

Interspecific Aggression between Two Parrotfishes (*Sparisoma*, Scaridae) in the Florida Keys

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When resources are economically defensible, interspecific aggression may occur when one species attempts to use the defended resources to the detriment of the defending species. In the Florida Keys, we investigated vigorous and frequently observed aggression between the Redband Parrotfish, *Sparisoma aurofrenatum*, and the Redtail Parrotfish, *Sparisoma chrysopterus*, along with microhabitat overlap and foraging overlap. *Sparisoma chrysopterus* home ranges extensively overlap *S. aurofrenatum* territories. Both parrotfishes are found over and feed upon *Halimeda opuntia*, a green calcareous alga, significantly more than all other microhabitats. Interspecific aggression by these parrotfishes is primarily directed toward conspecifics. Extensive overlap in distributions combined with overlap in microhabitat and foraging behavior likely play a role in fostering the disproportionately high interspecific aggression observed between these two parrotfishes in the Florida Keys.

INTERSPECIFIC aggression and territoriality have been well studied in a variety of animal taxa including fishes, dragonflies, and birds (e.g., Orians and Willson, 1964; Singer, 1989; Harrington and Losey, 1990) and are evidently manifested when certain resources (mates, mating opportunities, food, nest sites, or shelter from predators) are economically defensible, that is, the benefits gained by aggressive defense of resources outweigh the costs of defense (Brown, 1964). It follows that attacks against other species should occur only when they are attempting to use the resources to the detriment of the defender (Choat and Bellwood, 1985; Robertson and Gaines, 1986; Itzkowitz, 1990). Therefore, one would expect differing levels of aggression with differing intruders, and the intensity of aggression should vary with the potential competitive overlap of the intruder (Myrberg and Thresher 1974; Moran and Sale 1977; Itzkowitz and Slocum 1995). This study investigates social and foraging behaviors of two parrotfishes in the Florida Keys, *Sparisoma aurofrenatum* and *S. chrysopterus*, to specify the roles of microhabitat and foraging overlap in mediating interspecific aggression between them.

In Panama and the Virgin Islands, *S. chrysopterus* are generally associated with seagrass beds and have relatively little overlap with *S. aurofrenatum* (K. E. Clifton, pers. comm.; R. R. Warner, pers. comm.). However, in the Florida Keys, *S. chrysopterus* make extensive forays onto reefs to forage and so encounter patrolling terminal phase (TP, see Materials and Methods) *S. aurofrenatum*. On the reefs, *S. chrysopterus* are frequently the recipients of aggression from TP *S. aurofrenatum*, often involving lengthy vigorous

chasing as well as biting (RCM, pers. obs.). Presumably, TP *S. aurofrenatum* are directing aggression toward *S. chrysopterus* because the latter species is attempting to use territory resources needed by the former. Our research tests two hypotheses: (1) Microhabitat overlap between *S. aurofrenatum* and *S. chrysopterus* reflects preferential utilization of specific feeding substrata over others; and (2) The amount of aggression between the two parrotfishes is greater than that directed toward other reef fish species.

MATERIALS AND METHODS

Study species.—Parrotfishes usually have three distinct color and life-history phases: juvenile phase, initial phase (IP), and terminal phase (TP; Warner and Robertson, 1978). We focused on TP parrotfishes (usually the largest and socially dominant members of the population) because TP *S. aurofrenatum* were initiating the interspecific aggression.

Terminal phase *S. aurofrenatum* (most fish > 14 cm TL) are usually harem and territorial, forming contiguous territories on reefs that they defend against conspecifics (Robertson and Warner, 1978; Clavijo, 1982; RCM, pers. obs.). Their territories contain a group of females with whom the dominant male pair-spawns almost exclusively. Terminal phase *S. aurofrenatum* are rarely seen together except when involved in aggressive interactions, usually involving a territory border dispute. The diet of *S. aurofrenatum* consists mostly of benthic turf algae (Randall, 1967).

In contrast to *S. aurofrenatum*, *S. chrysopterus* are not harem or territorial, although temporary mating territories may be established by

TP individuals (usually fish > 13.5 cm TL) during daily afternoon spawning periods (Robertson and Warner, 1978). *Sparisoma chrysopterum* are often encountered in seagrass beds surrounding coral reefs, where both color phases (IP and TP) spend most of their nonreproductive portion of the day in foraging groups (Robertson and Warner, 1978). Individuals can be recognized on consecutive days in discrete home ranges (Burt, 1943), but multiple *S. chrysopterum* TPs often coexist peacefully in their foraging groups. The diet of *S. chrysopterum* is composed of seagrass and algae (Randall, 1967).

