cal Ecology, p. 136-140.

Sides, E. M. 1975. A study of niche separation in three species of Ophiocoma (Echinodermata: Ophiuroidea) in Jamaica. M. Sc. Thesis, Univ. West Indies.

Sides, E. M. 1981. Aspects of space utilization in shallow-water brittlestars (Echinodermata: Ophiuroidea) of Discovery Bay, Jamaica. Ph. D Thesis, Univ. West Indies.

Sides, E. M., and J. D. Woodley. 1985. Niche separation in three species of *Ophicoma* (Echinodermata: *Ophiuroidea*) in Jamaica, West Indies. Bulletin of Marine Science, 36: 701-715.

Tran, J. K., and B. Whited. 2004. Patterns of distribution of three brittle-star species (Echinodermata: *Ophiuroidea*) on coral reefs. Dartmouth Studies in Tropical Ecology, p. 177-180.

BENEFITS OF MIXED SPECIES SCHOOLS FOR THREE FISH SPECIES

TIMOTHY R. MATSUURA, MELISSA A. BARGER, GABRIEL H. CALVI AND DANIEL J. MADIGAN

Abstract: The mechanisms that drive mixed species schooling are not well understood, and may vary with different fish species. We examined schooling behavior and the benefits of schooling in three fish species (spotlight parrotfish, doctorfish, and bluehead wrasse) at Discovery Bay, Jamaica. We followed individuals of each species, recording time spent schooling, average school size, feeding efficiency and damselfish attacks in and out of schools. Bluehead wrasse spent less time schooling than the other two species, although all species benefited from schools through increased foraging efficiency, decreased damselfish attacks, or both. Because food resources are neither limiting nor completely defended in Discovery Bay, we suggest that some mechanism other than increased foraging efficiency, such as predator avoidance, drives the amount of time each species spent schooling.

Key Words: bluehead wrasse, doctorfish, foraging efficiency, predator avoidance, stoplight parrotfish

INTRODUCTION

Forming heterospecific foraging associations is a common behavior of many tropical reef-fish species. These mixed-species schools comprise complex and relatively understudied interactions between species, and many mechanisms have been suggested to explain them. The main benefits of schooling include predator avoidance and increased foraging rates (Lukoschek and McCormick 2000). Other studies show that groups of fish can help fish circumvent the territoriality of competitors (Robertson 1976). A school of fish can swamp a damselfish territory and fish can graze on algae while the damselfish is occupied chasing other members of the school (Foster 1985), thus allowing an individual fish within a school to take more bites and receive fewer damselfish attacks.

We chose three species of fish com-

mon in the back reef of Discovery Bay, Jamaica to compare the relative benefits gained by schooling across different fish species. Our three focal species were the stoplight parrotfish (*Sparisoma viride*), doctorfish (*Acanthurus chirurgus*), and the bluehead wrasse (*Thalassoma bifasciatum*). These fish are in different families and have distinct life histories, and all of these species are known to aggregate in loosely-knit feeding groups. Both the doctorfish and parrotfish are generalist feeders that consume algae, seagrass and microinvertebrates in the sediment. Terminal male bluehead wrasse forage upon invertebrates and zooplankton (Deloach 1999), and have been shown to prefer damselfish eggs when available (Foster 1987).

We wanted to assess any differences in schooling benefits between these species. We measured the differences in feeding rates and damselfish attack rates in and out of schools for each of these fish species. We also measured the proportion of time each fish spent in and out of schools. We predicted that the fish species with the greatest increase in feeding rate and the greatest decrease in damselfish attack rate would spend the greatest proportion of time schooling.

