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Appendix A. Forereef algal species richness. The number in parentheses is the total number of species for each site. Species listed above the bold line were found at both sites.

Discovery Bay (25)	Pear Tree Bottom (21)
Amphiroa fragilissima	*Amphiroa fragilissima*
Dictyota ciliolata	*Dictyota ciliolata*
D. dichotoma	*D. dichotoma*
Galaxaura oblongata	*Galaxaura oblongata*
Halimeda goreaui	*Halimeda goreaui*
H. opuntia	*H. opuntia*
H. tuna	*H. tuna*
Padina gymnospora	*Padina gymnospora*
Sargassum fluitans	*Sargassum fluitans*
S. hystrix	*S. hystrix*
S. polyceratium	*S. polyceratium*
Spyridia sp.	*Spyridia sp.*
Turbinaria tricostata	*Turbinaria tricostata*
Ventricaria ventricosa	*Ventricaria ventricosa*
Caulerpa racemosa	*Acanthophora spicifera*
Dasya harveyi	*Centroceras clavulatum*
D. mertensii	*Ernodesmis verticillata*
Gracilaria damaecornis	*G. subverticillata*
Laurencia intricata	*Hypnea cervicornis*
Lobophora variegata	*Laurencia poitei*
Rosenvingea intricata	*P. sanctae-crucis*
S. hystrix var. buxifolium	
S. platycarpum	
T. turbinata	
Valonia spp.	

Homing behavior and size variation of mysid swarms

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Abstract: *Mysidium gracile* occurs in swarms during the day and disperses at night on coral reefs. Homing behavior may be a mechanism for reforming these swarms each morning. We predicted that individuals within swarms occupy the same swarm location each day. Furthermore, we predicted swarms would be made up of similar sized individuals. Direct evidence for homing was not found. However, when swarms were completely removed, their locations were not occupied the following morning, suggesting that swarms are not composed of randomly associated individuals, and that homing occurs. Swarms were composed of different sized individuals.

Key Words: dispersal, Mysidium gracile, *predation, swarms*

INTRODUCTION

Swarms of *Mysidium gracile* are found on the backreef of Discovery Bay, Jamaica (Hahn and Itzkowitz 1985, Hoult and Neal 1988, Butler 1989, Deem 1998). Mysid swarming behavior has been proposed as a mechanism for predator protection and to increase reproductive and feeding efficiency (Clutter 1969 in O'Brien 1988, Wittman 1976 in O'Brien 1988). *M. gracile* in Discovery Bay commonly swarms during the day within damselfish territories, disperses at night to feed in the water column, and typically reforms into swarms at particular sites early in the morning (Hahn and Itzkowitz 1985, Hoult and Neal 1988, Deem 1998). Light cues seem to trigger dispersal and re-aggregation (Hoult and Neal 1988).

Homing behavior may be a mechanism for mysids to reform their swarms each morning. Hahn and Itzkowitz (1985) demonstrated short-distance homing behavior of displaced groups of individuals during the day. Despite the apparent re-aggregation of mysid swarms in the same locations in successive days, there is currently no evidence to indicate that the same individuals return to the same swarm location. We predicted that each individual homes to a single swarm location each day.

It has been suggested that swarms of *M. gracile* are made up of similar-sized individuals (Butler 1989, Deem 1998). This segregation by size may have differing costs and benefits for different sized mysids. Larger individuals may avoid swarms with small individuals as they may be easily detected by predators. Small individuals may avoid swarms with large individuals to avoid cannibalism. Intermediate sized individuals would be in more mixed groups. Therefore, as Butler (1989) and Deem (1998) observed, we predicted that swarms would be composed of similar-sized individuals.

METHODS

Mysid swarms were located in the back reef of Discovery Bay, Jamaica from 6-11 March, 1999. Each swarm was within the territory of a dusky of three-spot damselfish territory in the vicinity of coral overhangs. All swarms chosen for study were separated by at least 5 m. Swarms were marked with a buoy and glow sticks for night observations.

