

Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes

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Synopsis

Many parrotfishes (Scaridae) co-occur in mixed-species aggregations as juveniles, but diverge in resource use and social structure as adults. Focal observations of three juvenile parrotfishes (*Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*) were conducted on inshore patch reefs in the Florida Keys to determine how feeding and aggressive interactions vary with group participation. All three species spent more time in groups than alone, most often in groups of less than ten individuals. Feeding rates were significantly higher for *S. viride* when foraging in groups than when alone. All species fed most often from *Halimeda*, and overall diet composition was similar for fish whether feeding in groups or alone. The frequency of aggressive interactions varied with group participation. Focal *S. aurofrenatum* were more aggressive when in groups than when alone, and both *S. aurofrenatum* and *S. viride* were attacked more often by damselfishes when they were alone than when in groups. In contrast, feeding rates, diet breadth, and aggressive interactions of *S. coeruleus* were less affected by group participation. Small mixed-species aggregations of coral reef fishes may be large enough for individuals to assume some of the benefits of group participation while at the same time avoiding the costs of competition realized in larger groups.

Introduction

Mixed-species foraging groups of juvenile parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) are common on western Atlantic coral reefs (Itzkowitz 1977, Ogden & Lobel 1978, Wolf 1985b, Debrot & Myrberg 1988). Group membership may enable individuals to gain access to the defended resources of territory holders, decrease search times for patchily distributed resources, and provide increased protection from predation (Barlow 1974, Robertson et al. 1976, Foster 1985, 1987, Wolf 1987, Clifton 1991). These benefits may be offset by the costs of increased competition for food among group members and the 'oddity effect' whereby distinctive coloration increases the risk of

predation for relatively rare individuals within groups (Austin & Smith 1972, Waite 1984, Wolf 1985a).

Feeding on benthic algae, characteristic of these herbivorous fishes, requires multiple rapid bites that expose individuals to aggression from potential food competitors and increase their risk of predation (Robertson et al. 1976). Minimizing these risks is especially important for small juvenile reef fishes that are highly susceptible to predation (Hixon 1991). For most fishes, vulnerability to predation decreases with an increase in body size (Werner & Gilliam 1984, Shulman & Ogden 1987, Sale & Ferrell 1988, Forrester 1990, Hixon 1991, Hixon & Beets 1993, Levin 1994, Carr & Hixon 1995). Predation may directly affect food selection and/or feeding behavior for animals that are

at a greater risk of predation while foraging than during other activities (Lima 1987, McNamara & Houston 1992, Krause & Godin 1996). For example, the risk of predation for guppies foraging nose down is greater than for those foraging horizontally (Krause & Godin 1996). Likewise, juvenile parrotfishes also adopt a head-down foraging position (K. Overholtzer personal observation) that may increase their vulnerability to predation while feeding. Compared to solitary individuals, group foraging fishes may experience lower per capita attack rates by predators through dilution effects and may have more time to forage because they spend less time in vigilance, as shown for birds (Pulliam 1973, Caraco 1979).

Group foraging may enable small individuals to overwhelm the defenses of territorial herbivores and feed on defended algal resources unavailable to solitary fishes (Barlow 1974, Robertson et al. 1976, Foster 1985, Reinthal & Lewis 1986). Many damselfishes (Pomacentridae) are pugnacious territory holders and have been shown to chase parrotfishes from their territories, including juveniles (Low 1971, Itzkowitz 1990). In Panama, schooling striped parrotfish (both juveniles and adults) fed at higher rates and were attacked by territorial damselfishes less often than non-schooling conspecifics (Robertson et al. 1976). Species that overlap in diet may also benefit from mixed-species foraging by using other group members as food finders, as shown for cyprinids (Pitcher et al. 1982) and scarids (Clifton 1991).

