predation pressure causes *Diadema* to aggregate in canyons or crevasses on the ocean floor. Although we did find a positive relationship between urchin abundance and substrate complexity, our measure of complexity may not have provided the best estimate of potential refuge. For example, a relatively flat substrate with many crevices may have the same calculated complexity value as a mounded substrate, but may offer a different level of protection to *Diadema*.

Urchin abundance was probably a major factor determining the community composition. As predicted, areas with high urchin abundance had less macroalgal cover and more coral and microalgal turf cover. Although this is a well-documented large-scale trend (Aronson et al. 2000, Edmunds et al. 2001), our results suggest this trend is also evident on a microspatial scale even within areas of high urchin abundance. We found a positive correlation between urchin abundance and juvenile coral abundance, which suggests urchin grazing may promote coral recruitment by opening up suitable settlement space for larval corals (Howarth 1979). If herbivory by *Diadema* is opening up suitable settlement space for juvenile corals, a clumped urchin distribution may result in a clumped distribution of successful coral recruits at a microspatial scale.

Community composition on the reef has changed considerably in the past 10 years. Our background data reflect the macroalgae-to-coral phase shift that is being documented on Caribbean reefs. However, a more rapid phase shift may be occurring on the microspatial scale in more complex areas that experience greater grazing pressure. Our results suggest *Diadema* density and substrate complexity may drive microspatial patterns in substrate cover and coral recruitment. As urchin populations continue to recover from the die-off, they may distribute themselves differentially with regard to microspatial habitat complexity, and thus alter community composition differentially on a localized scale. Future research should attempt to examine how this phase shift may affect the distribution and composition of coral and alga species on a local scale.

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Diel variation in fish community composition and schooling behavior on the back-reef of Discovery Bay, Jamaica

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Abstract: A large number of fish species are able to coexist on tropical coral reefs by reducing competition through temporal and behavioral partitioning of resources. Some species may partition behavior and increase their foraging efficiency by traveling in single- or mixed-species schools. Fish that exhibit schooling behavior may be better able to find resources and overwhelm territorial fish that guard high quality resources. Schooling behavior is also thought to reduce a fish's vulnerability to predators, as each individual benefits from the vigilance of other members and many individuals together may confuse potential predators. This behavior should be more pronounced during the day when visual predators are active. We tested these ideas by conducting a census of fish populations during the day and night on the back-reef at Discovery Bay, Jamaica. We hypothesized that fish would partition resources in time, with different species being active during the day and the night. We further hypothesized that schooling behavior would differ between the day and night, and predicted that schooling would be more common during the day. Like past studies at this site, we found a difference in the species detectable during the day and the night, indicating that fish are partitioning resources in time. We also saw increased schooling behavior during the day, suggesting that some fish species are taking advantage of the increased foraging efficiency and predator avoidance associated with schooling. These results indicate that similar tropical reef species are able to coexist by partitioning common resources.

Key Words: diel activity, mixed-species school, resource partitioning, single-species school, solitary

Introduction

Tropical coral reefs are home to an incredible diversity of fish species, with 500 - 600 species in the Caribbean alone. There is a high degree of resource overlap as a result of such a large number of species, and there are many mechanisms that allow them to coexist. One mechanism is the evolution of resource partitioning in time and space, or specializing on certain foods or habitat types (Sale 1977, Galdfelter 1980). Many species of fish are active during daylight hours, while some reach their peak activity during the night. These diel differences could allow species that share habitat to reduce interspecific competition for resources (Rooker 1991). In addition, fish may partition resources behaviorally by foraging in different ways, either as solitary feeders, organized single species schools or opportunistic mixed-species schools, to increase foraging efficiency by overwhelming territorial fish protecting resources on the territory (Ehrlich 1973, Ogden 1977, Crook 1999). Schooling may also provide increased protection from predators due to greater combined vigilance and the "confusion effect" that these groups of potential prey would exhibit (Crook 1999).

We conducted a diel census of fish populations to explore various behavioral adaptations that may allow between 100 - 200 species of fish to coexist in the back-reef of Discovery Bay, Jamaica. Based on previous FSP studies, we hypothesized that there would be a difference in species composition between the two time periods, possibly reflecting behavioral responses to reduce resource overlap. We further hypothesized that there would be a difference in schooling behavior between day and night, predicting that more species would school during the day due to increased foraging activity and greater risk from visual predators.

