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# SCHOOLING AS A MECHANISM FOR CIRCUMVENTING THE TERRITORIALITY OF COMPETITORS<sup>1</sup>

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**Abstract.** The herbivorous striped parrotfish *Scarus croicensis* exhibits pronounced within-site variability in its social behavior: some individuals hold permanent feeding territories while others form feeding schools. Members of both of these classes are subordinate to the omnivorous damselfish *Eupomacentrus planifrons* which strongly inhibits the feeding of parrotfish in its own feeding territories. To a lesser degree, territorial *S. croicensis*, whose territories are superimposed on those of *E. planifrons*, also inhibit the feeding of nonterritorial conspecifics. Data show that nonterritorial *S. croicensis* in schools feed at higher rates, and are attacked by territory owners less often than nonschooling nonterritorials. This supports the hypothesis that schooling enables those individuals to circumvent the territoriality of their competitors. Nonterritorial *S. croicensis* apparently constitute that proportion of the population that cannot obtain feeding territories, probably primarily as a result of the aggressive activities of *E. planifrons*, and schooling thus promotes the coexistence of these territorial and nonterritorial forms. A number of other teleost species, benthic-browsing omnivores, and herbivores, that associate with *S. croicensis* schools and are subject to strong aggression from *E. planifrons*, derive benefits from this association in the same way as the schooling parrotfish do. Predators that associate with *S. croicensis* schools, and that are little attacked by *E. planifrons*, benefit instead by feeding on organisms disturbed by the feeding school.

**Key words:** *Coexistence; competition; herbivores; omnivores; Panama; San Blas Islands; schooling; territoriality.*

## INTRODUCTION

Schooling is common in a great number of fishes of many different ecotypes, living in a variety of environments. A large body of information has accumulated on schooling behavior, particularly since many schooling species are of economic importance. Suggestions as to the adaptive significance of schooling have concentrated largely on predator-prey relationships (Brock and Riffenburgh 1960, Cushing and Harden Jones 1968, Ehrlich 1975, Ehrlich and Ehrlich 1973, Eibl-Eibesfeldt 1962, Hobson 1968, Manteifel and Radakov 1961, Neill and Cullen 1974, Pitcher 1973, Seghers 1974, Vine 1973). Some thought has also been given to the mechanical advantages gained by fishes swimming in schools (Belyayev and Zuyev 1969, Weihs 1973) and the possibility that schooling facilitates reproductive activities and migrations (Shaw 1970).

Coral reefs contain an abundance of herbivorous,

carnivorous, and omnivorous territorial fishes, and the agonistic interactions between these and the many nonterritorial species present potential problems to the nonterritorial fishes. Jones (1968), in studying the ecology of a number of acanthurids in the central Pacific, observed that a small and inoffensive species, *Acanthurus triostegus*, formed schools, and suggested that this constituted a defense against the territoriality of aggressively more dominant congeners. Vine (1974) has similarly proposed that schooling enables the Red Sea surgeonfish *Acanthurus sohal* to feed in the territories of other species.

Although Barlow (1974) has extended Jones' (1968) idea with respect to *A. triostegus*, and presented some supporting data, there have been no thorough tests made of this hypothesis. It has not been shown either that territorial fishes do actually inhibit the feeding of nonterritorial species in their territories, or that members of feeding schools of such nonterritorial species have higher feeding rates than do nonschooling individuals; nor has it been shown that such differences in feeding rates can be accounted for by differences in the frequency

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with which individuals of these two classes receive attacks from territory owners.

The striped parrotfish, *Scarus croicensis* Bloch, is one of the commonest Caribbean scarids (Randall 1967), where it is widely distributed on coral reefs. Ogden and Buckman (1973) and Buckman and Ogden (1973) recognized three social classes in that species, with representatives of all classes living on the same reef: (1) territorial individuals, (2) "foraging groups" [= feeding schools], and (3) small "stationary groups" that remain in small undefended areas. They observed that territorial *S. croicensis* defended their territories against nonterritorial conspecifics and that members of both of these classes were vigorously attacked by the omnivorous, territorial damselfish *Eupomacentrus fuscus* Cuv. and Val. [= *E. dorsopunicans*—see Greenfield and Woods 1974]. With this in mind, we decided to test the possibility that by schooling, nonterritorial *S. croicensis* increased their chances of gaining access to food in the territories of both conspecifics and damselfishes and that schooling thus facilitated the coexistence of these territorial and nonterritorial forms. As our initial observations showed that *E. dorsopunicans* was rare in the study area chosen, but that a close relative, the three-spot damselfish, *E. planifrons* (Cuvier), which is also omnivorous, was both abundant there and aggressively dominant over *S. croicensis*, we examined the relationship between *E. planifrons* and *S. croicensis*.

On coral reefs, both mono and multispecific schools of benthic-browsing fishes are commonly encountered. Multispecific schools typically contain a nuclear species, one that numerically predominates in the school and frequently forms monospecific schools, and a number of associate species. Some of these associates form schools of their own and may act as the nuclear species of multispecific schools; other only join schools as associates. Ogden and Buckman (1973) documented the association of various herbivores and carnivores with *S. croicensis* schools. Our preliminary observations showed that some of these associates were also being regularly attacked by *E. planifrons*, and we decided to test whether participation in schools was adaptive for these species in the same way as we were proposing it was for *S. croicensis*.

#### METHODS

The study was conducted in the San Blas Islands of Panama. All quantitative data were collected, and all experiments performed on the reef named Airstrip Reef in Fig. 1 of Ogden and Buckman (1973), between August and November of 1974. Data were collected between 0800 and 1630 h.

To assess whether territorial conspecifics and *E. planifrons* could inhibit the feeding activity of non-

territorial *S. croicensis*, and if any such inhibition depended on whether the nonterritorials were schooling, we made two series of observations on nonterritorials and conducted two series of experiments. In each series of observations we recorded, per unit time, the number of bites made on the substrate by an individual parrotfish and the number of attacks on it by *E. planifrons* and by territorial *S. croicensis*. Separate series of observations were made on nonterritorial parrotfish in schools (school members or Schoolers) and on nonschooling individuals (lone parrotfish or Loners, i.e., < five individuals in a group). In 10 experiments, the feeding activity of nonterritorials in areas before and after the removal of either (a) all *E. planifrons* (four experiments) or (b) all territorial *S. croicensis* (six experiments) was recorded (see Table 1). Further, following two of the experiments in which territorial *S. croicensis* were removed, we removed *E. planifrons* from the same areas, with pre- and post-removal observations on feeding by nonterritorials again being made.