An increase in feeding rate or time devoted to foraging when in groups has been shown for fishes (Foster 1985, 1987, Wolf 1987, Kohda & Takemon 1996), birds (Sullivan 1984, Latta & Wunderle 1996), and mammals (Monaghan & Metcalfe 1985, Saino 1994). However, feeding efficiency may actually be highest in moderate-sized groups if group members are competing with one another for food (Saino 1994). In mixed-species flocks, birds modified their foraging behavior by limiting the microhabitats in which they fed or reducing diet breadth in such a way that agonistic interactions with other members of the group were reduced (Austin & Smith 1972, Waite 1984). If this pattern holds true for fish, some degree of resource partitioning may result in decreased competition between species within multi-specific schools. For example, large schools composed primarily of striped parrotfish have been observed to separate into smaller, single-species groups while feeding (Ogden & Lobel 1978).

Previous descriptions of mixed-species groups of small parrotfishes have emphasized the fluid nature of the association, noting constant changes in group composition (Robertson et al. 1976, Ogden & Lobel 1978, Wolf 1983). This is also true of the mixed-species groups of juvenile parrotfishes on inshore patch reefs in the Florida Keys (K. Overholtzer personal observation). However, these groups are significantly smaller than those reported in previous studies from Panama and the U.S. Virgin Islands, and typically contain ten or fewer individuals and as many as six species. Rare individuals may be highly visible and therefore vulnerable to predation in these groups, depending on their coloration. If these odd individuals spend most of their time in small foraging groups, either the benefits of group participation outweigh the costs, or group foraging is a relatively fixed behavior in these fishes.

The goal of this research was to examine the role of mixed-species foraging groups in the resource use and social behavior of three juvenile parrotfishes (*Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*). These particular species were chosen because they were easily identifiable, and we observed them to be among the most consistent members of these mixed-species aggregations. In addition, they are interesting in that they co-occur in mixed-species aggregations as juveniles, but then segregate by species as adults with vastly different social systems ranging from solitary, home-ranging individuals to territorial males with female harems. We specifically addressed the following questions: (1) Does the frequency of group participation differ among these species, and are there differences in the size and composition of the groups they join? (2) Does feeding rate increase with group participation? (3) How is diet breadth affected by group participation? (4) Does the frequency of aggression decrease with group participation?

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 (80°44'W, 24°51'N) from April to November 1996. The average depth at this site is approximately

5 m, and patch reefs range in area from 10 to 2000 m². The study area consisted of three moderate-sized (~1000 m²) adjacent patch reefs surrounded by halos of sand and seagrass (primarily *Thalassia testudinum*) beds. Dominant scleractinian corals on these reefs include *Diploria* spp., *Montastrea annularis*, *M. carvernosus*, and *Siderastrea* spp., and the dominant macroalga is *Halimeda opuntia*. Mixed-species aggregations of juvenile parrotfishes were common at this site and typically contained *Scarus iserti*, *Sparisoma aurofrenatum*, and *Sparisoma viride*, and occasionally *Scarus coeruleus* and *Sparisoma atomarium*. In addition, individuals from other families including Labridae, Acanthuridae, and Chaetodontidae frequently joined these groups.

Supplemental observations of *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. The opportunity to observe this species at a second location allowed us to compare resource use and group participation at a close, but dissimilar site. 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 astreoides*) is minimal. *Halimeda opuntia* is the dominant macroalga. Scarids were less abundant at this site; only three of the five juveniles common at Coral Gardens were present (*Scarus iserti*, *Sparisoma aurofrenatum*, *Sparisoma viride*).

Field observations

All behavioral observations were conducted using SCUBA between 10:00 h and 16:00 h, and were made only when horizontal visibility was at least 3 m. Twelve focal individuals each of *Sparisoma aurofrenatum* and *S. viride*, and 7 individuals of *Scarus coeruleus* were observed. (*S. coeruleus* was less abundant at Coral Gardens than the other two species.) Lengths of focal fishes were repeatedly checked by comparing length estimates to a variety of background landmarks. Sizes of focal individuals were similar for all three species, ranging from 40 to 100 mm with a pooled mean of 62 mm (SE = 11.5).