Study sites.—Research for this study was conducted at two sites in the Florida Keys. The Coral Gardens (CG) study site (approximately 80°44'W; 24°51'N) in Hawk Channel consists of numerous patch reefs of various sizes (1 m² to > 2000 m²) surrounded by seagrass beds consisting mostly of Turtle Grass (*Thalassia testudinum*) and Manatee Grass (*Syringodium filiforme*). Coral growth at the site is luxuriant, and the dominant hard corals in the area are Great Star Coral (*Montastrea cavernosa*) and Boulder Star Coral (*Montastrea annularis*). Because of inclement weather, a second study site, Alligator Reef (AR), was used to supplement the observations. The AR site (approximately 80°37'W; 24°51'N) is located on the outer reef tract approximately 11 km northeast and seaward from CG and consists mostly of old coral pavement dominated by gorgonians. Data from both sites were pooled because there were no significant differences between the two study sites in the number of focal species encountered and the amount of aggression directed toward those species, dietary preferences, and time spent feeding and in social interactions (RCM, unpubl.).

Field observations.—Data were collected between 0900 h and 1830 h from June 1994 to February 1996 with scuba and represent 139 h of underwater work. The territories of 10 *S. aurofrenatum* were marked and measured at the CG site. Seven *S. chrysopterum* home ranges were marked and measured, four at the CG site and three at AR. Territories and home ranges were delineated by observing predictable areas of intraspecific aggression between TP *S. aurofrenatum* or by dropping markers where the focal animal changed direction for *S. chrysopterum*. Measurements were taken of the two greatest dimensions (an approximate length and width) of the territory, and the area of the territory was then calculated from these measurements. Areas of irregularly shaped territories were estimated by

combining areas of separate parts of these territories. Sizes (in total length, TL) of focal individuals were estimated by comparing the size of the focal animal against an object on the reef, which was later measured.

For 11 individuals of each species, focal animal sampling with continuous recording (Martin and Bateson, 1993) over a 15-min period was used to determine time spent foraging and time spent in social interactions. Feeding data gathered during the behavioral observations were substrata fed upon [calcareous algae, algal-overgrown hard coral, seagrass, live hard coral (hereafter coral), and other miscellaneous substrata, including bites to sand, macroalgae such as *Dictyota* spp., and coprophagy] and number of bites per both foraging bout and observation period. Calcareous algae consisted primarily (approximately 98%, based on chain transects, see below) of *H. opuntia* and rarely *H. tuna*. Hereafter calcareous algae are referred to as *H. opuntia*.

To test the hypothesis that microhabitat overlap between the two species reflects preferential use of specific feeding substrata over others, the composition of the substratum immediately beneath the focal animal was recorded every 15 sec (instantaneous sampling, Martin and Bateson, 1993). Percent cover estimates of nine microhabitats (coral, seagrass, sand, algal turf, macroalgae greater than 4 cm, encrusting algae, gorgonian, sponge, and rubble) in the study area were determined by randomly placed multiple transects with three meter lengths of 1.5 cm diameter link chain (Porter, 1972). Counting the number of links overlaying various microhabitats gave an estimate of the relative percent cover of these substrata "available" to the parrotfishes. Ten replicate random transects were made per respective territory or home range for the individuals whose territories or home ranges were marked and measured. Three *S. chrysopterum* home ranges were not measured because of inclement weather. The minimum feasible number of transects needed for analyses was determined to be 10 by the method of Harnett (1982). However, the estimates for percent cover of coral should be interpreted with caution because of their patchy distribution.

To test the hypothesis that the amount of aggression between the two parrotfishes is greater than that directed toward other reef fish species, 10 focal individuals of each species were followed during which all fishes encountered by the focal individual were recorded. By comparing the identity of all fishes encountered by *S. aurofrenatum* and *S. chrysopterum* during obser-

vations with the identity of those species who were actually recipients of aggression, we were able to determine whether certain species received disproportionately more aggression than others (as in Low, 1971; Ebersole, 1977; Harrington and Losey, 1990). An encounter was defined as any fish that was directly in the path of the focal individual during the observation period such that either fish had to alter its swimming path to avoid collision. We quantified aggression during observations by recording all social interactions, emphasizing overt aggressive and agonistic displays and behaviors. These included dorsal fin raising, flaring the caudal or pelvic fins, "tail stands" (Clavijo, 1982), nips, and chases by the focal individual. We recorded the species identity of all fishes encountered during social interactions.

Statistical analyses.—All datasets were tested for normality with the Kolmogorov-Smirnov test and for homoscedasticity with the Levene Median test. Originally, time budget data were non-normal, heteroscedastic, and included zero values. The square root ($x + 0.5$) transformation corrected the problem. Consistently nonnormal or heteroscedastic data were analyzed with non-parametric procedures (Siegel and Castellan, 1988).