Both territorial and nonterritorial *S. croicensis* lived and fed in the habitat occupied by *E. planifrons*, and we recorded their feeding rates and rates of attack on them by *E. planifrons* so that we could make comparisons between them. We also performed four *E. planifrons* removal experiments with the territorials so that any inhibition of their feeding activity by the damselfish could be assessed.

Intensive observations were made on six species that associated with *S. croicensis* schools: *Acanthurus coeruleus* Bloch and Schneider, *Chaetodon capistratus* Linn., *Chaetodon striatus* Linn., *Chaetodon ocellatus* Bloch, *Hypoplectrus puella* (Cuv. and Val.), and *Aulostomus maculatus* Val. The same observation and experimental procedures (with four *E. planifrons* removal experiments) were used, as with *S. croicensis*.

Observation periods on schooling and lone individuals of both *S. croicensis* and the associates varied from 5–30 min. An attack, at its minimum intensity, was considered to have occurred when a movement (nonsexual in the case of interactions between *S. croicensis*) was directed at the receiver that the receiver was apparently capable of perceiving.

As with many other parrotfishes, *S. croicensis* is partially sexually dichromatic: juveniles, females, and smaller males belong to a plainly striped Initial Phase, while larger males are in the more brightly colored Terminal Phase (Randall 1963, 1968). Both color phases contribute to the three social classes described by Ogden and Buckman (1973). Small fish also formed separate schools from large ones, as schools tended to be composed of similarly sized individuals.

Because of this, separate observations were made on Juveniles (classed here as individuals  $\leq 70$  mm

TABLE 1. Procedure for the removal experiments

Class of experiment	Feeding activity observed of:	Experiments			Controls			
		Exp. no.	Area (m <sup>2</sup> )	Hours observation before/after removal	Control no.	Area (m <sup>2</sup> )	Hours observation before/after	
<i>Eupomacentrus planifrons</i> removals	Nonterritorial <i>Scarus croicensis</i>	1	7.8	8.5/10.5	1	7.5	2/2	
		2	6.6	8/8	2	10.5	2/2	
		3	16.0	2/2	3	9.0	2/2	
		4	12.0	2/2	4	16.0	2/2	
		5	20.0	2/2				
		6	20.0	2/2				
		Territorial <i>Scarus croicensis</i>	1	16.0	2/2	Same as above		
	2		16.0	2/2				
	3		16.0	2/2				
	4		4.0	2/2				
		School associate species	1	7.5	2/2	Same as above		
	2		15.0	2/2				
	3		9.5	2/2				
	4		22.5	2/2				
	Territorial <i>Scarus croicensis</i> removals	Nonterritorial <i>Scarus croicensis</i>	1	16.0	2/2	Same as above		
2			12.0	2/2				
3			20.0	2/2				
4			20.0	2/2				
5			20.0	2/2				
6			20.0	2/2				

\*<sup>1</sup> These experiments were conducted in the same areas as experiments \*<sup>2</sup>.

total length, although they are probably sexually mature), on initial-phase adults, and on terminal-phase adults to see if there were differences between them. While we were able to catch, tag (using color-coded glass beads sewn through the dorsal musculature), and make observations on specific individuals in the juvenile schools, this was not possible with schooling adults. Because of the fact that adult schools often contained hundreds of fish in a compact mass, we were unable to keep track of untagged individuals for more than a couple of minutes. Instead, since each adult school moved and fed as a cohesive, coordinated unit, for each half-hour observation period we used a composite individual—as soon as the fish under observation was lost in the milling mass, the observer's attention was switched to another nearby individual engaged in the same activity, and data recording continued.

With the removal experiments, pre- and post-removal observations were made on the same day in all the experiments of short duration, and over several days in two longer-term ones. In each case, the *E. planifrons* or territorial *S. croicensis* were removed by spearing immediately after the pre-removal observation period, and post-removal observations were begun  $\approx$  1 h after the finish of the removal procedure. In *E. planifrons* removal experiments, diffusion of damselfish into the cleared area from the surrounding coral began almost immediately after the removal procedure. This began

the post-removal observation period as these new "residents" immediately began attacking parrotfish.

Controls for these experiments consisted of the same sequence of activities, except that, although each area was disturbed by diver activity (disturbance of the substrate during spearing operations invariably attracted fishes to the area), no *E. planifrons* or territorial *S. croicensis* were removed. A total of four controls were run. The sizes of areas used in the experiments and controls, and the observation schedules are shown in Table 1.

In some of the experiments and controls the actual number of visits made and bites taken from the area was recorded. However, during periods of great activity this was not possible, and feeding activity was then usually estimated in the following manner. Individuals present in the area were counted at 5-min intervals, and a mean number of individuals present at any one time calculated from this. An estimate of the total number of bites was made by (1) counting the number of bites taken by various individuals in a number of 2.5-min periods and calculating a mean bite rate from that, then (2) multiplying this bite rate by the total observation time and by the mean number of individuals present. (While with *S. croicensis* twelve 2.5-min periods were usually used in calculating a mean bite rate, with the associate species only four 2.5-min periods were used, as data were collected on all six during each experiment.) In three of the early experiments

TABLE 2. Activity of *Scarus croicensis* schools: Means with 95% confidence limits for movement, feeding, and attacks from *Eupomacentrus planifrons* and territorial conspecifics

School	Rate of movement (m/half hour)	Min feeding <sup>a</sup> / half hour	No. attacks by <i>E.</i> <i>planifrons</i> /half hour	No. attacks by territorial conspecifics/half hour
Adult	137 ± 21.8 N = 16	20.9 ± 1.3 N = 18	546 ± 75 N = 20	144 ± 39 N = 20
Juveniles	51 ± 7.2 N = 14	21.6 ± 1.4 N = 22	477 ± 69 N = 29	87 ± 33 N = 29

<sup>a</sup> A school was defined as feeding when at least 20% of its members were feeding. In practice, almost all members of a school fed during a feeding bout.

feeding activity was recorded as the number of fish-feeding minutes. This was then converted to a number of bites, using the known mean feeding rate of schooling nonterritorials.