After a 5 min habituation period, two divers approached a group of fishes. One diver recorded foraging and social interaction data for each focal animal

for 15 min with continuous recording, while a second diver simultaneously recorded group size and composition data using instantaneous sampling at one minute intervals. Fish were scored as belonging to the same group containing the focal individual using an inter-fish distance of 0.5 m, i.e., within 0.5 m of either the focal fish or another fish in the group that was within 0.5 m of either the focal fish or another fish in the group. The exact number of fish per aggregation was tallied for groups of 10 or fewer fish, but larger groups necessitated use of categories of 11–15, 16–20 and 21–25 fish. Group composition was recorded in terms of the number of species present within each family (Scaridae, Labridae, Acanthuridae, and other) as well as the number of conspecifics of the focal fish.

For each focal sampling period, every feeding 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 was that required to reapply the jaws to the substrate. Substrate categories included two upright foliose macroalgae, *Halimeda opuntia* and *Dictyota* spp.; large algal turfs (≥ 10 mm frond height), referred to as 'turf'; sedimented, sparse algal turfs (< 10 mm frond height); seagrass, *Thalassia testudinum*; and sand. Both turf 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 fish feces. We also tallied the frequency of all overt aggressive and agonistic behaviors involving the focal individual (including chases, mouth to mouth displays, dorsal fin raising, and caudal or pelvic fin flaring). Participants in these encounters were identified to species.

Statistical analyses

All analyses were performed using the statistical software SigmaStat[®] version 2.0 (Jandel Scientific 1995). Data were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variances using the Levene Median test before performing any parametric statistics. Data that did not meet the assumptions of parametric statistics after transformations were analyzed by nonparametric means. Mann–Whitney U-tests were used to compare frequency of group participation, feeding rates, and frequency of aggressive interactions

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 two locations were pooled in all subsequent analyses.

One-way ANOVA was used in lieu of two-way ANOVA (one repeated factor) for among- and within-species comparisons of the frequencies of group participation and group composition because of violations of parametric assumptions. To ensure there was no significant interaction between factors, two-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 one-way nonparametric repeated measures ANOVA (Friedman's chi-square) and among species comparisons were conducted using one-way ANOVA. Student-Neuman-Keuls' (SNK) test was used for multiple comparisons of all significant ANOVA effects.

One-tailed paired t-tests were used to compare feeding rate and frequency of aggressive interactions for the minutes that focal individuals were alone versus minutes they spent in groups. The Wilcoxon signed-rank test was used in lieu of the t-test in cases where data did not meet parametric assumptions. Diet breadth (Shannon–Wiener diversity index) for each species foraging alone versus in groups was compared using the t-test method outlined by Hutcheson (1970). Feeding rate (bites min^{-1}) was regressed against categorical group size variables (2–5, 6–10, 11–15, 16–20, 21–25) for each of the three species using regression analysis for multiple values of Y (feeding rate of each individual) for each value of X (group size) (Zar 1996).

Results

Group participation

Frequencies of group participation were similar among *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* (Figure 1). All three species spent more time in groups of any size (combining all groups) than alone during 15 min observations. Among species, *S. viride* spent more time alone than the other two species (ANOVA, $F_{2,31} = 3.241$, $p = 0.054$), although this difference was only marginally statistically significant. However, no species spent more time in groups of any particular size [e.g., 2–5 ($F_{2,31} = 2.305$,

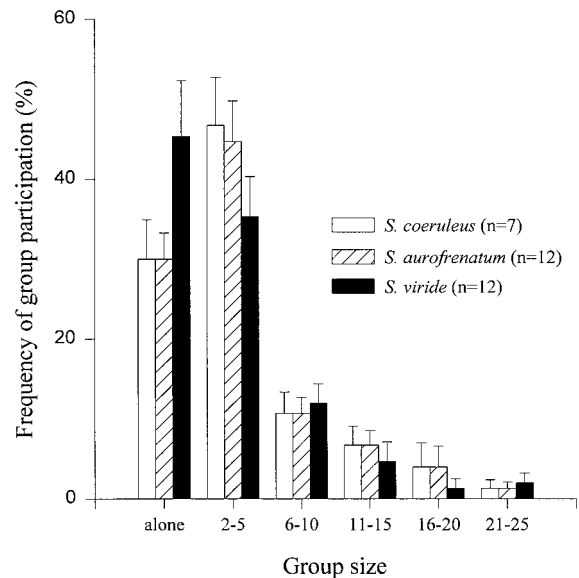


Figure 1. Mean frequency (+1 SE) of group participation (%) for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*.