METHODS

We observed fish from 4-10 March 2005 on the west back reef at Discovery Bay, Jamaica. We located focal individuals of bluehead wrasse, stoplight parrotfish, and doctorfish by snorkeling over the reef until an individual was sighted in a mixed-species school. Since we were interested in schooling behavior, we chose fish that were initially in schools; any bias towards schooling should be seen across all three fish species and not affect the comparison between species. To control for size, all observed individuals fell into the following size ranges: bluehead wrasse, 9-11 cm (terminal male); stoplight parrotfish, 9-12 cm (juvenile); doctorfish, 9-12 cm (juvenile). Since size range and coloration were kept approximately equal for each fish species, the observed fish within each species were at approximately equal life stages.

We followed each fish for 10 min, recording the time spent in schools and time spent alone. We counted feeding bites and attacks by damselfish (damselfish attacks were any acts of damselfish aggression that elicited a response in the focal fish). We also counted the number of times an individual left and rejoined a school. Each time an individual joined a school, we recorded the number of individuals in the school; these values were averaged to obtain the mean school size for each individual during the observation period.

Proportion of time spent schooling, in-school and solitary feeding rates and in-school and solitary rates of attack by damselfish were compared for different species using one-way ANOVAs (JMP 5.0.1).

RESULTS

Bluehead wrasse spent significantly less time in schools than doctorfish and parrotfish ($F = 50.22$, $df = 2, 66$, $P < 0.001$,

Tukey's α = 0.05; Fig 1). Doctorfish and parrotfish did not differ in the proportion of time they spent in schools.

There was an effect of species and schooling on feeding rate (2-way ANOVA, F = 7.76, df = 5, 127, P < 0.0001; Species F = 8.76, df = 2, P = 0.0003; School F = 15.90, df = 1, P = 0.0001; Interaction F = 2.27, df = 2, P = 0.11; Fig. 2). The lack of an interaction shows there was no difference between species in the magnitude of the change between feeding rates in and out of schools. For each species, feeding rates were significantly higher when schooling than when solitary (Doctorfish F = 22.36, df = 1, 41, P < 0.0001; Parrotfish F= 2.02, df = 1, 42, P = 0.16; Bluehead Wrasse F = 3.71, df = 1, 44, P = 0.06; Fig. 2).

There was an effect of schooling, but not species, on rate of damselfish attacks (2-way ANOVA, F = 2.16, df = 5, 127, P = 0.06; Species F = 0.16, df = 2, P = 0.85; Schooling F = 5.34, df = 1, P = 0.02; Fig. 3). The magnitude of the change between damselfish attacks made on fish in and out of schools was the same for doctorfish and parrotfish but it differed significantly between these species and the bluehead wrasse (2-way ANOVA, Interaction F = 2.67, df = 2, P = 0.07; Fig. 3). Doctorfish and parrotfish both experienced a reduced rate of damselfish attacks when schooling than when solitary; there was no difference for bluehead wrasse (Doctorfish F = 3.11, df = 1, 44, P = 0.09; Parrotfish F = 7.28, df = 1, 42, P = 0.001; Bluehead Wrasse F = 0.27, df = 1, 44, P = 0.61; Fig. 3).

DISCUSSION

All three fish species showed benefits from mixed-species schools. Doctorfish and bluehead wrasse exhibited higher feeding rates in schools (Fig 2.), and the doctorfish and parrotfish experienced lower attack rates in schools (Fig. 3). The proportion of time spent schooling was not the same among the three species, with the bluehead wrasses schooling one-third as much as the doctorfish and parrotfish (Fig. 1).

The main benefits suggested for mixed-species schools are reduced risk of predation and higher foraging efficiency (Lukoschek and McCormick 2000). The proposed mechanisms by which foraging efficiency has been shown to increase in