Methods

On 25 February 2002, we surveyed fish species on the western back-reef in Discovery Bay, Jamaica. Pairs of observers collected data along parallel transects starting at the boat launch in front of the Discovery Bay Marine Laboratory and ending at the reef crest (see Nagy et al. 2000 for illustration). Nine pairs of observers conducted an hour-long survey during the morning (08:30 - 09:30; cloudy, rough waves) and eight pairs conducted an hour-long survey at night (20:30-21:30; clear, full moon). We recorded the presence of fish species for each transect. To estimate abundance, we calculated the proportion of transects on which a species was seen and used a t-test to compare the data.

We also recorded the behavior of fish as solitary, in a single species school or in mixed species schools. We defined a school simply as a group of fish traveling together. Due to this loose definition of schooling, groups of fish not showing real schooling behavior were included. To determine whether schooling behavior changed between the day and night, we calculated the proportion of fish species found alone, in a single- or mixed-species school or exhibiting both behaviors. For species found both day and night, we calculated the number of species that changed schooling behavior and the reported the type of change.

Results

We observed 101 different fish species, with 49 species found exclusively during the day, 21 species found exclusively at night and 31 species found during both the day and the night (Table 1). The species observed during the day were more evenly distributed across the back-reef than those observed at night. Across all species, the proportion of transects on which species were seen was significantly greater during the day than at night ($t = 5.64$, $df = 15$, $P < 0.001$).

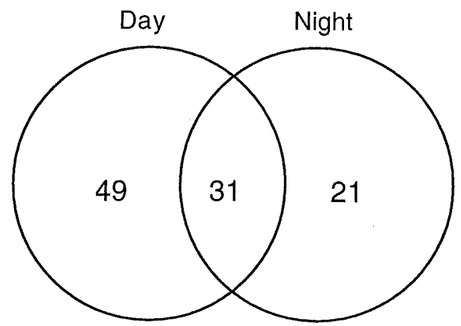

FIG. 1. Number of fish species found in the day, night, and in both censuses in the back reef of Discovery Bay, Jamaica.

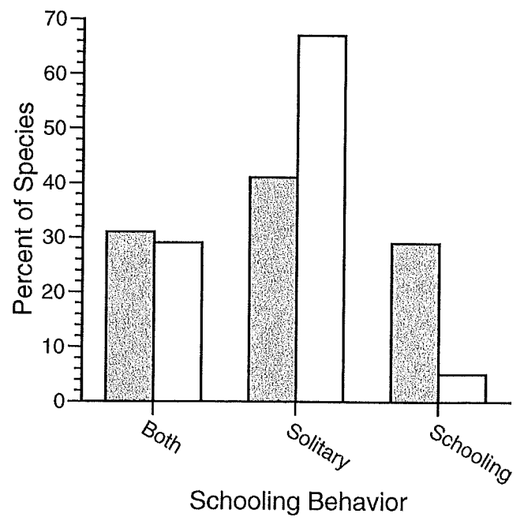

FIG. 2. The percent of species found both solitary and schooling, exclusively solitary, and exclusively schooling during the day (gray) and night (white).

Schooling behavior changed between the day and night (Fig. 2). During the day, 40% of fish species were found only as solitary individuals, 29% were found exclusively in schools and 31% exhibited both types of behavior. During the night, 66% of species were solitary, 5% of species were only schooling and 29% of species exhibited both behaviors. The schooling behavior of half of the 32 species observed both day and night did not

TABLE 1. Day and night fish survey of the back reef at Discovery Bay, Jamaica. The number of transects is the number of transects in which a fish was observed, out of 9 total transects.