$p = 0.12$) or 6–10 ($F_{2,31} = 0.113$, $p = 0.89$)]. Within species, both *S. coeruleus* and *S. aurofrenatum* were found in groups of 2 to 5 individuals more often than alone or in larger groups, while *S. viride* was alone as often as it participated in these small groups (Friedman's RM ANOVA on ranks; *S. coeruleus*: $X^2_5 = 47.9$, $p < 0.0001$, *S. aurofrenatum*: $X^2_5 = 27.7$, $p < 0.0001$, *S. viride*: $X^2_5 = 44.2$, $p < 0.0001$; SNK, $p < 0.05$). All three species joined larger groups infrequently, and no group contained more than 25 individuals.

Aggregations joined by focal individuals contained other juvenile parrotfishes (*Scarus iserti* and *Sparisoma atomarium*) and juveniles or small adult butterflyfishes, surgeonfishes, and wrasses. Of participants from these other families, wrasses were the most common (mostly *Halichoeres bivittatus* and *H. maculipinna*). Mean species richness of groups was similar for all three parrotfish species (Figure 2). The mean scarid richness per group was also similar among species, but *Sparisoma viride* joined more groups composed of only parrotfishes. Most groups joined by *S. coeruleus* and *S. viride* contained no conspecifics (70.7% and 56.8%, respectively). Conversely, most groups joined by *S. aurofrenatum* did contain other conspecifics (67.3%).

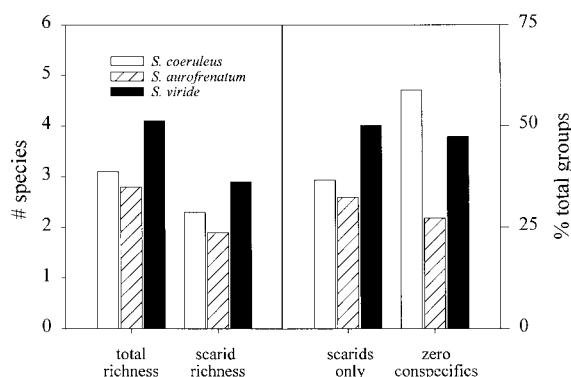


Figure 2. Composition of groups joined by juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*. Groups are characterized in terms of richness (total and scarid) and the frequency of total groups containing scarids only and containing no conspecifics. Numbers indicate pooled means calculated from the total minutes that each species occurred in groups of any size [*S. coeruleus* (n = 75), *S. aurofrenatum* (n = 126), *S. viride* (n = 87)].

Effects of group participation on feeding

Feeding rates (bites min^{-1}) were significantly higher for *S. viride* when in groups than when alone (one-tailed paired t-test, $t_{11} = 3.346$, $p = 0.007$; Table 1). However, there was no significant difference in feeding rates for either *S. coeruleus* or *S. aurofrenatum* when feeding alone compared to feeding in groups (*S. coeruleus*: $t_6 = -0.481$, $p = 0.67$, *S. aurofrenatum*: Wilcoxon signed-rank test, $W = 3.000$, $p = 0.91$). Feeding rate was unrelated to group size for *S. coeruleus* (Figure 3). There was also no increase in feeding rate with group size for *S. aurofrenatum* or *S. viride*, but our ability to detect an effect was reduced by few observations at larger group sizes.

Diet breadth (H') of *S. aurofrenatum* was significantly greater for individuals when they were in groups versus when they were alone (Table 1, $t_{23} = 24.57$, $p < 0.001$). For *S. viride*, diet breadth decreased when foraging in groups versus when alone ($t_{14} = 43.76$, $p < 0.001$). Diet breadth was not significantly different for *S. coeruleus* whether foraging alone or in groups ($t_{14} = 0.37$, $p > 0.50$). Comparisons of the number of bites per min on individual substrata yielded few differences between group and solitary foraging individuals (Table 2). When foraging alone or in groups, all species fed most often from the calcareous macroalga *Halimeda*. Comparing solitary to group foraging, *S. aurofrenatum* took significantly more bites

Table 1. Comparison of feeding and aggressive interactions (mean \pm 1 SE) for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* when solitary versus in groups.

