Effect of macroalgae and damselfish on the composition of mixed-species fish schools in a tropical coral reef

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Abstract: Coral reef fish often use schooling to avoid predation and facilitate resource acquisition. What is less well known are the factors which determine the composition of schools. We examined the effects of macroalgal cover and damselfish territories on several aspects of mixed-species schools. Schools were largely dominated by juveniles, and Striped Parrotfish was the core species in almost every school. While we found no effect of macroalgae or damselfish on the number of schools or species richness of schools, we found larger schools in areas without macroalgae and areas without damselfish territories. We found an opposite effect of damselfish and macroalgal cover on school size from that found in previous studies, and we propose several alternate hypotheses.

Key Words: Scarus croicensis, *schooling behavior,* Stegastes fuscus, Stegastes planifrons

INTRODUCTION

Schooling is a common strategy that many coral reef fish use to avoid predation and increase resource acquisition. Schooling protects fish from predators by increasing the amount of vigilance and decreasing the risk of attack on any one individual (Partridge 1982, Reinthal and Lewis 1986, Debrot and Myrberg 1988). Schooling may also be advantageous for acquiring resources. Fish in schools have greater ability to locate resources and higher foraging rates (Reinthal and Lewis 1986). In areas of high damselfish density, mixed-species schools may form to infiltrate highly defended territories and feed on macroalgal turfs that would be otherwise inaccessible (Robertson et al. 1976, Reinthal and Lewis 1986, Shannon et al. 2000). Schooling behavior may also be influenced by changes in substrate cover that result from wave action and grazing pressure. For example, in the shallow forereef of Discovery Bay, Jamaica, areas with high cover of macroalgae differ greatly from barren-zone areas grazed intensely by the sea urchin *Diadema antillarum.*

In this study, we examined how the presence of aggressive, territorial damselfish and macroalgal cover influence characteristics of mixed-species schools. Specifically, we predicted that there would be more and larger schools in areas with damselfish territories, because larger schools would more easily overwhelm damselfish defenses. We also expected that species richness of schools in areas with damselfish would be lower, because a high proportion of conspecifics, or species of similar size, shape and color, in a school may confuse the resident damselfish and decrease the effectiveness of its defenses (Ehrlich and Ehrlich, 1973).

We predicted that schools would be fewer and smaller in areas with macroalgae because fewer fish would be necessary to locate resources when they are abundant. Furthermore, there is often a clear separation of adult and juvenile schools. Field et al. (1993) speculated that adults school to benefit foraging, whereas juveniles school to avoid predators. Because juveniles may use algae for refuge more frequently than adults, we predicted that juveniles would make up a greater fraction of total fish in areas with macroalgal cover.

METHODS

We observed multi-species schools on 4 - 11 March 2003 at Dancing Lady and Caricomp mooring sites at Discovery Bay Marine Laboratory, Jamaica, W. I. All observations were made using SCUBA at depths between 4 and 7 m. To observe schooling behavior and structure, we selected eight replicate 3 x 3 m plots in each of four treatments: (1) high abundance of macroalgae with high density of Three-spot (*Stegastes planifrons*) and Dusky Damselfish (*Stegastes fuscus*), (2) high abundance of macroalgae with no damselfish, (3) no macroalgae with high density of Three-spot and Dusky Damselfish, and (4) no macroalgae or damselfish. Some sites for treatment 4 contained the less aggressive Bicolor Damselfish (*Stegastes partitus*). We assumed that the presence of this smaller territorial damselfish would have negligible effects on foraging schools as compared to the larger, more aggressive damselfishes.

We observed each plot for 25 min, recording the age structure and number of fish of each species in mixed-species schools entering the plot. We determined species and size class of each individual based on markings and sizes depicted in Humann (1994). We also noted if the school was actively foraging or just passing through the sample site. Any individual associating with the school for at least 20 seconds was counted.

Since the number of schools observed varied between treatments, we calculated average values per school for the number of species and number of individuals at each plot. Main effects and the interaction between macroalgae and damselfish were calculated using two-way ANOVA.