No data were collected on any of the species at times when large amounts of zooplankton were moving through the study area, as then many normally substrate-feeding fishes, including *S. croicensis*, *E. planifrons*, and some of the school associates, rose up and fed in midwater.

## RESULTS

### I. *Scarus croicensis*

*Activity of nonterritorials in the E. planifrons habitat.*—Schools of adult *S. croicensis*, which typically comprised several hundred individuals, were characteristically associated with areas of good coral cover (Ogden and Buckman 1973). They rarely moved more than a meter onto the surrounding sand and turtle grass flats. In the study area, schools moved unpredictably to and fro across the entire half-hectare coral patch in depths of from 2 to at least 7 m. Aptly named "Foraging Groups" by Ogden and Buckman (1973), they spent most of their time feeding (Table 2). Juvenile schools did not attain the same size as typical adult schools, and we never observed any containing more than ≈ 50 individuals. They were much more sedentary than adult schools (Table 2), rarely covering more than 100 m<sup>2</sup> during several hours of observation, and remaining within the same 200–300 m<sup>2</sup> area throughout the 3-mo study period. Several tagged juveniles remained in the same school for at least 3 mo. Juvenile schools spent the same proportion of their time feeding as adult schools did (Table 2). Up to three adult schools were known to be in the study area at any one time. Upon meeting, they often coalesced, and large schools sometimes split into smaller ones.

Contrary to Ogden and Buckman's (1973) report that on overcast days, and in dirty water, schools sometimes did not form at all, we observed them under all weather and water conditions. While on

a number of occasions we were unable to find an adult school in the study area, we feel that they failed to form only on the infrequent occasions when large numbers of nonterritorials were dispersed throughout the study area feeding on zooplankton that flowed through it.

*Eupomacentrus planifrons* was abundant throughout the coral zone (a sample of 50 × 1-m squares scattered throughout the study area yielded a mean density of 3.6/m<sup>2</sup>, with a range of from 2–5/m<sup>2</sup> [these included individuals using only part of the m<sup>2</sup>]). Adult schools were under continual harassment from attacks by them and, to a lesser degree, territorial *S. croicensis*, regardless of whether or not they were feeding (Table 2). Juvenile schools were also subjected to frequent attacks from both *E. planifrons* and territorial *S. croicensis*, although they suffered fewer attacks from conspecifics than did adult schools (Mann-Whitney *U*-test, *p* < .005) (and probably fewer from *E. planifrons*, since the numbers of its attacks on adult schools were in some cases undoubtedly underestimated). These attacks were largely ineffective in preventing adult schools settling and feeding.

Lone *S. croicensis*, although often difficult to find, moved about and fed in the same habitat as schools and were attacked by both *E. planifrons* and territorial *S. croicensis*. Juvenile and adult loners of both color phases, fed at lower rates than equivalent schoolers (Table 3, *U*-test, *p* < .001 in all cases) and were also attacked by *E. planifrons* more frequently than were equivalent schoolers (*U*-test, *p* < .001 in all three cases). However, while adult loners were attacked by territorial conspecifics as frequently as were adult schoolers, juvenile loners were attacked less frequently than were juvenile schoolers (*U*-test, *p* < .05). Also, while there were no differences between the rates at which adult loners of the two color phases were attacked, either by *E. planifrons* or by territorial conspecifics, juvenile loners were attacked more often by *E. planifrons* and less often by territorial conspecifics than were adult loners (*U*-test, *p* < .01 in all cases).

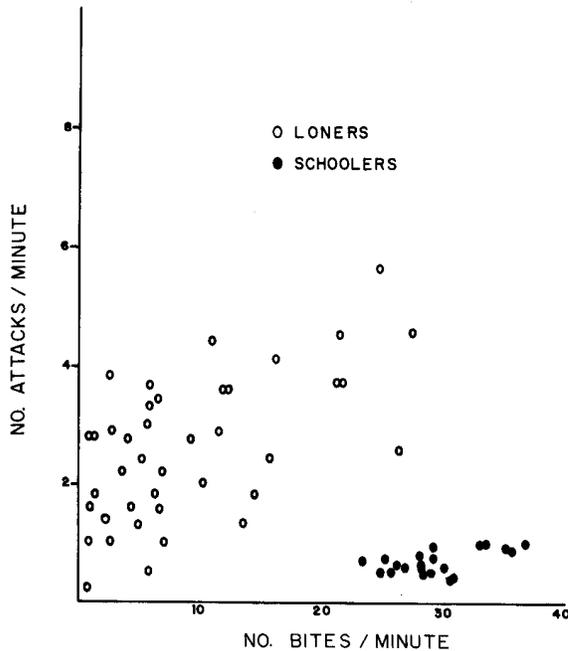


FIG. 1. Feeding rates of individual adult *Scarus croicensis* in relation to the frequency of attacks on them by *Eupomacentrus planifrons*.

Similarly, while adult schoolers of the two color phases were attacked at the same rates by *E. planifrons* and the same rates by territorial *S. croicensis*, juvenile schoolers were attacked more often than adult schoolers by *E. planifrons* and less often by territorial conspecifics (*U*-test,  $p < .001$  in all cases).

Nonterritorial *S. croicensis* differed in their re-

sponses to attacks from territory owners, depending on whether or not they were in schools. A school member typically showed only low-intensity avoidance reactions to the attacks and moved only a short distance before resuming feeding in the school. Lone parrotfish responded more strongly to attacks, often ceasing feeding completely and fleeing large distances before attempting to return to the substrate. Attacks occurred regardless of whether or not the loners were feeding. Territorial attacks by both species were also characteristically more prolonged when directed at loners, with the intruder being chased well away; whereas, with schoolers, the attacker's attention was usually quickly transferred to another fish. Thus, few school members suffered as much harassment as loners.

