WITH A LITTLE HELP FROM MY FRIENDS: BENEFITS OF SCHOOLING IN OCEAN SURGEONFISH

YIRAN GU AND ALANNA H. PURDY

Faculty editor: David R. Peart

Abstract: Fish schooling provides individuals with potential benefits such as predator avoidance, increased foraging efficiency and access to food resources. We tested whether schooling affects foraging rates of adult and juvenile Ocean Surgeonfish in Grape Tree Bay on Little Cayman Island. We hypothesized that 1) individual feeding rates would be greater in heterospecific than conspecific groups, and 2) individual feeding rates would be greater in groups than alone. Juveniles foraged mostly in heterospecific groups while adults foraged mostly alone. Juveniles fed significantly faster in heterospecific groups than with conspecifics or alone, in contrast to adults, whose feeding rates did not change when individuals associated with either con- or hetero-specifics. The number of Ocean Surgeonfish did not differ between conspecific and heterospecific groups, but heterospecific groups were always larger. Thus, we could not determine whether the benefits of heterospecific associations were a function of individual behavior influenced by species composition, or group size. Large, heterospecific groups may reduce predation risk in addition to increasing foraging rates, leading to the prediction that juveniles should associate with heterospecific groups whenever possible.

Key Words: Acanthurus bahianus, *schooling, predation, competition*

INTRODUCTION

Mixed-species schooling is common in herbivorous coral reef-fish. Potential benefits include predator avoidance, increased foraging efficiency, and improved access to food resources (Lukoschek and McCormick 2000, Foster 1985). In many species, individuals have different schooling behavior and diet preferences at different lifestages (Overholzter et al. 2000).

Ocean Surgeonfish (*Acanthurus bahianus*) is a generalist herbivore that occurs individually, in mixed-species groups, and (as adults) in conspecific groups (Deloach and Human 1999). We evaluated the effects of schooling and lifestage on feeding rate of Ocean Surgeonfish in the back reef of Grape Tree Bay on Little Cayman Island. Con- and heterospecific schooling may allow individuals to spend more time foraging via increased predator detection (Lukoschek and McCormick 2000). If so, feeding rate of individuals in groups would be higher than that of solitary foragers. Alternatively, schooling could increase competition among individuals, leading to decreased feeding rate, which would favor solitary foraging. Competition may also be higher among conspecifics than among heterospecifics, leading to a lower

feeding rate of individuals in conspecific groups than those in heterospecific groups.

Juvenile Ocean Surgeonfish may school more often than adults, as diet, habitat and behavior changes with lifestage (Lawson et al. 1999). Predator-vigilance could be more important for juveniles than adults, favoring schooling behavior (Wolf 1984). Damselfish defend patches of algal garden in their territories and limit access of other herbivorous fish (Deloach and Human 1999). Overcoming damselfish territoriality may be more difficult for solitary juveniles than solitary adults and juveniles in foraging groups, favoring schooling in juveniles.

METHODS

We measured feeding rates of adult and juvenile Ocean Surgeonfish on Feb 29 and Mar 1- 2, 2008 along a 400 m stretch of the back reef in Grape Tree Bay, in front of the Little Cayman Research Center. During both morning and afternoon each day, we haphazardly sampled Ocean Surgeonfish by snorkeling over the reef until an actively traveling or feeding individual was located 1-10 m from the reef crest. We observed one focal fish per group encountered. We categorized individuals of 10-13 cm in length as adults, 4-6 cm as juveniles, and ignored fish outside these size classes.

After habituating fish to our presence for ca. 1 min, we counted # bites made by the focal fish for up to 5 minutes, and calculated bite rate (bites min^{-1}). We recorded schooling behavior (solitary, conspecific, or heterospecific groups), group size, species composition, and whether foraging during each observation period occurred in damselfish territory. We ended an observation period before 5 minutes if the individual changed group association, began non-foraging activities (such as hiding, visiting cleaning station), or swam out of sight. For analysis, we retained all observations longer than 30 s.

We equalized variances with a $\log_{10}$ transformation of bite rate and ran two, two-way ANOVAs for the effects of grouping and damselfish territory on feeding rates; one for adults, one for juveniles. We did not include interactions between the two factors because we had no a priori hypotheses about the effect of damselfish territory on grouping. We were also unable to include the interaction term in the model since we observed no solitary juveniles feeding in damselfish territories.

We tested for the specific hypothesized differences in feeding rate using linear contrasts. We compared feeding rates of solitary individuals and individuals in heterospecific and conspecifics groups ($\mu_H + \mu_C - \mu_S = 0$), and of individuals in

heterospecific and conspecific groups ($\mu_H + \mu_C = 0$).