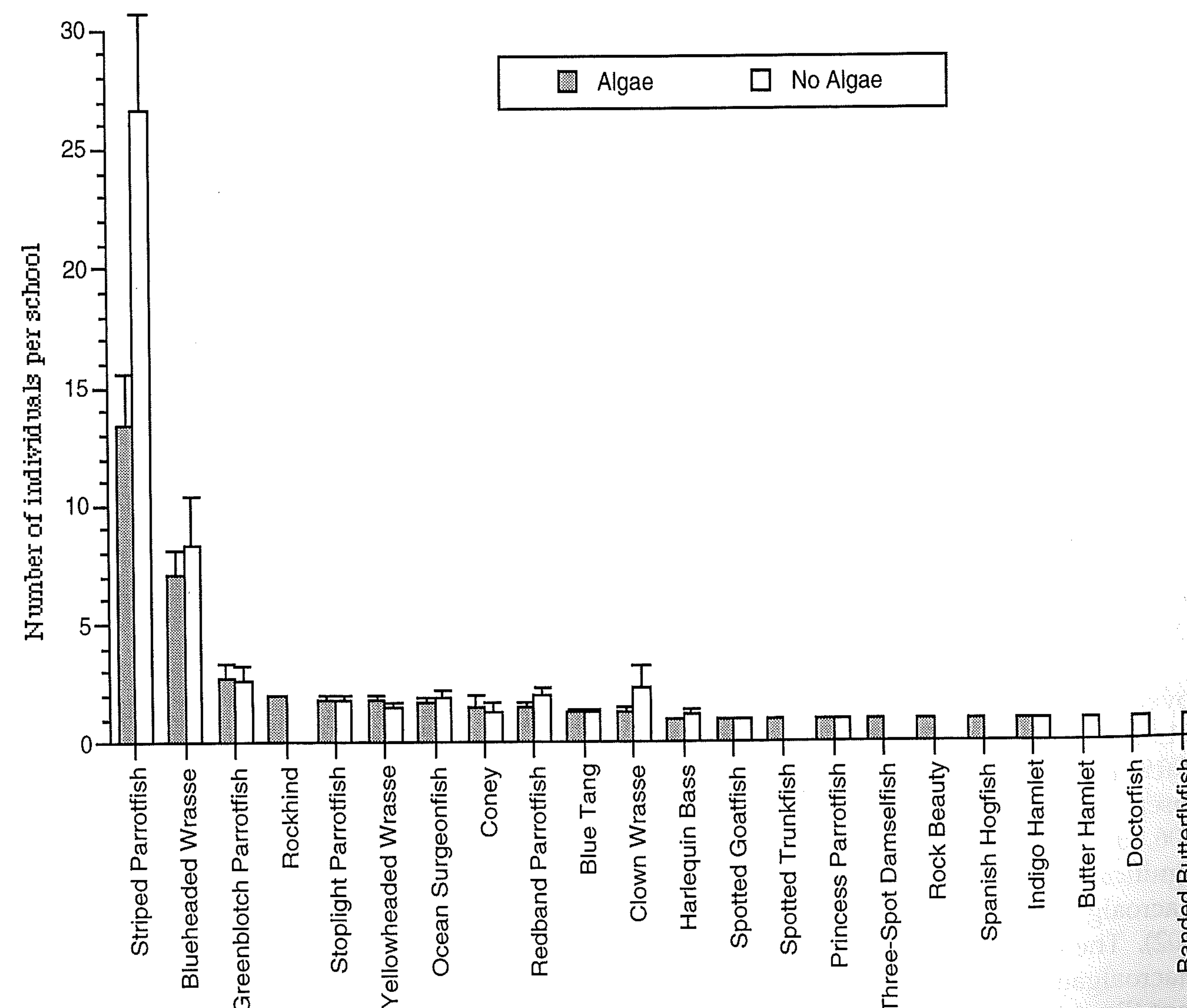

FIG. 1. Number of individuals (mean ± SE) of each species observed in areas with and without macroalgal cover.