Variable	Group participation	
	solitary	group
Feeding rate (bites per min)		
<i>S. coeruleus</i>	7.7 ± 1.2	7.7 ± 0.7
<i>S. aurofrenatum</i>	5.7 ± 0.7	6.0 ± 0.6
<i>S. viride</i>	5.6 ± 0.6^a	7.2 ± 0.7^a
Diet breadth (H')		
<i>S. coeruleus</i>	0.91 ± 0.09	0.89 ± 0.09
<i>S. aurofrenatum</i>	0.55 ± 0.03^b	0.82 ± 0.03^b
<i>S. viride</i>	1.40 ± 0.04^b	0.84 ± 0.03^b
Aggressive interactions (# per min)		
as aggressors		
<i>S. coeruleus</i>	0.4 ± 0.3	1.3 ± 0.6
<i>S. aurofrenatum</i>	0.3 ± 0.2^c	2.2 ± 0.7^c
<i>S. viride</i>	0.8 ± 0.5	1.1 ± 0.4
as recipients		
<i>S. coeruleus</i>	0.7 ± 0.3	0.7 ± 0.3
<i>S. aurofrenatum</i>	1.5 ± 0.8	1.6 ± 0.7
<i>S. viride</i>	2.4 ± 0.6	3.0 ± 0.4

^apaired t-test.

^bHutcheson (1970) t-test for comparing diversity indices.

^cWilcoxon signed-rank test.

solitary vs. group = ** $p < 0.025$, *** $p < 0.001$.

from *Dictyota* ($t_{11} = 3.387$, $p = 0.006$) when in groups than alone and did not feed from 'other' foods when alone. *Sparisoma viride* took more bites per min from sedimented algal turfs ($t_{11} = 2.271$, $p = 0.044$) when in groups than when alone, and did not feed from sand when alone. Bites taken from individual substrata by *S. coeruleus* in groups did not differ from those taken when alone, although this species did not feed from *Thalassia* when alone.

Effects of group participation on aggression

Focal juvenile individuals of all three species were aggressive toward conspecifics, other juvenile parrotfishes, damselfishes, and occasionally towards grunts and wrasses. Attacks were directed toward both other group members and fish outside of the group. Aggression directed toward adult parrotfishes was never observed with the exception of two interactions with initial phase *Scarus iserti*, a relatively small parrotfish

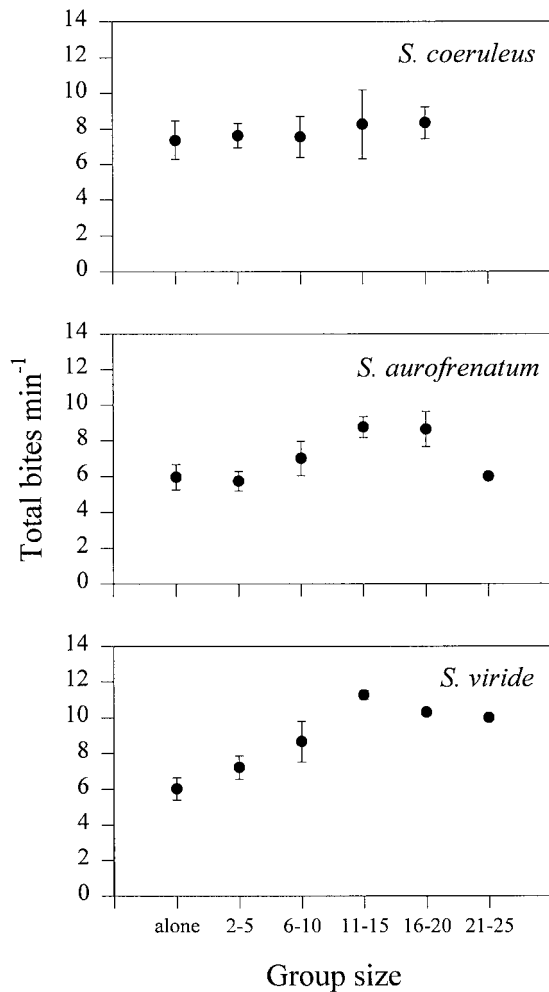


Figure 3. Feeding rate (total bites min^{-1}) as a function of group size for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*. Each point represents the mean bites per min for one focal individual in a particular group size. Regression-with-replication analyses were not significant for any species ($p > 0.05$).