For chi-square tests of feeding, encounter rate, and microhabitat data, some categories were combined to increase expected frequencies (Siegel and Castellan, 1988; Zar, 1996). Shannon-Wiener diversity indices (H') were calculated from the parrotfishes' foraging behaviors and microhabitat use. A two-way ANOVA of parrotfish time budgets revealed a significant interaction effect between species and social behavior. Consequently, a Tukey test was employed to test differences among subgroup means separately for each species (Day and Quinn, 1989; Sokal and Rohlf, 1995).

RESULTS

General social and feeding behavior.—The TP *S. aurofrenatum* ranged from 23–29 cm TL (mean \pm SD = 24.5 \pm 1.9 cm, $n = 10$), whereas the TP *S. chrysopterus* ranged from 23–41 cm TL (29.0 \pm 5.3 cm, $n = 11$). At both study sites, TP *S. aurofrenatum* spent most of their time feeding on various reef substrata as they patrolled their territories, rarely crossing territorial boundaries. When two TP *S. aurofrenatum* sighted one another, an aggressive display or chase almost always ensued, with cessation of chasing after the intruder had passed over the territory boundary. Patrolling TP *S. aurofrenatum* some-

times ignored females that they encountered, and occasionally the male would join the female at a feeding site, but more often, females were displayed to (which caused them to swim away from the male), supplanted from the foraging site, chased, or nipped.

In contrast, TP *S. chrysopterus* foraged over relatively larger areas of the reefs and moved freely into surrounding seagrass beds up to 15 m from the reef. *Sparisoma chrysopterus* would sometimes forage in groups of three to 15 individuals, containing other TP *S. chrysopterus* or females of various sizes, or other species of fishes such as Redfin Parrotfish, *Sparisoma rubripinne*, Blue Tang, *Acanthurus coeruleus*, Ocean Surgeon, *A. bahianus*, and Doctorfish, *A. chirurgus*. Aggression from TP *S. chrysopterus* consisted of short chases directed mostly at foraging group members, although these fishes rarely elicited or received aggression from *S. chrysopterus* relative to aggression received from *S. aurofrenatum*. We observed no evidence of TP *S. chrysopterus* discontinuing a chase after passing over certain landmarks or boundaries.

Parrotfish territories and home ranges.—*Sparisoma chrysopterus* occupied home ranges (mean \pm SD = 4371.5 \pm 5869.5 m², $n = 7$), which were significantly larger than territories (240.0 \pm 137.4 m², $n = 10$) defended by *S. aurofrenatum* (Mann-Whitney Rank Sum test, $t = 88.0$, $n_1 = 7$, $n_2 = 10$, $P < 0.02$), and any given home range almost always overlapped territories. There was no significant relationship of parrotfish territory or home range size to time spent in aggressive interactions or to time spent feeding for either species (Muñoz, 1996).

Feeding.—Both *S. aurofrenatum* and *S. chrysopterus* spent significantly more time feeding than engaged in social behaviors. *Sparisoma aurofrenatum* fed an average of 85.9 \pm 1.9% (mean \pm SE, $n = 11$) and *S. chrysopterus* fed an average of 94.5 \pm 0.9% ($n = 11$) of 15-min observations [two-way ANOVA on square root ($x + 0.5$) transformed data, behavioral category: $F_{2,60} = 309.2$, $P < 0.0001$; species \times behavioral category: $F_{2,60} = 7.2$, $P < 0.001$; species: $F_{1,60} = 0.02$, NS; Tukey's test: $q_{60,2} = 3.4$, $P < 0.05$; Fig. 1]. Although both parrotfishes spent more time feeding than in social interactions, *S. chrysopterus* spent more time feeding than *S. aurofrenatum*, but this parrotfish spent more time in social interactions (both intra- and interspecific) than *S. chrysopterus*. These two parrotfishes fed differently from different substrata ($\chi^2_4 = 22.84$, $P < 0.001$; Figs. 2–3). *Sparisoma aurofrenatum* took more bites from *H. opuntia* than did *S. chrysopterus*, where-