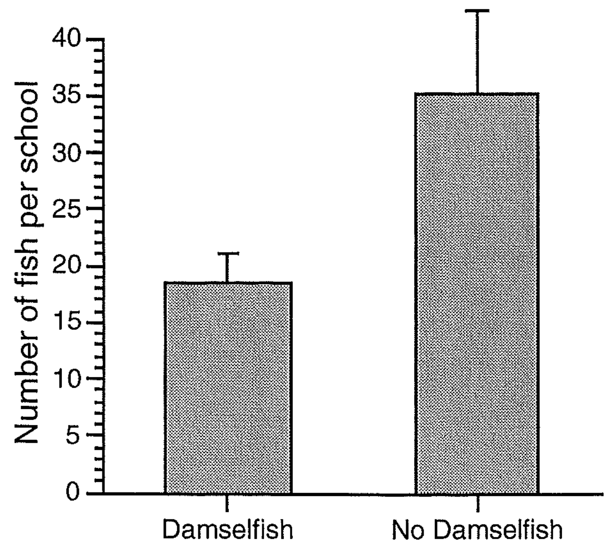

FIG. 2. Mean size of multi-species schools in the presence and absence of territorial damselfish (n = 16). Data were pooled across sites.

RESULTS

We observed 95 distinct multi-species schools and 22 species of fish during 32 observation periods. Striped Parrotfish (*Scarus croicensis*) was the most common species, appearing in 88.4% of the schools (Fig. 1). We found no effect of damselfish on the number of schools (F = 1.60, df = 1,30; P = 0.22). There was also no effect of damselfish on the number of species observed in schools for each treatment (F = 0.48, df = 0.48; P = 0.50). School size was significantly larger in sites lacking aggressive damselfish (Fig. 2; F = 4.62, df = 1, 30; P = 0.04). There was no effect of damselfish on the proportion of juveniles in schools (F = 1.83, df = 1, 30; P = 0.19).

We found no effect of macroalgal cover on the number of schools (F = 1.02, df = 1,30; P = 0.32). There was also no effect of macroalgal cover on the number of species observed in schools for each treatment (F = 0.06, df = 1, 30; P = 0.80). School size was significantly larger in sites with no macroalgae (Fig. 3; F = 6.16, df = 1, 30; P = 0.02). The interaction of the effects of macroalgae and damselfish was not significant (F = 1.50, df = 1, 30; P = 0.23). Finally, we observed a change in the size structure of schools between habitats. Schools observed in sites with high macroalgal cover had a significantly lower proportion of juveniles (Fig. 4; F = 6.07, df = 1, 30; P = 0.02).

DISCUSSION

The number of schools did not change among treatments, but school size was larger in areas without Three-spot or Dusky Damselfish. These findings are contrary to the finding of Shannon et al. (2000) that school sizes were larger in the presence of damselfish territories. Our observations may reflect the inability of these schools to successfully infiltrate heavily defended territories. They may have been excluded by aggressive behavior of damselfish. Nonetheless, schools in areas without damselfish may be maintained by benefits of lower predation risk and increased foraging rate (Reinthal and Lewis, 1986). On the other hand, we may have observed smaller schools in the presence of damselfish, because smaller schools could potentially pose less of a threat to the resident damselfish and draw less attention.

Alternatively, large schools in areas without damselfish may have been in transit

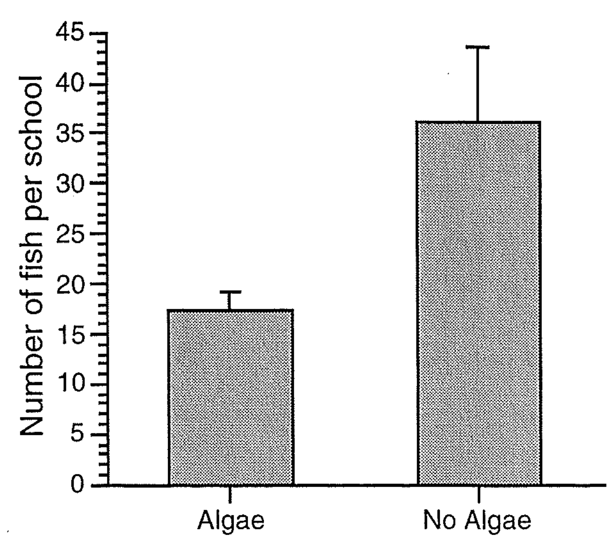

FIG. 3. Mean size of multi-species schools in areas with and without macroalgal cover (n = 16). Data were pooled across sites.