with an average size of 7.5 cm TL (Robertson & Warner 1978). Adults of this species were not distinguished from juveniles by observers. The frequency of aggressive interactions varied with group participation (Table 1). As aggressors, focal *S. aurofrenatum* were involved in many more interactions when in groups than when alone (Wilcoxon signed-rank test, $W = 45.00$, $p = 0.004$), and this aggression was directed primarily toward conspecifics. Group participation did not produce statistically significant effects on the frequency of aggressive interactions

for either *S. coeruleus* or *S. viride* as aggressors (*S. coeruleus*: $t_6 = -1.549$, $p = 0.17$; *S. viride*: $t_7 = -1.109$, $p = 0.30$). However, the absolute increase in aggression while in groups for *S. coeruleus* was sizeable, and neither of these species displayed aggression towards other parrotfishes when alone.

Although differences were evident in the overall amount of aggression directed toward focal juveniles when they were alone versus in groups, these differences were not statistically significant. Because aggressive interactions were relatively infrequent behaviors, there was low statistical power (< 0.50) to detect differences. Both *S. aurofrenatum* and *S. viride* were attacked more often by damselfishes when they were alone than when they were in groups. Focal *S. aurofrenatum* were the recipients of aggression from damselfishes a total of 14 times when alone and only 6 times when in groups ($W = -7.000$, $p = 0.56$). Focal *S. viride* were the recipients of aggression from damselfishes a total of 25 times when alone and only 14 times when in groups ($t_{11} = 1.372$, $p = 0.20$). These two species were the recipients of aggression from conspecifics more often when in groups than when alone. Focal *S. aurofrenatum* were the recipients of aggression from conspecifics only when in groups, but this difference was not statistically significant. Focal *S. viride* were the recipients of aggression from conspecifics a total of 11 times when in groups and only twice when alone ($W = 23.00$, $p = 0.047$). Aggression directed towards *S. coeruleus* did not vary with group participation.

Discussion

Participation in small, mixed-species groups

In the Florida Keys, juveniles of three species of parrotfish (*Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride*) occur more often in mixed-species aggregations than alone, and frequencies of group participation are similar among species. This lack of a difference between *Scarus coeruleus* and the two *Sparisoma* spp. contradicts previous findings. Winn & Bardach (1960) and Dubin (1981) described members of the genus *Sparisoma* as more solitary than *Scarus* in Bermuda and Barbados, respectively. Similarly, Barlow (1975) found that *Sparisoma* were always solitary in Puerto Rico. Itzkowitz (1974) reported that juvenile *Sparisoma* in Jamaica were solitary and *Scarus* were gregarious. Based on the present findings, such

Table 2. Mean number of bites per min (± 1 SE) on various substrata for juvenile *Scarus coeruleus*, *Sparisoma aurofrenatum*, and *Sparisoma viride* when solitary versus in groups.