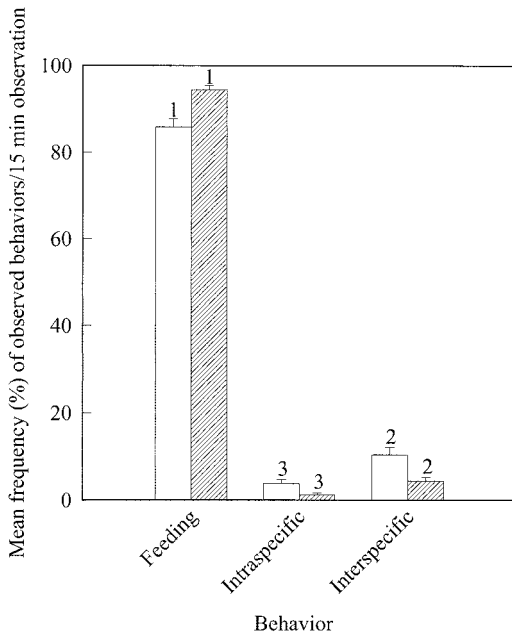


Fig. 1. Mean frequency (%) of observed behaviors of *Sparisoma aurofrenatum* and *Sparisoma chrysopterus* TPs in selected activities. Vertical bars show + 1 SE. Both intra- and interspecific behaviors included chases, displays, and flights. White bars = *S. aurofrenatum*, striped bars = *S. chrysopterus* (n = 11). Differing numbers above bars indicate significant differences with Tukey's test ($P < 0.05$).

as the latter species fed more on both macro- (partitioned $\chi^2_1 = 9.04$, $P < 0.01$) and turf algae (partitioned $\chi^2_1 = 5.82$, $P < 0.05$), and miscellaneous substrata (sand, gorgonian, coral, rubble, encrusting algae, and sponge; partitioned $\chi^2_1 = 6.86$, $P < 0.01$; Figs. 2–3). Despite these differences, both parrotfishes took more bites from *H. opuntia* and fewer bites from coral than would be expected from the percent cover of different microhabitats on territories and home ranges (*S. aurofrenatum*: $\chi^2_2 = 86.21$, $P < 0.001$; *Halimeda*: partitioned $\chi^2_1 = 77.09$, $P < 0.001$; coral: partitioned $\chi^2_1 = 11.48$, $P < 0.001$; Fig. 2; *S. chrysopterus*: $\chi^2_4 = 68.96$, $P < 0.001$; *Halimeda*: partitioned $\chi^2_1 = 53.05$, $P < 0.001$; coral: partitioned $\chi^2_1 = 15.10$, $P < 0.001$; Fig. 3). When feeding on *H. opuntia*, both parrotfishes bit and consumed whole pieces of the thallus rather than grazing on attached epiphytes. *Sparisoma chrysopterus* fed from a greater diversity of substrata than *S. aurofrenatum* (H' for *S. chrysopterus*: 1.30; H' for *S. aurofrenatum*: 0.74). Both parrotfishes took the fewest number of bites per bout when feeding on coral. The mean number of bites per foraging bout for *S. aurofrenatum* (mean \pm SD = 1.56 ± 0.35 , n = 11) was similar

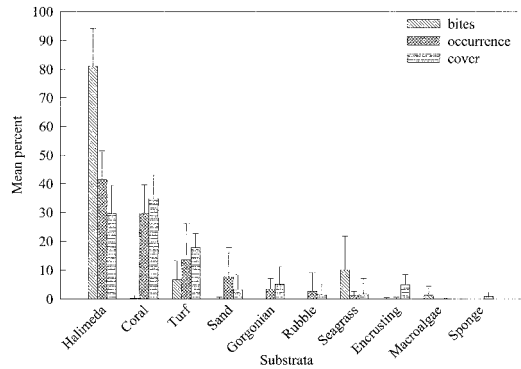


Fig. 2. Feeding and microhabitat use behavior and percent cover of different microhabitats on *Sparisoma aurofrenatum* territories. Vertical bars show + 1 SD. Sample sizes = 11 for feeding and microhabitat observations and 10 for percent cover estimates.

to *S. chrysopterus* (1.12 ± 0.1 , n = 11; Two-Sample Kolmogorov-Smirnov test, two-tailed: $D_{6,6} = 0.204$, NS).

Microhabitat use.—*Sparisoma aurofrenatum* spent more time over *H. opuntia* than all other substrata (Fig. 2), and *H. opuntia* and corals occupied more cover on their territories than all other substrata (Fig. 2). *Sparisoma aurofrenatum* used microhabitats in the proportions in which they occurred in their territories ($\chi^2_3 = 3.98$, NS).