There were differences between the relationships of the frequencies of attacks by territorial conspecifics and *E. planifrons* on the different age classes of nonterritorial parrotfish to the feeding rates of those parrotfish:

1) While there were no correlations between the feeding rates of individual juvenile schoolers and the frequencies of attacks on them by either territorial species, individual adult schoolers experienced slightly higher rates of attack from *E. planifrons* when they fed at higher rates (Fig. 1, Spearman Rank Correlation Coefficient,  $r = .46$ ,  $p < .05$ ) and slightly lower rates of attack from territorial conspecifics (Fig. 2, Spearman Rank Correlation Coefficient,  $r = -.41$ ,  $p < .05$ ). However, the frequency of attacks by either *E. planifrons* or territorial conspecifics on an adult or juvenile school

TABLE 3. Mean feeding rates and mean rates of attack by *Eupomacentrus planifrons* and by territorial conspecifics, for individual *Scarus croicensis* of each class. Numbers in parentheses indicate standard deviation

Color phase	Social class	Bites/min	<i>E. planifrons</i> attacks/min	Territorial <i>S. croicensis</i> attacks/min	Sample size
<b>Initial</b>					
Juvenile	Schoolers	28.5 (6.0)	1.33 (0.41)	0.26 (0.24)	750 min $N = 25$
	Loners	14.6 (8.3)	4.17 (1.91)	0.21 (0.27)	300 min $N = 28$
	Territorials	32.9 (7.8)	2.16 (1.03)		300 min $N = 20$
Adult	Schoolers	30.4 (4.6)	0.74 (0.20)	0.42 (0.10)	300 min $N = 10$
	Loners	7.3 (11.7)	2.53 (1.59)	0.92 (0.77)	209 min $N = 18$
	Territorials	25.0 (11.0)	0.71 (0.43)		450 min $N = 15$
<b>Terminal</b>					
Terminal	Schoolers	29.0 (3.0)	0.72 (0.23)	0.49 (0.19)	300 min $N = 10$
	Loners	11.9 (7.7)	2.86 (1.09)	0.86 (0.61)	200 min $N = 23$
	Territorials	32.6 (6.1)	0.94 (0.32)		450 min $N = 15$

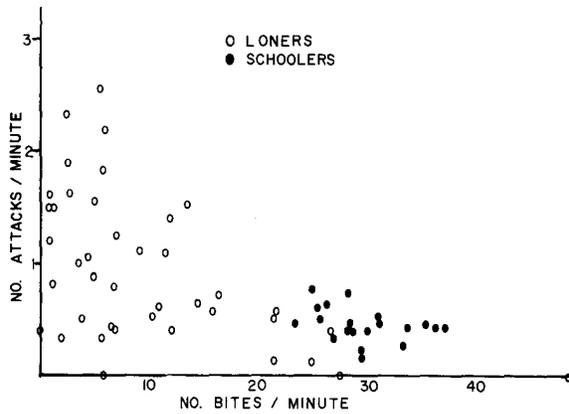


FIG. 2. Feeding rates of individual adult *Scarus croicensis* in relation to the frequency of attacks on them by territorial conspecifics.

as a whole was not correlated with the proportion of its time that the school spent feeding.)

2) Also, while high feeding rates of adult loners were correlated with high rates of attack from *E. planifrons* (Fig. 1, Spearman Rank Correlation Coefficient,  $r = .52$ ,  $p < .01$ ) and low rates of attack from territorial conspecifics (Fig. 2, Spearman Rank Correlation Coefficient,  $r = .46$ ,  $p < .01$ ), there were no significant correlations between the feeding rates of juvenile loners and the rates at which they were attacked by either species.

*Activity of territorials in the E. planifrons habitat.*—Territorial *S. croicensis* were scattered throughout much of the coral patch study area, as isolated terminal-phase males and in groups composed of a single terminal-phase male and up to five initial-phase individuals (Buckman and Ogden 1973, our own observations). All group members fed within the group's territory and the occupant terminal-phase males also spawned there (Randall and Randall 1963, Buckman and Ogden 1973).

Territorial juveniles and adults of both color phases fed at the same rates as equivalent schoolers but at greater rates than equivalent loners (Table 3, *U*-test,  $p < .001$  in all three cases). Territorials of all three classes were also attacked by *E. planifrons* less frequently than were equivalent loners (*U*-test,  $p < .001$  in each case), and adult territorials as often as were equivalent schoolers. However, juvenile territorials were attacked more often than were juvenile schoolers (*U*-test,  $p < .001$ ). Juvenile territorials were also attacked by *E. planifrons* more frequently than were adult territorials of either color phase (*U*-test,  $p < .001$  in both cases). This continuous aggressive activity from *E. planifrons* disrupted those fishes' feeding activities.

Initial- and terminal-phase territorials were both defensively active against adult schools (each delivered almost 50% of 2,628 attacks against schools).

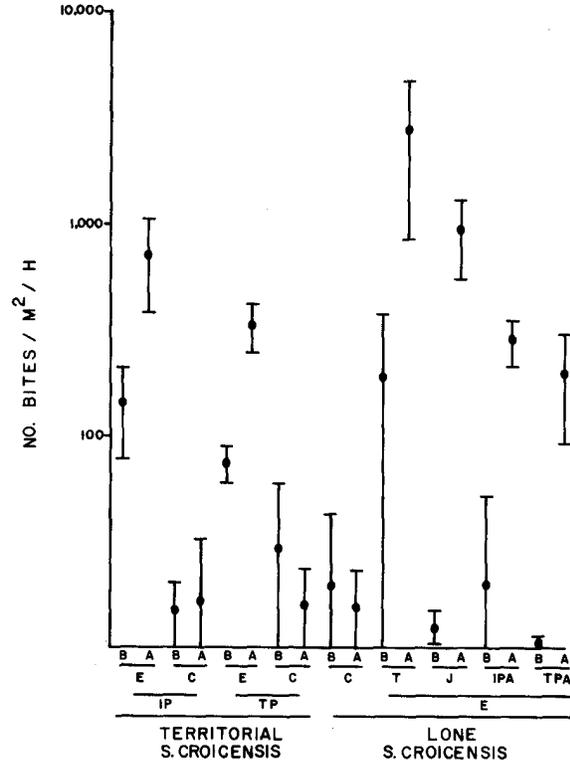


FIG. 3. Feeding activity of individual *Scarus croicensis* in the *Eupomacentrus planifrons* removal experiments: mean feeding rates with 95% confidence limits. B = before removals, A = after removals, J = juveniles, IPA = initial phase adults, TPA = terminal phase adults, T = total (J + IPA + TPA), E = experiments, C = controls.

As the large amounts of aggression that territorials directed at schools moving near and intruding into their territories were immediately obvious, we were surprised to find that territorials sometimes interspersed this aggressive activity with bouts of intensive feeding during which they joined adult schools feeding in their territories.