Substrata	<i>S. coeruleus</i>			<i>S. aurofrenatum</i>			<i>S. viride</i>		
	solitary	group	p	solitary	group	p	solitary	group	p
<i>Halimeda</i>	3.69 \pm 0.85	3.95 \pm 0.79	NS	3.91 \pm 0.73	3.68 \pm 0.54	NS	2.76 \pm 0.40	3.22 \pm 0.53	NS
SAT	1.58 \pm 0.73	0.85 \pm 0.38	NS	1.37 \pm 0.48	1.42 \pm 0.36	NS	1.89 \pm 0.49	2.91 \pm 0.65	0.04
<i>Dicyota</i>	0.11 \pm 0.11	0.11 \pm 0.04	NS	0.15 \pm 0.07	0.49 \pm 0.12	0.006	0.34 \pm 0.24	0.17 \pm 0.14	NS
turf	0.67 \pm 0.38	0.58 \pm 0.28	NS	0.12 \pm 0.06	0.15 \pm 0.09	NS	0.77 \pm 0.07	0.85 \pm 0.33	NS
<i>Thalassia</i>	0	0.07 \pm 0.07	NS	0.17 \pm 0.17	0.08 \pm 0.08	NS	0.07 \pm 0.07	0.01 \pm 0.01	NS
sand	1.36 \pm 0.64	1.93 \pm 1.08	NS	0.02 \pm 0.02	0.05 \pm 0.03	NS	0	0.04 \pm 0.03	NS
other	0.25 \pm 0.10	0.16 \pm 0.08	NS	0	0.09 \pm 0.03	NS	0.08 \pm 0.04	0.14 \pm 0.04	NS

generalizations may not be true for juveniles of all parrotfish species in all geographic locations.

Groups joined by these parrotfishes contain up to 20 fish, but the typical group size is five or fewer individuals. Because small groups contain mostly a fourth species, *Scarus iserti*, individuals of these three parrotfishes tend to be conspicuous. This is especially true for *S. coeruleus* and *S. viride* because these species are most often in groups containing no other conspecifics. Their juvenile coloration (*S. coeruleus*: yellow head, pale blue body; *S. viride*: white spots on red background) is distinct from most other reef-dwelling small parrotfishes in the Western Atlantic (generally a dark, striped pattern), and is therefore likely to stand out in a mixed-species aggregation. *Scarus coeruleus*, however, may decrease its conspicuousness by altering its coloration to a striped pattern comparable to that of *S. iserti*; this behavior was observed for *S. coeruleus* while in groups at our study site (K. Overholtzer personal observation). Juvenile *S. viride* apparently are not able to change their coloration in this manner, but may instead seek refuge within the reef itself, rather than in groups (Wolf 1985a). Because even conspicuous individuals spent more of their time in small foraging groups than alone, the benefits of mixed-species group participation likely outweigh the costs. Based on the present study as well as previous research, potential advantages of group participation appear to include enhanced feeding and decreased aggression (Barlow 1974, Robertson et al. 1976, Foster 1985, Hourigan 1986, Reinthal & Lewis 1986, Wolf 1987).

Effects of group participation on feeding

For *Sparisoma aurofrenatum*, group participation had little effect on feeding rate. However, diet breadth was higher for this species when in groups than when alone.

Previous research has shown that parrotfishes will eat a variety of foods despite fluctuating abundances of those foods in the environment (Lobel & Ogden 1981). This behavior may function to ensure survival in an unpredictably patchy environment. Therefore, one advantage of group participation for *S. aurofrenatum* may be the ability to maintain a more varied diet than when foraging alone.

For *Sparisoma viride*, feeding rate was higher in groups than when alone, but diet breadth was lower for individuals foraging in groups than solitary foragers. Despite the fact that *S. viride* can feed on a wider variety of foods when solitary, and thereby maintains a varied diet as discussed previously, feeding rate is higher when in groups. An increase in feeding rate has been shown for numerous coral reef fishes in large groups (Barlow 1974, Robertson et al. 1976, Foster 1985, Hourigan 1986, Wolf 1987). For example, surgeonfish *Acanthurus chirurgus* increased the amount of time devoted to foraging when in groups, and individuals that derived a greater foraging benefit spent more time in groups (Wolf 1987). In Panama, non-territorial *Scarus iserti* in schools fed at higher rates and were attacked by territorial damselfish *Stegastes planifrons* less often than non-schooling territorial *S. iserti* (Robertson et al. 1976).