Like its congener, *S. chrysopterus* also spent more time over *H. opuntia* than all other substrata, yet turf algae growing on coral pavement occupied more percent cover than all other substrata on home ranges (Fig. 3), indicating that *S. chrysopterus* actively selected *H. opuntia* (χ^2_6

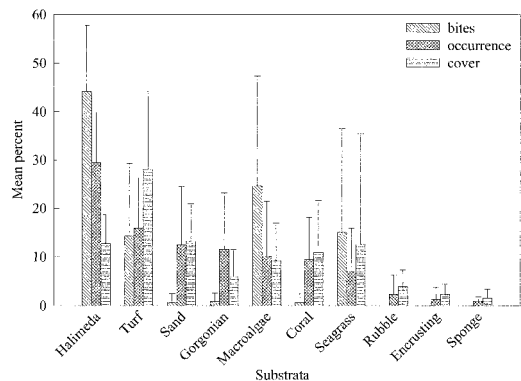


Fig. 3. Feeding and microhabitat use behavior and percent cover of different microhabitats on *Sparisoma chrysopterus* home ranges. Vertical bars show + 1 SD. Sample sizes = 11 for feeding and microhabitat observations and 10 for percent cover estimates.

= 18.1, $P < 0.01$; partitioned $\chi^2_1 = 15.35$, $P < 0.001$). *Sparisoma chrysopterym* had broader microhabitat use patterns than did *S. aurofrenatum* (H for *S. chrysopterym*: 1.98; H for *S. aurofrenatum*: 1.47). Additionally, microhabitat composition of home ranges was different from that of territories ($\chi^2_8 = 112.7$, $P < 0.001$), because of differing percent cover of *H. opuntia* (partitioned $\chi^2_1 = 19.2$, $P < 0.001$), macroalgae and sponges (combined, partitioned $\chi^2_1 = 20.9$, $P < 0.001$), sand (partitioned $\chi^2_1 = 14.4$, $P < 0.001$), seagrass (partitioned $\chi^2_1 = 15.1$, $P < 0.01$), and coral (partitioned $\chi^2_1 = 39.7$, $P < 0.001$) occurring on territories compared to home ranges.

Sparisoma aurofrenatum and *S. chrysopterym* overlapped significantly and intermediately in microhabitat use (Kendall's Coefficient of Concordance test, $W = 0.5$, $n = 10$, $k = 22$; W ranges from zero to one, with a value of zero indicating no overlap and a value of one indicating complete overlap; $\chi^2_9 = 108.0$, $P < 0.001$). However, comparing overall microhabitat use between the two parrotfishes revealed no significant difference (two-sample Kolmogorov-Smirnov test, two-tailed: $D_{10,10} = 0.323$, NS).

Aggressive interactions.—Both *S. aurofrenatum* and *S. chrysopterym* directed most of their aggression (i.e., overt aggressive displays and attacks) toward confamilials (Mann-Whitney Rank sum test: *S. aurofrenatum*— $t = 51.0$, $n_1 = 15$, $n_2 = 3$, $P < 0.01$; *S. chrysopterym*— $t = 48.0$, $n_1 = 15$, $n_2 = 3$, $P < 0.03$). Further, for both parrotfishes, their encounter rates with other fishes did not affect the distribution of their aggression toward those species ($R \times C$ test of independence: *S. aurofrenatum*— $G_{adj,5} = 62.6$, $P < 0.001$; Fig. 4A; *S. chrysopterym*— $G_{adj,4} = 13.6$, $P < 0.01$; Fig. 5A). For example, *S. aurofrenatum* encountered snappers (Lutjanidae) and grunts (Haemulidae) as frequently or more than other parrotfishes (Fig. 4B), yet these two groups received comparatively little aggression. Similarly, *S. chrysopterym* only encountered grunts as frequently as other parrotfishes (Fig. 5B), yet haemulids received comparatively little aggression from this parrotfish. The two study species were more aggressive when they encountered parrotfishes than when they encountered other species of fishes (Figs. 4–5). Both *S. aurofrenatum* and *S. chrysopterym* were most aggressive toward conspecifics, then toward each other, and then toward other parrotfishes and other fishes from different families.

Sparisoma aurofrenatum and *S. chrysopterym* engaged in significantly more interspecific encounters than intraspecific encounters ["encounters" here include both aggressive encoun-