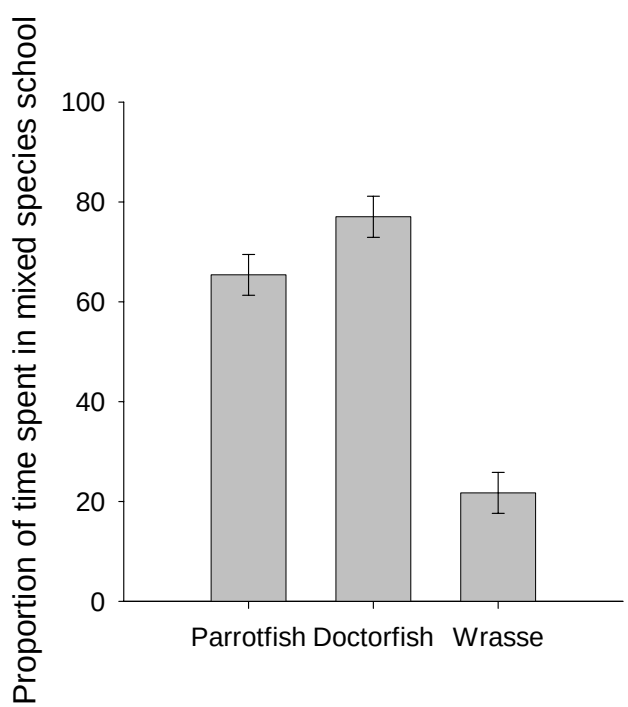

Figure 1. Proportion + 1 SE of time spent in mixed species schools. Doctorfish and Stoplight parrotfish spent more time in schools than out of schools. Bluehead wrasse spent more time out of schools than in schools.

mixed species schools are 1) resource location, in which school members expedite the finding of a rare or limited resource, and 2) swarming of territorially defended resources, such as fish eggs or damselfish algal mat territories (Foster 1985, 1987). In Discovery Bay, we saw doctorfish and parrotfish foraging on algal and turtle grass substrates, food resources that are neither limited nor entirely defended. Therefore, enhanced feeding is unlikely to be the only mechanism directly driving schooling behavior in these species.

Predator avoidance may be an important benefit of mixed-species schooling in these fish. Previous studies have shown that when in groups, fish spend less time showing 'vigilant' (predator-detecting) behavior, and thus more time foraging (Lukoschek and McCormick 2000). This was also supported by our behavioral observations of the doctorfish and parrotfish. In groups these fish fed in the open, but when solitary, they hid under rocks and fed little. This suggests that the doctorfish and parrotfish school to decrease their risk of predation, and that while schooling, decreased time is spent on predator detection, leading to increased foraging efficiency. This could be a response to naturally occurring predation threats; it is more likely to be an ingrained, evolutionarily-favored behavior, as predators are thought to be relatively uncommon at Discovery Bay (Ruel and Zug 1994).

The bluehead wrasse spent less time

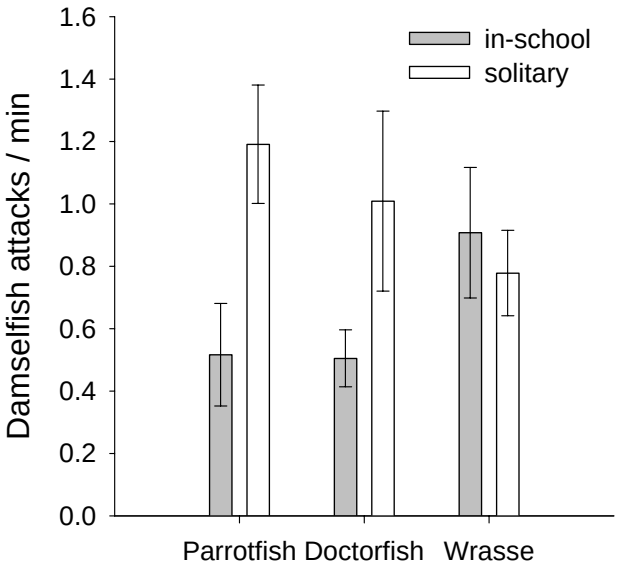

Figure 3. In-school and solitary damselfish attack rates + 1 SE for stoplight parrotfish, doctorfish, and bluehead wrasse in Discovery Bay, Jamaica (n = 69). Attack rates for parrotfish and doctorfish were higher when solitary. There was no difference in damselfish attack rates on bluehead wrasse while schooling or solitary.