For all three species, there were few differences in the number of bites taken from individual substrata. Each of the three species was never observed feeding from certain substrata (e.g. *Thalassia*, sand, sponges, gorgonians) when foraging alone, although they fed on these substrata when in groups. However, these substrata were all fed upon relatively infrequently. At our study site, the predominant macroalga, *Halimeda opuntia*, is the primary food source for all three of these juvenile parrotfishes (Overholtzer & Motta 1999). This

calcareous alga occurs within the territories of damselfishes. Therefore, if the main function of group participation is to overwhelm the defenses of damselfishes on these patch reefs, the number of bites taken from *Halimeda* should be higher for fish in groups than solitary individuals. However, for all three species of juvenile parrotfishes observed in this study, solitary fish fed from *Halimeda* as often as individuals in groups. Food selection for these species may simply be a function of how often they encounter particular microhabitats when foraging with the group, rather than an effort to specifically feed on defended resources such as *Halimeda*.

Effects of group participation on aggression

Group participation increased the frequency of aggressive interactions for *S. aurofrenatum* as aggressors, but had little effect for the other two species. This aggression was directed primarily toward conspecifics, suggesting that intraspecific antagonism increases for *S. aurofrenatum* when in groups. *Sparisoma aurofrenatum* tended to have more conspecific group members than the other two species, and the increase in aggression may result from encountering more conspecifics when in groups. Juveniles may recognize conspecifics as potential competitors with whom they will begin to establish a dominance hierarchy in preparation for territoriality as adults, as shown for chaetodontids (Reese 1991).

Group participation also decreased the frequency of aggression by damselfishes toward *S. aurofrenatum* and *S. viride*. Foster (1985) found that two-thirds of the feeding bouts of solitary tangs (surgeonfish) in damselfish territories ended with attacks by territory owners; additionally, rates of attack were inversely correlated with group size. Likewise, three surgeonfish species in Belize received more attacks from damselfishes when solitary than when schooling (Reinthal & Lewis 1986). However, the increased aggression toward solitary parrotfishes in the present study did not appear to limit feeding on *Halimeda* or algal turfs. Algal turfs in damselfish territories are thought to be relatively immune to attack from small groups of fishes (Montgomery 1981). It is not known whether these juveniles would actually eat more turf algae in the absence of damselfishes. Based on these preliminary results, group participation appears to have an effect on the frequency of attacks on *S. aurofrenatum* and *S. viride* by damselfishes, but it is unclear what

effects, if any, this increased aggression has on feeding behavior.

*Why does *Scarus coeruleus* join groups?*

Feeding rates, diet breadth, and aggressive interactions of *S. coeruleus* were only weakly affected by group participation. As suggested by Wolf (1985a), the benefits of group participation may be different for each species. The results of this study show no evidence of any clear advantages or disadvantages for this species when in mixed-species aggregations. *Scarus coeruleus* may join these groups as they pass through its home range to temporarily decrease vulnerability to predators despite gaining no obvious foraging advantages. Alternatively, this species may become a member of a group simply by feeding on resources that are concentrated in discrete patches at the same time an aggregation passes through. Further study is necessary to determine what advantages (e.g. increased survivorship) this species derives from group participation.

Conclusions

All previous research demonstrating the benefits of group participation has involved substantially larger groups of fish (80–500) than those included in this study (e.g. Robertson et al. 1976, Wolf 1985b, Debrot & Myrberg 1988). We have shown that small aggregations of reef fish (< 10 individuals) may be large enough for individuals to assume some of the benefits of group participation (e.g. increased feeding rates for *S. viride* and increased diet breadth for *S. aurofrenatum*). At the same time, these groups may be small enough that members can avoid the intragroup agonism characteristic of larger groups that may reduce feeding efficiency or attract predators. Avoidance of certain foods when fish are solitary may be related to an increased risk of predation associated with more exposed microhabitats, but overall diets were similar for fish in groups compared to solitary fish. Group participation decreased the frequency of aggressive interactions from damselfishes, but the implications of this difference in aggression for parrotfish feeding are not yet understood. There were few interspecific differences in group participation, with all three species found less often alone than in groups.

Future research should concentrate on understanding the effects of a range of group sizes on the ecology of juvenile parrotfish, and pinpointing the factors involved

in food selection, frequency of aggressive interactions, and the potential increased risk of predation for 'odd' individuals. Manipulations of the size and composition of mixed-species reef fish aggregations would be useful to test for interspecific variation in the costs and benefits of group participation, including determining how survivorship is affected by group participation.

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