#### Results of the removal experiments

*The E. planifrons removal experiments.*—In all six experimental areas there were increases, often massive, in the feeding and visiting activity of both lone and schooling nonterritorial *S. croicensis* after the removal of *E. planifrons*. Activity in the control areas remained unchanged (see Figs. 3 and 4).

The feeding activity of territorial *S. croicensis* also increased markedly following the removals while there were no changes in the control areas (Fig. 3). These increases resulted from both an increased presence of territorials in the cleared areas (they virtually ignored those parts of their territories outside the cleared areas), as well as increased in their feeding rates—the mean number of individuals of

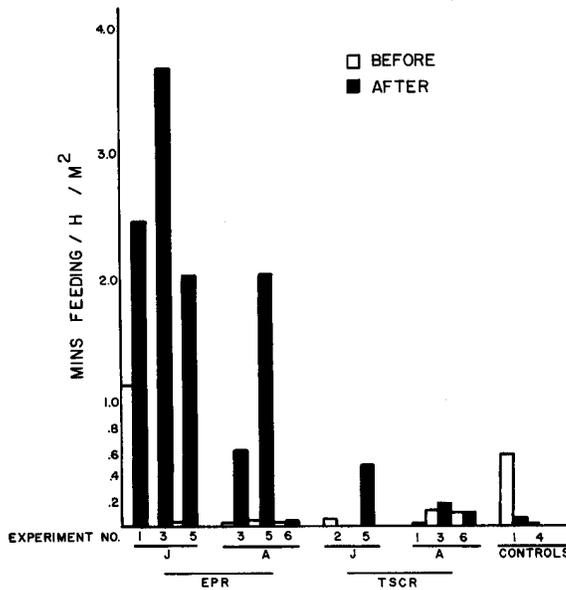


FIG. 4. Feeding activity of *Scarus croicensis* schools in the removal experiments. EPR = *Eupomacentrus planifrons* removals, TSCR = territorial *S. croicensis* removals.

each color phase present per unit area doubled, on the average, and their feeding rates increased by more than half, on the average.

*The territorial S. croicensis removal experiments.*—Lone nonterritorial *S. croicensis* did not consistently increase their feeding activity in areas from which territorial conspecifics were removed (Fig. 5); large increases were observed in only two areas, and moderate increases in another two, while no changes occurred in the remaining two. There was only a slight tendency for the feeding activity of schools to increase (see Fig. 4). These increases in the feeding activity of nonterritorial parrotfish following the removal of territorial conspecifics were of a lower order than those that occurred following the removal of *E. planifrons* from equivalent areas (see Figs. 4 and 5).

When the total feeding activity of nonschooling *S. croicensis* (territorials plus loners) before and after the removals of territorials is considered, it can be seen (Fig. 6) that this activity tended to decline following the removals. In only one of the six experiments did post-removal feeding activity of loners exceed (slightly) the pre-removal level of activity of territorials, or the total level of pre-removal activity.

## II. The associate species in the *E. planifrons* habitat

*Feeding activity in and out of schools.*—*Acanthurus coeruleus* and *C. capistratus* were both com-

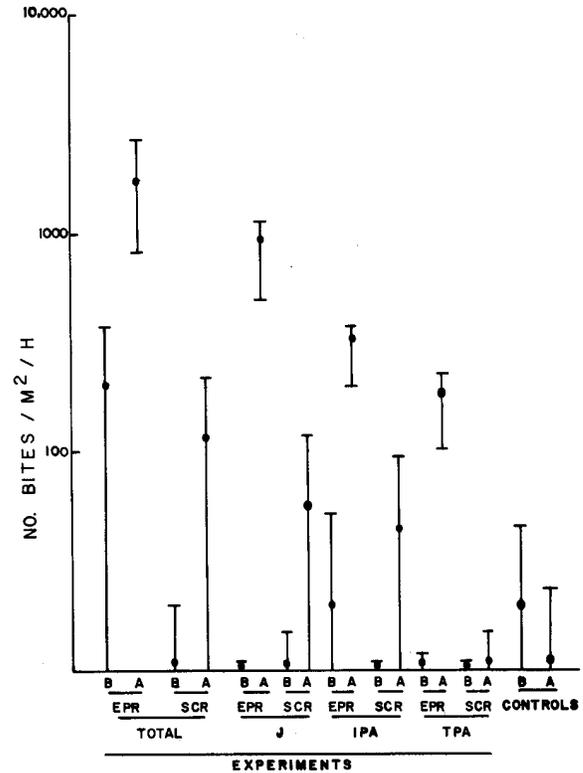


FIG. 5. Feeding activity of lone *Scarus croicensis* in the *Eupomacentrus planifrons* and *S. croicensis* removal experiments: mean feeding rates with 95% confidence limits. B = before removals, A = after removals, EPR = *E. planifrons* removal experiments, SCR = *S. croicensis* removal experiments, J = juveniles, IPA = initial phase adults, TPA = terminal phase adults.

mon in the coral-covered parts of the study area. *Acanthurus coeruleus* fed singly and in groups containing up to almost all the two dozen individuals in that area. *Chaetodon capistratus* were encountered alone and in small, transient, loosely knit groups. The less common *C. ocellatus* and *C. striatus* we only saw in ones and twos. *Hypoplectrus puella* and *Aulostomus maculatus* were almost invariably seen singly. All six species regularly associated with parrotfish schools, then behaving as school members in their feeding behavior and movement patterns.

*Acanthurus coeruleus* and the three *Chaetodon* species were frequently and vigorously attacked by *E. planifrons*. When associating with adult *S. croicensis* schools, all four experienced lower rates of attack from *E. planifrons* than they did when not, and had higher feeding rates (Table 4). School associates of these species also reacted less strongly to *E. planifrons* attacks than did individuals out of schools, and their feeding was less disturbed by these attacks.