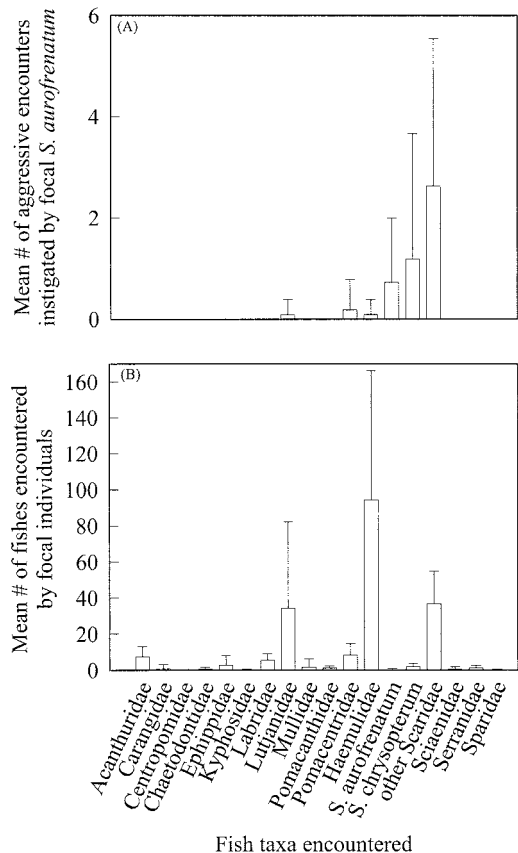


Fig. 4. (A) Mean number of aggressive encounters by *Sparisoma aurofrenatum* TPs during 15-min observations ($n = 11$). (B) Families of fishes encountered by *S. aurofrenatum* TPs during 15-min observations ($n = 10$). Vertical bars show $+1$ SD. For (A) and (B), the categories *S. aurofrenatum* and *Sparisoma chrysopterym* refer to TPs. Initial phases of these species are included in the "other Scaridae" category, which also includes *Sparisoma rubripinne*, *Sparisoma viride*, Midnight Parrotfish, *Scarus coelestinus*, Rainbow Parrotfish, *Scarus guacamaia*, Striped Parrotfish, *Scarus iserti*, and Queen Parrotfish, *Scarus vetula*.

ters instigated and received by focal animals, two-way ANOVA on square root ($x + 0.5$) transformed data, behavioral category: $F_{2,60} = 309.2$, $P < 0.0001$; species \times behavioral category: $F_{2,60} = 7.2$, $P < 0.001$; species: $F_{1,60} = 0.02$, NS; Tukey's test: $q_{60,2} = 3.4$, $P < 0.05$; Fig. 1]; $10.4 \pm 1.7\%$ (mean \pm SE, $n = 11$) versus $3.8 \pm 1.0\%$, respectively, for *S. aurofrenatum*, and $4.3 \pm 0.8\%$ versus $1.2 \pm 0.5\%$, respectively, for *S. chrysopterym*. Territorial *S. aurofrenatum* were more aggressive than home-ranging *S. chrysopterym* and were involved in more aggressive encounters than the latter parrotfish. When only interspecific aggressive interactions were considered

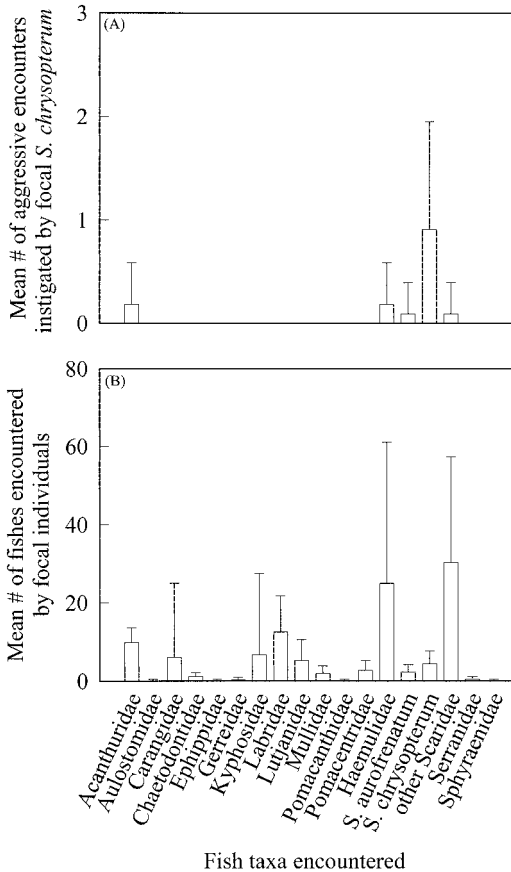


Fig. 5. (A) Mean number of aggressive encounters by *Sparisoma chrysopterym* TPs during 15-min observations (n = 11). (B) Families of fishes encountered by *S. chrysopterym* TPs during 15-min observations (n = 10). Vertical bars show + 1 SD. For (A) and (B), the categories *Sparisoma aurofrenatum* and *S. chrysopterym* refer to TPs. Initial phases of these species are included in the "other Scaridae" category, which also includes *Sparisoma rubripinne*, *Sparisoma viride*, Blue Parrotfish *Scarus coeruleus*, *Scarus guacamaia*, *Scarus iserti*, and *Scarus vetula*.