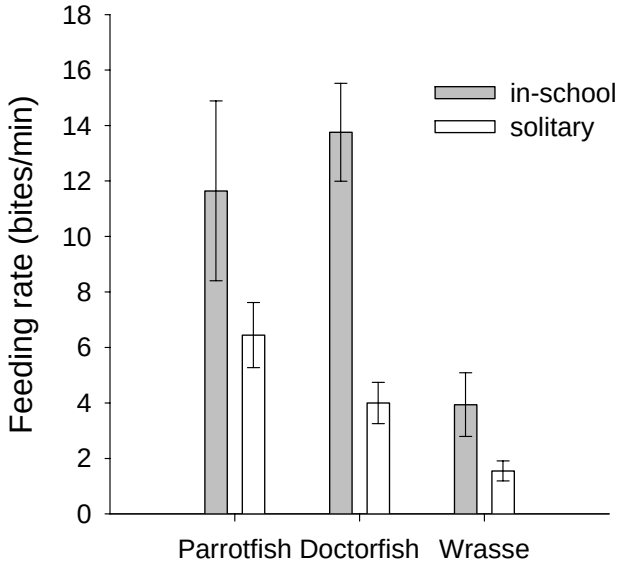

Figure 2. In-school and solitary feeding rates + 1 SE of stoplight parrotfish, doctorfish, and bluehead wrasse in Discovery Bay, Jamaica (n = 69). All fish showed greater feeding rates in schools than when solitary. There was an affect of species with parrot fish and doctorfish having higher overall feeding rates than bluehead wrasse (Tukey α = 0.05). There was no difference in the magnitude of change between in-school and solitary feeding rates across species.

in schools than doctorfish and parrotfish, though feeding efficiency increased while schooling. Solitary bluehead wrasse behavior was different from that of solitary doctorfish and parrotfish. While the latter two species were relatively inactive when alone, the solitary bluehead wrasses were highly active and seemed to forage often in damselfish territories. These wrasses may have been foraging for damselfish eggs, a preferred food resource (Foster 1987). If the acquisition of this resource was a priority for wrasses, blueheads may be more likely to leave the perceived safety of schools to search for damselfish eggs. We did not observe mixed-species schools swarming damselfish territories, and therefore schooling would not give the wrasse any advantage in egg foraging. Additionally, damselfish may target bluehead wrasses, as damselfish have been shown to defend specifically against egg-eating species (Foster 1987); therefore schooling would give bluehead wrasses no benefit against damselfish attacks.

Recent studies have indicated that several factors may encourage mixed species schooling, and these factors may be constantly changing with changing environmental conditions (Crook 1999). Our results suggest that although feeding efficiencies increased in schools for all three fish species, this may be an indirect effect of a behavior that evolved as a result of different benefits, possibly predator detection and avoidance.

LITERATURE CITED

Crook, A. C. 1999. Quantitative evidence for assortative schooling in a coral reef fish. Marine Ecology Progress Series., 176: 17-23.

Deloach, N. 1999. Reef Fish Behavior. New World Publications, Inc: Jacksonville, Florida.

Foster, S. A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. Animal Behavior, 33: 782-792.

Foster, S. A. 1987. Acquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, Thalossoma lucasanum. Environmental Biology Fishes, 19: 215-222.

Lukoschek, V. and M. I. McCormick. 2000. A review of multi-species foraging associations in fishes and their ecological significance. Proceedings of the 9th International Coral Reef Symposium.

Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher, and M. G. Cleland 1976. Schooling as a mechanism for circumventing the territoriality of competitors. Ecology, 57: 1208-1220.

Ruel, J. J. and D. B. Zug, Jr. 1994. The use of mixed-species foraging groups by the stoplight parrotfish, *Sparisoma viride*. Dartmouth Studies in Tropical Ecology, p. 162-166.