between damselfish territories. The patchiness of damselfish territories may encourage the need for schools to cross over areas of low damselfish density. The presence of larger schools may also be due to the high rates of flux and merging of schools. We frequently observed temporary merging of schools. This behavioral flexibility may increase each school's ability to find food, avoid predators, and feed efficiently on a variety of resources. Our results may have been confounded by this variability of school size over time and space.

We observed no effect of damselfish presence on the species richness of schools. We had expected species richness to be low in the presence of damselfish, because schools with more conspecifics and few individuals of different morphology may be most likely might confuse territorial damselfish. It is possible that predation pressures and pressures from damselfish have similar influences, keeping richness low in all areas.

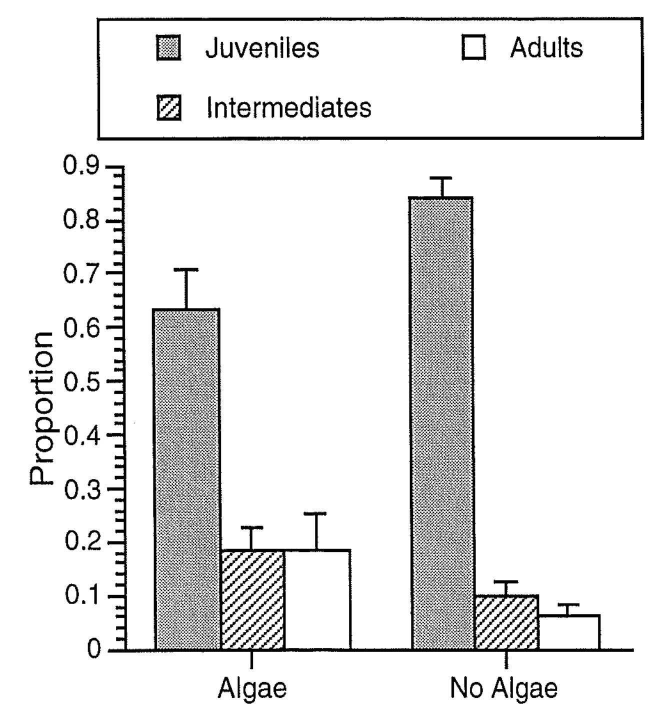

FIG. 4. Proportion of each size class in mixed-species schools observed in sites with and without macroalgal cover (n = 16). Data were pooled from across sites.

Macroalgae did not influence the number of schools, but school size was greater in the absence of macroalgal beds. The lack of algal cover may decrease the availability of refugia, increasing the need for fish seeking protection to form schools. This explanation is especially relevant to juvenile fish that use schooling most often for predator protection. Our findings that schools in the barren zone had a greater proportion of juveniles supports this hypothesis.

Species richness did not vary with macroalgal cover, suggesting that foraging benefits were not influencing schooling as much as predation pressure. Different species within a mixed-species school often have different feeding preferences, preventing intense interspecific competition and rapid depletion of resources (Itzkowitz 1977). More diverse mixed-species schools would, therefore, be more efficient foragers. The lack of an effect of macroalgal cover suggests species richness of schools may be balanced by increased predation pressure where there are more resources.

The influence of macroalgal cover and territorial damselfish on the composition of mixed-species schools remains unclear. While we found that these factors did not affect number of schools or species richness of schools, our results regarding school size differ from the findings of previous studies (Robertson et al. 1976; Shannon et al. 2000). This may suggest that additional factors influence the composition of mixed-species schools. A study looking at the influence of location, site fidelity and flux of individuals could determine composition dynamics of mixed-species schools.

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