(chases and displays instigated by focal animals), *S. aurofrenatum* engaged in $2.0 \pm 2.61\%$ (mean \pm SD, n = 11) aggressive interactions per 15 min versus $0.45 \pm 0.52\%$ interactions for *S. chrysopterym*, a greater than fourfold difference despite a less than twofold difference in interspecific encounter rate (Table 1). Size (TL in cm) was not significantly related to the aggressive behaviors instigated by *S. aurofrenatum* or *S. chrysopterym* (Muñoz, 1996).

DISCUSSION

Sparisoma aurofrenatum and *S. chrysopterym* overlap significantly in microhabitat use and foraging behavior. Both species of parrotfishes are found over *H. opuntia* and feed more on *H. opuntia* than on all other substrata. The two species feed at similar rates from similar substrata, and the average number of bites per feeding bout for both species is similar regardless of substratum type. However, it is not known whether an equal quantity of food is taken by each species per bite. Most of the parrotfishes' time is spent feeding (80–95% of time budgets), results that agree with those of other authors (Horn, 1989; Bellwood, 1995; van Rooij et al., 1996b) for parrotfishes and other herbivorous reef fishes.

Sparisoma aurofrenatum is confined to a territory and grazes substrata (primarily *H. opuntia*) in proportion to their occurrence in its territory. *Sparisoma chrysopterym*'s larger home ranges give it the liberty to forage from a broader variety of substrata than *S. aurofrenatum*, but it still feeds primarily from *H. opuntia*, even though this substratum is less abundant on home ranges than on territories. Thus, *S. chrysopterym* actively selects *H. opuntia* over all other types of food substrata. In contrast, large (≥ 100 individuals) feeding schools of *S. chrysopterym* are common in Panamanian seagrass beds

TABLE 1. AGGRESSIVE AND NONAGGRESSIVE ENCOUNTERS OF TP PARROTFISHES. Values are mean (\pm SD) per 15 min. Nd = no aggressive encounters observed.

Encountered species	Focal species			
	<i>S. aurofrenatum</i> encounters		<i>S. chrysopterym</i> encounters	
	Aggressive n = 11	Nonaggressive n = 10	Aggressive n = 11	Nonaggressive n = 10
<i>S. aurofrenatum</i>	0.73 (1.27)	0.3 (0.48)	0.09 (0.30)	2.3 (1.83)
<i>S. chrysopterym</i>	1.18 (2.48)	1.9 (1.79)	0.91 (1.04)	4.4 (3.27)
other Scaridae	2.64 (2.91)	36.6 (18.06)	0.09 (0.30)	30.3 (26.89)
Haemulidae	0.09 (0.30)	94.3 (71.83)	0.18 (0.40)	24.9 (36.09)
Lutjanidae	0.09 (0.30)	34.3 (47.85)	nd	5.2 (5.33)
Pomacentridae	0.18 (0.60)	8.3 (6.18)	nd	2.7 (2.45)
Acanthuridae	nd	7.5 (5.4)	0.18 (0.40)	9.8 (3.79)

(Robertson and Warner, 1978), and large (> 27 cm) individuals there take most of their bites from seagrass (McAfee and Morgan, 1996), as do TP *S. aurofrenatum* (Dubin, 1981). Additionally, Panamanian *S. aurofrenatum* have the broadest diet of five parrotfishes studied (McAfee and Morgan, 1996). Dietary and parrotfish distribution differences between Panamanian and Florida Keys populations may be a result of differences in seagrass or algal productivity and abundance. *Halimeda opuntia* may be the most abundant and available resource for these two parrotfishes in the Florida Keys.

Greater flexibility in habitat use for a home ranging species does not necessarily imply that a territorial species is at a disadvantage. Bruggemann et al. (1994a) found that territories of Stoplight Parrotfish, *Sparisoma viride*, had richer and more accessible food patches than the rest of the reef. Territorial *S. viride* spent less time foraging than nonterritorials, but the lower foraging effort still produced a similar food intake because of higher yields per bite on territories (Bruggemann et al., 1994b). In the Florida Keys the relatively higher percent cover of *H. opuntia* on territories than compared with home ranges may afford an advantage to resident *S. aurofrenatum* (if percent cover relates to total abundance), enabling them to spend less time feeding than *S. chrysopterus*. The abundance of refuges on the reef compared to off the reef may also benefit territorial *S. aurofrenatum*.

The amount of aggression between *S. aurofrenatum* and *S. chrysopterus* in the Florida Keys is significantly greater than that directed toward other reef fish species and is not proportional to the encounter rates among species. Together, both parrotfishes encounter at least 71 different species of fishes from 18 families, yet interspecific aggression by *S. aurofrenatum* and *S. chrysopterus* is primarily confined toward other parrotfishes. Harrington and Losey (1990) identified intruder species as the most important proximate effect on chasing behavior of a damselfish. The pattern of aggression displayed by the two parrotfishes (more aggression toward conspecifics, less toward congeners, and less toward confamilials or other fishes) agrees with most results for other parrotfishes and pomacentrids, probably because the more closely related fishes are to each other the more likely they require similar resources (but see Ebersole, 1977; Itzkowitz, 1990; van Rooij et al., 1996a).