Day Only		Night Only		Day and Night	
Species	no. transects	Species	no. transects	Species	no. transects
Anglefish, French	2	Bigeye	1	Anchovies	1
Angelfish, Gray	1	Butterflyfish, four-eyed	1	Balloonfish	8
Angelfish, Rock Beauty	1	Cardinalfish, Barred	3	Cornetfish, bluespotted	1
Barracuda, Great	3	Cardinalfish, Belted	3	Damselfish, Sergeant Major	2
Bass, Harlequin	1	Cardinalfish, Bridled	1	Damselfish, Yellowtail	1
Basslet, Fairy	2	Cardinalfish, Dusky	4	Drum, Spotted	1
Blenny, Palehead	1	Cardinalfish, Twospot	2	Eel-Moray, Spotted	1
Blenny, Redlip	1	Damselfish, Dusky	3	Goatfish, spotted	1
Blenny, Rosey	2	Damselfish, Night Sergeant	2	Grunt, French	4
Butterflyfish, Banded	1	Eel, Green	1	Hamlet, Indigo	2
Butterflyfish, Spotfin	3	Flamefish	2	Houndfish	1
Chromis, Brown	2	Herring	1	Jack, Bar	3
Chromis, Blue	2	Needlefish	2	Lizardfish	1
Damselfish, Beaugregory	8	Porcupinefish	6	Mojarra, Mottled	3
Damselfish, Bicolored	9	Ray, Lesser Electric	1	Mojarra, Yellowfin	5
Damselfish, Cocoa	1	Ray, Spotted Eagle-	3	Needlefish	2
Damselfish, Dusky	8	Ray, Yellow	1	Parrotfish, Redband	2
Damselfish, Longtail	1	Schoolmaster	1	Parrotfish, Redtail	1
Damselfish, Threespot	9	Snapper, Gray	1	Parrotfish, Stoplight	1
Eel, Goldspotted	1	Squirrelfish	8	Reef Croaker	4
Eel, Sharptail	2	Soapfish, Greater	6	Silverside	7
Filefish, Orange-spotted	2	Soldierfish, Barred	4	Snapper, Mutton	2
Flounder, Peacock	2			Squirrelfish, Dusky	4
Goatfish, Yellow	3			Squirrelfish, Longspine	4
Goby, Bridled	2			Squiirrelfish, Longjaw	2
Goby, Goldspotted	1			Squirrelfish, Reef	4
Goby, Sharknose	1			Soldierfish, Blackbar	1
Guitarfish, Atlantic	1			Surgeon, Doctorfish	4
Hamlet, Barred	1			Surgeon, Ocean	2
Hogfish, Spanish	1			Sweeper, Glassy	5
Mojarra, Flagfin	2			Trumpetfish	4
Parrotfish, Bucktooth	2			Wrasse, Slippery Dick	2

TABLE 1. (Continued)

Day Only		Night Only		Day and Night	
Species	no. transects	Species	no. transects	Species	no. transects
Parrotfish, Princess	8				
Parrotfish, Striped	8				
Parrotfish, Yellowtail	2				
Puddingwife	1				
Puffer, Sharpnose	1				
Sand Diver	2				
Sheepshead	1				
Snapper, Yellowtail	1				
Squirrelfish	9				
Stingray, Southern	1				
Surgeon, Ocean	9				
Surgeon, Blue Tang	9				
Tobaccofish	1				
Tomtate Grunt	2				
Torpedo, Atlantic	1				
Wrasse, Blackear	1				
Wrasse, Blueheaded	8				
Wrasse, Clown	6				
Wrasse, Yellowhead	2				

change from day to night. However, the schooling behavior of 12 of these species changed from schooling during the day to solitary at night. Three species showed the reverse pattern and were observed solitary during the day and schooling at night.

Discussion

As expected, we found a difference in fish species composition between day and night. This could be a result of different foraging behaviors, with species specializing on resources available at the different times. By temporally partitioning feeding activity, reef fishes reduce competition and take full advantage of the resources in their shared habitat. The number of fish observed both day and night probably underestimates temporal partitioning, as some of these were likely active only during the day or night.

Although most species found during both time periods were solitary, both single- and mixed- species schools were more common during the day. By schooling, fish potentially increase competition for resources, but are able to increase their foraging efficiency by locating resources quicker and overwhelming territorial fish defending quality resources not available elsewhere. These schools also increase predation defense by increasing the chance that a predator will be

spotted. In addition, schools of potential prey can confuse predators and reduce their capture efficiency. Mixed-species schools benefit less abundant species by increasing their numbers, and some have adapted mimic behavior by schooling only with species of similar shape, size and coloration (Dafni 1984, Crook 1999).

Fifteen species that were observed both day and night showed a transition between solitary and schooling behavior. Two species of squirrelfish, the dusky and longspine, were solitary during the day but occurred in schools at night. It is possible that these species are resting during the day in crevices and forming schools at night to forage efficiently. Twelve species were found in schools during the day and solitary at night. Many of these species feed in schools during the day, breaking apart to bed down in crevices alone at night. Solitary nocturnal species, such as the soldierfish and long jaw squirrelfish, may join mixed schools during the day for protection. Ehrlich (1973) suggested that a limited number of crevices are available to fishes resting during the day, hence daytime schooling could provide solitary, nocturnal individuals with increased safety from predators.

Overall we found that fish are partitioning resources such as food and shelter, both temporally and behaviorally. Further studies could explore the specific benefits to different times of peak activity and the relative costs and benefits of schooling behavior. Further research could investigate other adaptations amongst species that might promote the coexistence of such a high diversity of fish.

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