Although both *H. puella* and *A. maculatus* were regularly attacked by *E. planifrons*, they experienced

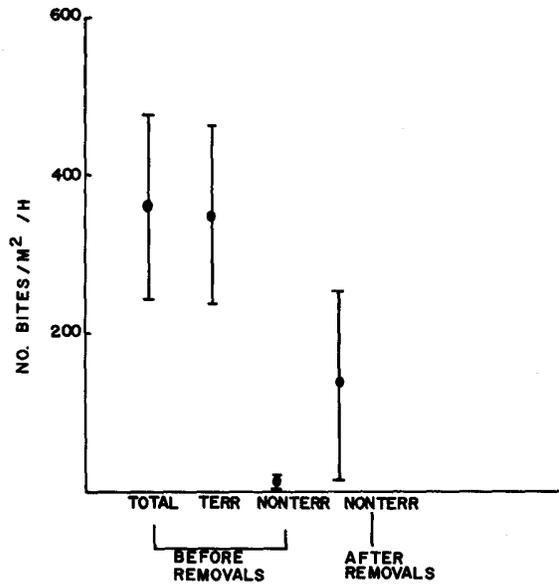


FIG. 6. Feeding activity of nonschooling *Scarus croicensis* in areas before and after the removal of territorial *S. croicensis*: mean feeding rates with 95% confidence limits. TERR = territorials, NONTERR = nonterritorials.

much lower rates of attack than any of the other four species of school associates (Table 4; *U*-test,  $p < .001$  in all cases). Both experienced lower rates of attack from *E. planifrons* when associating with *S. croicensis* schools than when not, and both had higher feeding rates in schools.

*The E. planifrons removal experiments.*—There were enormous increases in the feeding activity of *A. coeruleus*, *C. capistratus*, *C. ocellatus*, and *C. striatus* in all four experimental areas following the removal of *E. planifrons*, but no changes in the control areas (Fig. 7). These increases resulted from

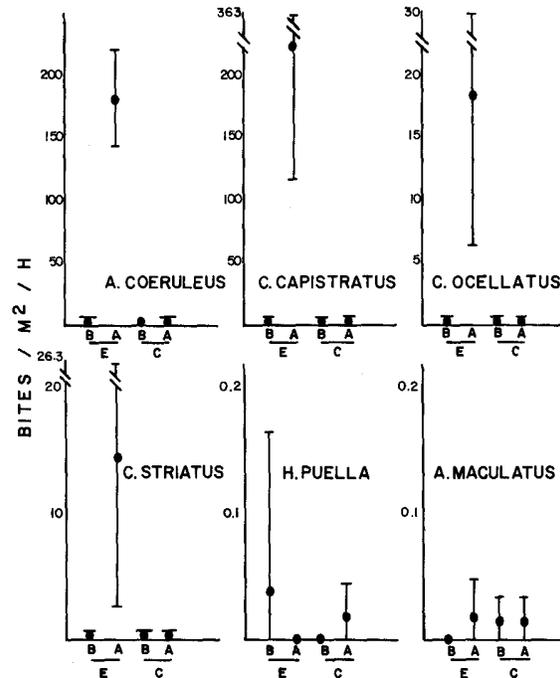


FIG. 7. Feeding activity of the associate species in the *Eupomacentrus planifrons* removal experiment: mean feeding rates with 95% confidence limits. B = before removals, A = after removals, E = experiments, C = controls.

fishes aggregating in the cleared areas and feeding steadily throughout the post-removal observation periods. (In *A. coeruleus* and *C. capistratus*, the species on which the most data are available, the mean numbers of individuals per unit area increased by an average of 35× and 21× respectively, and the mean number of bites per individual by 11 and 10×.) There were no changes in the activity of

TABLE 4. Six associate species—mean feeding rates and mean rates of attack from *Eupomacentrus planifrons*, of schooling and lone individuals. Numbers in parentheses indicate standard deviation. Probabilities based on Mann-Whitney *U*-test

Species	No. bites/min		No. <i>E. planifrons</i> attacks/min		Sample size	
	Loners	Schoolers	Loners	Schoolers	Loners	Schoolers
<i>A. coeruleus</i>	16.10 (7.94)	26.98 ( $p < .001$ ) (8.57)	1.52 (0.93)	0.78 ( $p < .001$ ) (0.29)	17 periods 211 min	15 periods 181 min
<i>C. capistratus</i>	1.33 (0.76)	3.48 ( $p < .001$ ) (2.00)	3.98 (2.04)	1.68 ( $p < .001$ ) (0.99)	20 periods 180 min	20 periods 206 min
<i>C. ocellatus</i>	1.25 (0.84)	4.44 ( $p < .001$ ) (2.39)	1.66 (1.23)	0.88 ( $p < .001$ ) (0.63)	16 periods 180 min	15 periods 181 min
<i>C. striatus</i>	0.67 (0.43)	3.70 ( $p < .001$ ) (2.15)	2.81 (2.44)	1.21 ( $p < .01$ ) (0.66)	18 periods 195 min	19 periods 181 min
<i>H. puella</i>	0.05 (0.09)	0.23 ( $p < .001$ ) (0.18)	0.25 (0.19)	0.04 ( $p < .001$ ) (0.06)	13 periods 180 min	15 periods 183 min
<i>A. maculatus</i>	0.06 (0.08)	0.25 ( $p < .01$ ) (0.26)	0.18 (0.23)	0.06 ( $p < .05$ ) (0.08)	12 periods 180 min	15 periods 185 min

*H. puella* and *A. maculatus* in either the experimental or control areas (Fig. 6).

#### DISCUSSION

*Scarus croicensis* and *E. planifrons* share the same parts of the same habitat and, to a large degree, the same general food resources and specific food items: *S. croicensis* as a herbivore, and *E. planifrons* as a browsing omnivore (Randall 1967, Emery 1973). As the interspecific dominance of *E. planifrons* over *S. croicensis* inhibits the feeding activity of members of all social classes of that species, *S. croicensis* has the problem of obtaining food in the face of aggression from an abundant and pugnacious competitor. The aggressive activities of territorial *S. croicensis* also inhibit the feeding of nonterritorial conspecifics in the same habitat, though to a lesser degree than do those of *E. planifrons*. This places an added burden on the nonterritorials over that experienced by territorials.

Despite the large amounts of aggression that are directed against them, schools spend most of their time feeding. In adult schools at least individuals that feed at higher rates are attacked slightly more frequently by *E. planifrons* and slightly less frequently by territorial conspecifics. This situation may result from schoolers being most interested in feeding in those areas containing the fewest territorial conspecifics and the most damselfish, perhaps because of differences in food quality or density. (However, our data also show that the proportion of its time that a school as a whole spends feeding is not related to the frequency of attacks on it. Here we feel that our data collection technique was not efficient enough to cope with the very high frequencies of attacks often observed and that this relationship may not be real.)