Although the general pattern of aggression observed in our study is consistent with previous work, the frequency with which *S. aurofrenatum* and *S. chrysopterus* engage in social interactions is higher in the present study than in other stud-

ies of parrotfishes. Previous research with Panamanian and Puerto Rican *S. aurofrenatum*, *S. chrysopterus*, and other Caribbean parrotfishes, showed they engaged rarely in interspecific aggressive interactions (Dubin, 1981; Clavijo, 1982; van Rooij et al. 1996b). However, McAfee and Morgan (1996) found that, although all five parrotfish species they examined used similar resources, each species had a unique pattern of resource use. Numerous studies have examined dietary or habitat overlap in fishes and found apparent high overlap in certain dimensions to be offset by differences in another dimension (e.g., Robertson and Gaines, 1986; Bellwood and Choat, 1990; Bruggemann et al., 1994c).

How do we explain the patterns of relatively high rates and frequent occurrences of interspecific interactions for *S. aurofrenatum* and *S. chrysopterus*? The extensive overlap with the coral reef habitat that *S. chrysopterus* has in the Florida Keys, coupled with its home-ranging behavior, may place this parrotfish in potentially more encounters with aggressive fishes (such as TP *S. aurofrenatum*), in contrast to studies of the same species elsewhere. In comparison, *S. aurofrenatum* is restricted to living and feeding from within the confines of a territory. The "dear enemy" effect (Fisher 1954), or recognition of neighbors combined with respect for neighboring territorial boundaries, may be operating in *S. aurofrenatum* social systems. This would result in very low numbers of intraspecific interactions with neighboring TPs. The dear enemy effect, together with *S. chrysopterus*'s overlap onto the reef would translate into more observable inter- than intraspecific interactions for *S. aurofrenatum*. In the present study, TP *S. aurofrenatum* encountered conspecific TPs more than six times as infrequently as they encountered TP *S. chrysopterus* and more than 120 times as infrequently as they encountered other parrotfishes. Alternatively, *S. aurofrenatum* may attack *S. chrysopterus* irrespective of their overlap in resources but simply because *S. chrysopterus* is closer than another intruding fish to an attacking male *S. aurofrenatum* attempting to clear his territory of intruders. For herbivorous species, often, the chasing of one individual results in clearing the territory of all other intruders (Low 1971; Harrington and Losey 1990; RCM, pers. obs. for parrotfishes).

The overlap in microhabitat utilization and foraging behavior complements the extensive overlap that *S. chrysopterus* home ranges have on multiple *S. aurofrenatum* territories in the Florida Keys study sites. Our estimates of average *S. aurofrenatum* territory size (240.0 m²) are larger than Clavijo's (1982) estimate of 88 m²

and smaller than Hoffman's (in Dubin, 1981) estimates which ranged from 500–1000 m². Multiple factors may influence territory size such as the distribution of the resource being defended (Pottle and Green, 1979; Hixon, 1987; Grant, 1993) or competitor density (Norman and Jones, 1984; review by Carpenter, 1987; Tricas, 1989), both that may vary widely within and among reefs (Shapiro, 1991). The results of our study (e.g., variation in *S. aurofrenatum* territory size, relatively high rates of interspecific encounters, overlap of microhabitat and similar foraging behavior) further support the recent suggestion that intraspecific alternative forms of social organization (e.g., geographic variation in behavior) are common (Lott, 1991; Warner, 1991; Foster, 1996). Among-site differences in behavior may be dependent on factors such as reef size, food availability, population density, or individual mortality rates (Aldenhoven, 1986; Roberts and Ormond, 1992; Sakai, 1997). The phenotypic plasticity of parrotfish social and mating systems suggests that different types of individuals (i.e., territorial, bachelors, pair or group spawning, etc.) may attain differential success in different habitats (Randall and Randall, 1963; Warner and Downs, 1977; Warner, 1991).

Our study shows that, in the Florida Keys, there is significant microhabitat overlap between *S. aurofrenatum* and *S. chrysopterygus*; the amount of aggression between the two parrotfishes is significantly greater than that directed toward other fish species, and the two parrotfishes' encounter rates with other fishes has no influence on the manner in which they distribute their aggression toward those species. These two herbivores broadly overlap in use of microhabitat and distribution and have similar foraging strategies. Together with their differing social systems, these factors likely contribute to the disproportional interspecific aggression that exists in the Florida Keys.

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