RESULTS

We observed a total of 38 adult and 48 juvenile Ocean Surgeonfish over the period of 3 days. Fourteen focal adults and 36 juveniles foraged in groups. On average, conspecific groups contained 2.12 ± 0.08 fish (mean ± SE), while heterospecific groups contained 6.88 ± 0.52 fish. Of the 20 fish species observed foraging with Ocean Surgeonfish in heterospecific groups, juvenile Blueheaded Wrasse, juvenile Striped Parrotfish, and adult Striped Parrotfish were the most common (Table 1).

Schooling behavior affected feeding rate of juveniles and adults differently (Table 2, Figure 1). Feeding rate of individuals in con- and heterospecific groups differed for juveniles (linear contrast $F_{1,44} = 10.11$, P = 0.003) but not adults (linear contrast $F_{1,33} = 1.33$, P = 0.23). When combined, feeding rate of individuals in conspecific and heterospecific groups did not differ from those of solitary foragers, for either adults (linear contrast $F_{1,33} = 1.17$, P = 0.29) or juveniles (linear contrast $F_{1,44} = 2.64$, P = 0.11). Juveniles in heterospecific groups fed the fastest (Figure 1).

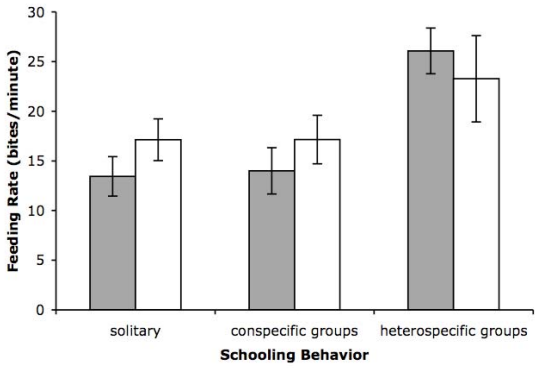

Figure 1. Feeding rate (mean ± SE) of adult and juvenile Ocean Surgeonfish (*Acanthurus bahianus*) with different schooling behaviors in a back reef of Grape Tree Bay, Little Cayman Island. Gray bars = juvenile (N=48), white bars = adults (N=38).

Feeding rate of adults and juveniles did not differ significantly (t = 0.74, df = 85, P = 0.46). Feeding rates also did not differ in and out of damselfish territories for adults or juveniles (Table 2). Although neither adults nor juveniles foraged extensively in damselfish territory, adults and juveniles did spend similar percentages of foraging time in damselfish territories (22.9% and 16.2% of observations respectively; Pearson's $\chi^2 = 0.59$, P = 0.44). Adults, which mainly fed alone (57.9%), differed from juveniles, which fed mostly in heterospecific groups (59.2%; Pearson's $\chi^2 = 15.75$, P = 0.0004). Although heterospecific groups were larger (mean ± SE, 6.88 ± 0.52) than conspecific groups (2.12 ± 0.08; F = 80.43, df = 1, P < 0.0001), the mean number of Ocean Surgeonfish in conspecific (mean ± SE, 2.7 ± 0.27) and heterospecific groups (2.1 ± 0.21)

did not differ (df = 1, 47, t = 3.14, P = 0.08).

Discussion

Adult feeding rate was unaffected by schooling behavior, whereas juveniles fed faster when associated with heterospecifics. Larger, mixed-species groups increase predator detection and allow individuals to spend more time foraging (Lukoschek and McCormick 2000). If predator detection is more important for juveniles than adults, and juveniles can feed faster in heterospecific groups, juveniles should forage in groups whenever possible.

The significantly lower feeding rate of juveniles in conspecific vs. heterospecific groups may be due to difference in behavior influenced by species composition of groups, or by group size. Since heterospecific groups were always larger than conspecific groups, we were unable to isolate the effect of group composition vs. group size on feeding rate.

Previous studies suggest that juvenile Ocean Surgeonfish avoid conspecifics in favor of mixed-species schools to minimize the cost of direct competition, while still benefiting from schooling (Debrot et al. 1988, Overholtzer et al. 2000). We found no evidence of conspecific avoidance, as both conspecific and heterospecific groups contained the same number of Ocean Surgeonfish. Assuming intraspecific competition in con- and heterospecific groups is equal, juveniles' tendency to school in heterospecific groups must be explained by mechanisms other than competition avoidance (i.e. increased predator detection or improved foraging efficiency).

By estimating the proportion of damselfish territory in potential foraging areas, it would be possible to test whether Ocean Surgeonfish feed in damselfish territories more than by chance alone (suggesting they do so to gain access to higher quality food), or less than by chance (suggesting active avoidance).

Insights into how schooling affects individual behavior could be gained by measuring the time individuals spend schooling vs. alone, and evaluating the potential costs of schooling, e.g. within group aggression and resource competition, and how these differ between con- and heterospecific groups.