The high feeding rates of school members arise, we maintain, from a relative immunity to attack from territory holders. Feeding in schools is probably socially facilitated, as it is in many gregarious animals, including fishes (Marler and Hamilton 1966, p. 132; Shaw 1970); however, the high feeding rates of schoolers do not result from this alone, since schools as well as nonschooling fish have their feeding inhibited by territory owners. With schools, the effectiveness of territory defense is reduced since (1) the number of defensive acts a territory owner can perform per unit time is limited and, although the school as a whole is subject to continuous aggression, its members individually experience low rates of attack (Jones 1968); and (2) when attacked, a school member does not have to completely disrupt its feeding and leave the area; instead it need only move to elsewhere in the school, where its anonymity protects it. It can thus partly ignore such attacks.

Nonterritorials out of schools are often apparently only temporarily so, as they join a school when they locate one. Much of the time they make little attempt to feed; when they do, they suffer high rates of attack from *E. planifrons*. They are not protected from attacks in the same way as school members are since they can be singled out and chased well away by a territory owner. This, we maintain, prevents them from achieving the same rate of feeding as school members. The regularity with which schools form and the relative infrequency of sightings of lone nonterritorials show how effective the protection is that schools provide. The existence of an inverse correlation between the feeding rates of adult, lone *S. croicensis* and the frequency with which they receive attacks from territorial conspecifics results, apparently, from individuals that are moving about, rather than attempting to feed, being those that intrude more frequently into conspecifics' territories and thus expose themselves more often to attack. While *E. planifrons* was abundant throughout the study area, territorial *S. croicensis* were not and much of the feeding done by lone *S. croicensis* was in areas not densely occupied by territorial conspecifics, that is, in areas defended by only one set of territory owners.

Although juvenile and adult *S. croicensis* both gain protection from *E. planifrons* and territorial conspecifics by schooling and then have high feeding rates, there exist a number of differences between them. Juveniles are less mobile than adults and tend to avoid areas occupied by territorial conspecifics more than nonterritorial adults do, which results in juvenile loners being attacked less often by conspecifics than adult loners. Schools of juveniles intrude more often into conspecifics' territories than do lone juveniles (probably because of the protection they receive from being in a school) and schoolers are thus attacked more frequently than are loners. The higher rates of *E. planifrons* attacks that individual juveniles of all classes suffer are probably due to (1) the small size of juvenile schools affording less protection to members than the larger adult schools do, and (2) juveniles, when not actually feeding, tending to remain closer to the substrate than adults, and thus exposing themselves more frequently to attacks. Juvenile territorials, being at the bottom of a dominance hierarchy, might also be relegated to those parts of the group's territory where attacks by damselfish are more likely.

The coexistence of two very different social classes of the one species in the same area raises questions about their relationship and the possibility of the interchange of individuals between classes. Buckman and Ogden (1973) found long-term occupation of parrotfish territories by their owners, and we observed both long-term presence in the one class

and relatively permanent movements between classes. We also observed one instance of the temporary (several hours) movement of a territorial terminal-phase male into a school. Based on the mean sizes of individuals collected from the different social classes, Warner and Downs, in an as yet unpublished manuscript, have erected a life history sequence in which such interclass movements of individuals are also figured. Buckman and Ogden (1973) performed one experiment in which they removed initial-phase individuals from their territories and found that they were replaced within several days. From this they suggested that a surplus of potentially territorial fish existed from which vacancies were readily filled. We performed nine additional similar experiments involving nine terminal-phase and 22 initial-phase fishes, and obtained similar results: all but one of the terminal-phase males were replaced within 2 days and all of the initial-phase individuals within a week. Where these particular replacements came from—schools or outside the coral area—was not determined; it is probable that at least some came from schools.

The relationships between *E. planifrons* and *S. croicensis*, and between the classes of *S. croicensis* that we suggest exist, are that (1) a certain level of feeding can be accomplished by single *S. croicensis* in the habitat in which *E. planifrons* lives (a level that is attained by the territorial *S. croicensis*), and (2) the nonterritorials comprise that portion of the population that, primarily as a result of the activities of *E. planifrons*, cannot obtain satisfactory territories. This indicates that for *S. croicensis*, in this particular area, territoriality is intrinsically superior to schooling as a mode of existence. While territorials and school members feed at the same rate, there could perhaps be differences in the quality of the food they obtain. Again, territoriality might be superior to schooling as an antipredator mechanism as a result of the territory owner being familiar with both shelter and sites from which predators are liable to attack in its small home area. With terminal-phase males, a territory is probably also necessary for reproduction as there are no noticeable breakdowns of terminal-phase male schools during periods of sexual activity and we regularly saw such schooling males ignoring spawning activity in their immediate vicinity.

Territorial *S. croicensis* live in large territories that encompass those of a number of *E. planifrons*. They appear to feed both between and within those damselfishes' territories. The *E. planifrons* apparently tolerate low levels of interspecific feeding in their territories, perhaps as a result of some combination of (1) the energetic costs of total exclusion of competitors being too high, and (2) the weaker defense of the less desirable parts of their territories. A

territorial *S. croicensis* would then be exploiting resources that were available to it only in low density and would need a comparatively large area. The success territorials have in gaining food is evident in the high feeding rates they have and is related to the low level of punishment they experience. The failure of nonterritorial parrotfish to rapidly, in most cases, achieve the same level of feeding activity as that of territorials before they are removed suggests that individuals filling a vacancy may need to learn what parts of their new territories they can feed in most efficiently. Participation by territorial parrotfish in the feeding schools in their own territories could represent a residual tendency to school. It could also be adaptive, by enabling territorials to gain access to food otherwise unavailable to them, that is, in areas heavily defended by *E. planifrons*.

While maintaining that schooling by *S. croicensis* is a response to the aggression of competitors, we are not implying that it is not adaptive in other ways. Nearly all (19 out of 20) the predation attempts we observed on schools of adult *S. croicensis* were made by demersal predators that attacked from the concealment of coral while a school was feeding. The condensation that a school undergoes during feeding bouts can then be construed as a response to confuse predators at a time when the prey are particularly vulnerable (concentrating their attention on feeding). The evident breakdown of schooling during midwater plankton feeding episodes may result from a combination of a reduced demersal predator threat and a tendency to disperse to accommodate dispersed food, as well as a lack of aggression from competitors.

