bruggemann et al. 1994a). Therefore, taking into account the considerable differences between the 2 habitats, the diet of juvenile *S. viride* at Coral Gardens is comparable to that found at other Caribbean sites.

The diets of these juvenile parrotfishes support the growing body of evidence that herbivorous fish are not randomly feeding from all potential food items they encounter. Selectivity among food types under natural conditions has been demonstrated for several scarid species (Wolf 1983, Bruggemann et al. 1994a,c, Muñoz 1996). In contrast, Dubin (1981) found that 3 parrotfishes (*Scarus iserti*, *S. taeniopterus*, and *Sparisoma aurofrenatum*) in Barbados fed on substrates in proportion to their abundance in the environment. McAfee & Morgan (1996) also found that 5 parrotfishes in Panama generally fed non-selectively. However, the latter study determined food availability on an entire

reef rather than in the home ranges of individual species, and all species may not include all microhabitats in their home ranges.

Potential for social structure among juveniles

Focal individuals of all 3 species of juveniles are involved in aggressive interactions with conspecifics, other juvenile parrotfishes, damselfishes, and occasionally grunts and wrasses. In contrast, Dubin (1981) observed no occurrences of juvenile parrotfishes as aggressors during 155 h of observation in Barbados. Likewise, McAfee & Morgan (1996) observed only 4 'competitive, non-sexual interactions' between parrotfishes in Panama after hundreds of hours of observation. The discrepancy between these studies and the present one may be explained by actual differences among sites (e.g. fish density, whether resources are limiting, relative importance of competition) or simply methodological differences. Observational methods (such as those used in the 2 former studies) that do not involve substantial sampling of focal individuals are more likely to overlook less frequent behaviors such as aggressive interactions. Aggression directed towards juveniles by adult parrotfishes was never observed in this study, with the exception of infrequent interactions with IP *Scarus iserti*. The lack of aggression by adults contradicts patterns exhibited by chaetodontids, embiotocids, and pomacentrids in which adults aggressively defend territories from juveniles (Hixon 1980a, 1981, Reese 1991, Harrington 1993).

As aggressors, juveniles tend to chase conspecific juveniles more often than other fishes, but are the recipients of aggression primarily from damselfishes. Aggressive interactions are most likely correlated with the degree of overlap in ecological requirements (Myrberg & Thresher 1974, Choat & Bellwood 1985). Based on the high degree of overlap in the use of space and food among these 3 species, we would expect them to display aggression toward one another as often as toward conspecifics. However, both *Sparisoma aurofrenatum* and *Sparisoma viride* are more aggressive toward conspecifics than any other parrotfishes. More subtle differences in resource requirements may exist among these species than were detected by this study. Alternatively, juveniles may recognize conspecifics as potential competitors with whom they will begin to establish a dominance hierarchy in preparation for territoriality as adults. Interspecific defense of an area by herbivores probably involves learning and may be influenced by early chance encounters with particular species (Choat & Bellwood 1985). Our results indicate that juvenile parrotfishes selectively displayed aggression toward conspecifics, challenging the idea that

naïve juvenile reef fishes chase a broader range of species than adults (Harrington & Losey 1990).

Numerous authors have noted frequent chases of parrotfish (including juveniles) by damselfishes (Low 1971, Ebersole 1977, Dubin 1981, Itzkowitz 1990, van Rooij et al. 1996a). Itzkowitz & Slocum (1995) showed that the attack intensity of *Stegastes leucostictus* against *Scarus iserti* was correlated with the total biomass of algae that the pomacentrid was defending. This implies defense of the food itself, rather than space. Attacks by damselfishes reduce the area in which these juveniles can feed, and may make it easier for predators to capture juveniles that are distracted by having to avoid territorial herbivores (Sweatman & Robertson 1994). At our study site, damselfishes frequently chase juvenile parrotfishes from their territories, but there is no evidence of aggression by damselfishes toward adult parrotfishes (Muñoz 1996, K. Overholtzer pers. obs.).

Implications for community structure

The coexistence of ecologically similar, closely-related fishes on reefs has been explained by 4 major classes of hypotheses including: (1) niche diversification through competition, (2) the competitive lottery hypothesis, (3) recruitment limitation, and (4) predation or disturbance limitation (reviewed by Ebeling & Hixon 1991). These 3 juvenile parrotfishes show no evidence of resource partitioning in terms of either food or space. Therefore, these observations do not support conventional models of niche diversification through past or present interspecific competition. Alternatively, resources may not be limiting for these juveniles, or these fishes are competing and a non-equilibrium mechanism such as limitation by recruitment, abiotic disturbance, or predation is allowing them to coexist.

Conclusions

There is little evidence for substantial resource partitioning of space or food among juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* on patch reefs in the Florida Keys. Moreover, the behavior of these fishes challenges conventional wisdom in at least 2 ways. (1) These juveniles selectively exploited a heavily calcified food source (*Halimeda opuntia*) despite its potentially high energetic costs of procurement, low food value, and predicted avoidance by herbivores (Littler & Littler 1980, Lewis 1985, Hay et al. 1988, Hay 1991). (2) Focal individuals disproportionately displayed aggression toward conspecifics,

challenging the hypothesis that juvenile reef fishes chase a broader range of species than adults, and were the recipients of aggression primarily from other herbivorous fishes.

Although juveniles do not remove as much biomass per bite as larger scarids, their relative abundance, high feeding rates, and selective foraging may contribute to a substantial effect on the distribution and abundance of benthic algae (reviewed by Hixon 1997). Future research should concentrate on the experimental manipulation of densities of territorial pomacentrids and manipulation of juvenile parrotfish to determine their relative effects on the demography and spatial distribution of larger age classes of parrotfish.

Acknowledgements. We thank S. Bell, M. Hixon, J. Ogden, and M. Robinson for constructive comments on various drafts of the manuscript; S. Binard, K. Choe, T. Curtis, D. Motta, N. Noone, T. Pledger, S. Schuler, and J. T. Streelman for generous field assistance; R. Muñoz for insights on experimental design; and the staff of the Keys Marine Laboratory for logistical support. This research was supported by the Lerner Gray Fund for Marine Research, Theodore Roosevelt Memorial Fund, the Florida Institute of Oceanography, and the University of South Florida. This paper is from a thesis submitted by K.L.O. in partial satisfaction of the requirements for a Master's degree in zoology from the University of South Florida.

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: April 14, 1998; Accepted: October 19, 1998
Proofs received from author(s): January 26, 1999