The benefits of heterospecific schooling for juvenile Ocean Surgeonfish seem clear and unequivocal. Literature on schooling behavior in fish focuses on two main components of fish fitness, feeding rate and predation risk. While there may be tradeoffs between these in some cases, no such tradeoffs are apparent here. Our findings indicate a substantial advantage in feeding rate. The extensive literature on how schooling reduces predation risk (Lukoschek and McCormick 2000, Morse 1977) makes it implausible that predation risk would be increased by joining a large, het-

erospecific group, especially for these relatively small juveniles, who could be vulnerable to a wide range of predatory fish on the reef.

Indeed, the benefits of reduced predation risk may contribute strongly to the feeding benefits of heterospecific group membership that we demonstrated. High juvenile feeding rates in these groups may be largely due to the reduced need to spend time on predator vigilance. Further, large heterospecific groups may be able to forage in areas rich in resources but relatively exposed to predators.

In summary, our findings lead to the prediction that juvenile Ocean Surgeonfish should associate with heterospecific schools wherever possible. Individual juveniles that tend to associate with the smaller, conspecific groups, or forage alone, should have lower fitness, and this behavior selected against. It is possible that these benefits of heterospecific schooling differ across the range of the species; in that case gene flow could maintain some variance in individual juvenile behavior.

LITERATURE CITED

Debrot, A.O., A.A. Myberg. 1988. Intraspecific avoidance as a proximate cause for mixed-species shoaling by juveniles of a western Atlantic surgeonfish, Acanthurus bahianus. Bulletin of Marine Science. 43:104-106.

Deloach, N. and P. Human. 1999. Reef fish behavior: Florida, Carribbean, Bahamas. Jacksonville: New World Publications Inc., pp. 180, 315.

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

Lawson, G.L., D.L. Kramer, W. Hunte. 1999. Size-related habitat use and schooling behavior in two species of surgeonfish (Acanthurus bahianus and A. coeruleus) on a fringing reef in Barbados, West Indies. Environmental Biology of Fishes. 54: 19-33.

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.

Morse, D.H. 1977. Feeding Behavior and Predator Avoidance in Heterospecific Groups. BioScience. 27: 332-339.

Overholtzer, K.L., P.J. Motta. 2000. Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. Environmental Biology of Fishes. 58: 345-354.

Wolf, N.G. 1984. Odd fish abandon mixed-species groups when threatened. Behavioral Ecology and Sociobiology. 17: 47-52.

Table 1. Abundance and frequencies of species observed in foraging groups (N=50) containing Ocean Surgeonfish (*Acanthurus bahianus*) in a back reef on Little Cayman Island. Bold captions indicate most common species observed in heterospecific groups.

Common Name	Scientific Name	Lifestage	Total Number of Individuals Observed	Number of Groups containing each Species
Blue Tang	*Acanthurus coeruleus*	Adult	2	2
		Juvenile	1	1
Bucktooth Parrotfish	*Sparisoma radians*	Adult	2	1
		Juvenile	2	2
Doctorfish	*Acanthurus bahianus*	Adult	1	1
		Juvenile	2	2
Foureye Butterflyfish	*Chaetodon capistratus*	Adult	1	1
French Grunt	*Haemulon flavolineatum*	Adult	33	4
Blueheaded Wrasse	***Thalassoma bifasciatum***	**Juvenile**	**18**	**11**
Bluelip Parrotfish	*Cryptotomus roseus*	Juvenile	1	1
Slippery Dick	*Halichoeres bivittatus*	Juvenile	6	5
Spotfin Butterflyfish	*Chaetodon ocellatus*	Juvenile	1	1
Stoplight Parrotfish	*Sparisoma viride*	Juvenile	6	6
Redtail Parrotfish	*Sparisoma chrysopterum*	Juvenile	3	1
Mutton Snapper	*Lutjanus analis*	Adult	4	2
Princess Parrotfish	*Scarus taenipoterus*	Adult	2	2
		Juvenile	2	1
Rainbow Wrasse	*Halichoeres pictus*	Adult	4	2
Sergeant Major	*Abudedduf saxatilis spelling?*	Adult	2	1
Slippery Dick	*Halichoeres bivaittatus*	Juvenile	16	6
Spotted Goatfish	*Pseudupeneus maculatus*	Adult	1	1
Striped Parrotfish	***Scarus criucensis***	**Adult**	**24**	**10**
		Juvenile	**20**	**10**
Yellowtail Snapper	*Ocyurus chrysurus*	Adult	3	1
Yellowtail Goatfish	*Mulloidichthys martinicus*	Adult	2	1
		Juvenile	2	1

Table 2. Two-way ANOVA of effects of schooling behavior and damselfish territories on feeding rate of adult and juvenile Ocean Surgeonfish on a back reef at Little Cayman Island.

	Adults			Juveniles		
Source	**df**	**F**	**P**	**df**	**F**	**P**
Damselfish Territory	1	0.01	0.92	1	0.11	0.74
Schooling Behavior	2	1.14	0.33	2	9.01	0.0005
Error	34			44		