The six associate species share the same parts of the same habitat with *E. planifrons*. Four of them also share the same general, and sometimes specific, food resources with that species—*A. coeruleus* as a browsing herbivore (Randall 1967), and as browsing carnivores, *Chaetodon capistratus*, *C. striatus* (Randall 1967), and *C. ocellatus* (our own observations). *Eupomacentrus planifrons* is dominant over these four species and its aggressive activities inhibit their feeding. The high feeding rates that members of these four species have when they associate with *S. croicensis* schools result, we think, directly or indirectly from the reduced effectiveness of *E. planifrons* territoriality. We maintain, therefore, that the association of these four species with parrotfish schools in the study area is a direct adaptive response to the problem posed by *E. planifrons*, and probably other territorial competitors, and that *S. croicensis* schools provide protection in the same way as they provide it for parrotfishes themselves.

For *H. puella* and *A. maculatus* the situation is different as they are not competing for food with *E. planifrons*. *Hypoplectrus puella* is a predator that

feeds primarily on shrimps and *A. maculatus* preys mainly on fishes (Randall 1967). They are also attacked very little by *E. planifrons* and neither species has its feeding activity inhibited by what attacks they do receive. Such selectivity by territorial pomacentrids of what types of species they attack, with attacks being concentrated on competitors (and sometimes egg predators), has been found with other damselfishes by Low (1971) and Myrberg and Thresher (1974). *Hypoplectrus puella* and *A. maculatus* gain no protection from *E. planifrons* by associating with *S. croicensis* schools, even though they are attacked less often by the damselfish when they are acting as school associates. What benefits they do derive from this association has been suggested for *H. puella* by Ogden and Buckman (1973), who thought that this species ate small free-swimming organisms disturbed by the feeding school. Our data, which show higher feeding rates for *H. puella* and *A. maculatus* when they are acting as associates, support this idea as applying to both species. Barlow (1974) has also suggested the same function for the association of various wrasses with *Acanthurid* schools, and similar associations in which one carnivorous fish feeds on organisms disturbed by another have been observed by other workers (e.g., Hobson 1968). The association of both *H. puella* and *A. maculatus* with *S. croicensis* schools is probably adaptive in two further ways: (1) *Hypoplectrus puella*, while in schools, were frequently observed "stalking" small *E. planifrons*. Schooling might assist their efforts at preying on such small territorial fishes when these are distracted by the school (in this respect the general resemblance of *H. puella* to *S. croicensis* may be sufficiently close to give *H. puella* an advantage). (2) *Aulostomus maculatus*, in schools, occasionally attacked parrotfish members of these schools. Schooling might also enable them to prey on school members (in moderation, since repeated attempts were observed to lead to avoidance reactions by the prey).

A variety of other Caribbean fishes, species with which we have not dealt in detail here, form monospecific feeding schools or act as the nuclear species or associates of multispecies schools. Others apparently act only as associates. These, which probably derive the same sort of benefits from schooling as we have described here, include the benthic feeding herbivores that act as nuclear species—*A. coeruleus*, *A. chirurgus*, and *Sparisoma viride*—and, as associates—the herbivores *Scarus coelestinus*, *Scarus vetula*, *Sparisoma rubripinne*, *Sparisoma aurofrenatum*, *Sparisoma chrysopterum*, the browsing carnivore *Pomacanthus paru*, and the predators *Halichoeres maculipinna* and *Mulloidichthys martinicus* (feeding habits from Randall [1967], school-

ing observations were by Ogden and Buckman [1973] and ourselves).

It is significant that the species of reef fishes that commonly form well-defined monospecific feeding schools, such as those of *S. croicensis*, are benthic-browsing herbivores that spend much of their time feeding. This emphasis on feeding activity means that they are being continually placed in situations that expose them to aggression from territorial competitors and probably makes them highly susceptible to predation. Both of these factors probably constitute strong selection pressures for school formation. The general lack of such monospecific school formation by benthic-browsing carnivores that have territorial competitors, even though they act as school associates, might be related to proximate factors such as their low population densities: a minimum number would be necessary for an effective school to be formed (*C. capistratus*, which was abundant in the study area, did occasionally form school-like aggregations; the significance of these is not known, although they did not feed intensively). Again it might be more efficient for carnivores to join existing groups of herbivores rather than attempt to form their own, since herbivores are far more abundant than they. Alternatively, the formation of monospecific schools by such species might be actually selected against. Differences in the distribution and abundance of the food resources used by members of this group of species, as compared to those of food used by the herbivores, could have some effect on whether an individual was able to gain an adequate amount of a food resource while in a large, tightly knit group of conspecific competitors, or whether it would be better off on its own. Increased dispersion of food items could favor greater dispersion of the feeding fishes, which would reduce the protective effectiveness of a group and thus any selection for its formation. If *Chaetodon* spp. were in the latter category, by associating with parrotfish schools they could gain protection from grouping without suffering the disadvantages of being in a large group of conspecifics. Anticompetitor schooling would probably also be successful only when sessile foods were involved—the response of motile prey organisms to the approach of a large, dense school of a predator can easily be imagined. Such predators would probably also be faced with the problem of low density food.

The damselfishes are a pantropical group, highly characteristic of coral reefs, both in terms of their abundance and large numbers of species. The extreme pugnacity of the many benthic-feeding members of this group that hold permanent feeding territories and the pronounced interspecific nature of much of their territoriality is well recognized (Barbach 1958, Reese 1964, Rasa 1969, Clarke 1970,

Low 1971, Myrberg 1972, Emery 1973, Brockman 1973, Sale 1974, Myrberg and Thresher 1974, Vine 1974, Itzkowitz 1974). The existence of such a group of species that are usually either herbivores or omnivores that consume large amounts of algae, and that despite their small size are characteristically dominant over members of other taxonomic groups, in combination with the presence of a number of territorial, herbivorous species of other teleost groups, presents very real problems to their competitors. Mono or multispecific schooling evidently represents a widespread adaptation by nonterritorial competitors to cope with this problem. In turn, the existence of an abundance of competitors has selected for pugnacity in these pomacentrids which, as a group, have evidently opted for the territorial strategy.

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