Fifty to seventy-five individuals were removed from four swarms using a hand-net. Removed individuals were placed in a clear, screw-top container and brought back to the lab. In the lab, the mysids were dyed using a solution of 50mg neutral red dye and 5 liters water (Modlin 1990), which was prepared approximately 1.5 hrs before the mysids were collected. After 1.5 hrs in the stain, mysids were removed from the solution. Ten to fifteen individuals were kept in the lab in a basin with running seawater as a control, and the remaining 40 to 50 individuals were returned to their original swarm. Returned individuals were watched for 5 to 10 min to make sure that they remained with the swarm.

At sunset, about 1800 h, we returned to the swarm site to observe the dispersal behavior of the swarm. We also returned to the site around 1930 h to make sure that the swarm had dispersed. The following morning at 0730 h, we

returned to the site again to see if a swarm had returned to the same location. We then collected all individuals in the swarm.

Red individuals, if any were present, were separated from the rest of the swarm and placed into a basin in the laboratory with running seawater. These individuals were then compared with the control individuals to determine if the color of the red individuals collected was the same as the dyed ones we had placed in the swarm. The remainder of the swarm was preserved in 10% formalin, and the size of each individual was measured to the nearest 0.5 mm (from eyes to statocysts).

Six entire swarms were collected and sized during the study period. Each day, we returned to the locations of previously collected swarms to see if a new swarm had recolonized the area. We also collected approximately 150 individuals from 8 additional swarms to look for naturally occurring red-pigmented individuals. Individuals from these swarms were not sized.

RESULTS

Observations conducted at swarm sites around sunset, revealed that mysid swarms disperse in random directions. As light levels diminish small groups of individuals break off from the swarm and move up in the water column. Once near the surface, groups immediately break up and individuals dispersed in all directions.

For the four swarms that we dyed, returned individuals, and collected the entire swarm the following morning, we found 49, 23, 26, and 36 red individuals. These individuals were compared with our control dyed individuals using a microscope. No differences were seen between the red and control individuals.

To further determine whether the red mysids collected from these swarms were indeed the ones we dyed, we randomly collected mysids from 8 other swarms to see if any were red. When collected, mysids were held against a white background in the field. All mysids were white in color. However, back at the lab, the individuals in 4 out of 8 swarms were predominantly red. After a few hours, they became white again. Over the course of the next 24 to 36 hrs, mysids changed color from white to red and back to white several times in no apparent pattern.

Observations on whether a swarm was present the following morning after an entire swarm was collected were conducted for five of the six swarms. For all sites, no swarms in the exact same location the following morning. However, at one location a group of approximately 15 mysids were found the following morning. As no swarms in general were observed to be that small, we considered these mysids to be part of the swarm that we thought we had collected in entirety the previous day. At two locations, new swarms formed two days after collection (Table 1).

The lengths of 2,599 individual mysids were measured. Lengths ranged from 1.0 mm to 6.0 mm. Although the mean size of the individuals in the six swarms ranged from 2.54 mm to 3.66 mm, each swarm had a broad size distribution (Fig. 1). All swarms differed significantly in mean individual size with the exception of two, the swarm with 317 mysids and the swarm with 599 mysids (Wilcoxon: X^2 estimate=214.9, df=5, $p<0.05$; Table 2).

Table 1. Presence of new swarms after collection of entire mysid swarm the previous morning. N indicates no swarm present. Y indicates new swarm present.

Date Collected	6-Mar	7-Mar	8-Mar	9-Mar	10-Mar	11-Mar
6-Mar	----------	N	N	N	N	N
7-Mar	----------	----------	N	Y	Y	Y
8-Mar	----------	----------	----------	N	Y	Y
9-Mar	----------	----------	----------	----------	N	N
10-Mar	----------	----------	----------	----------	----------	N

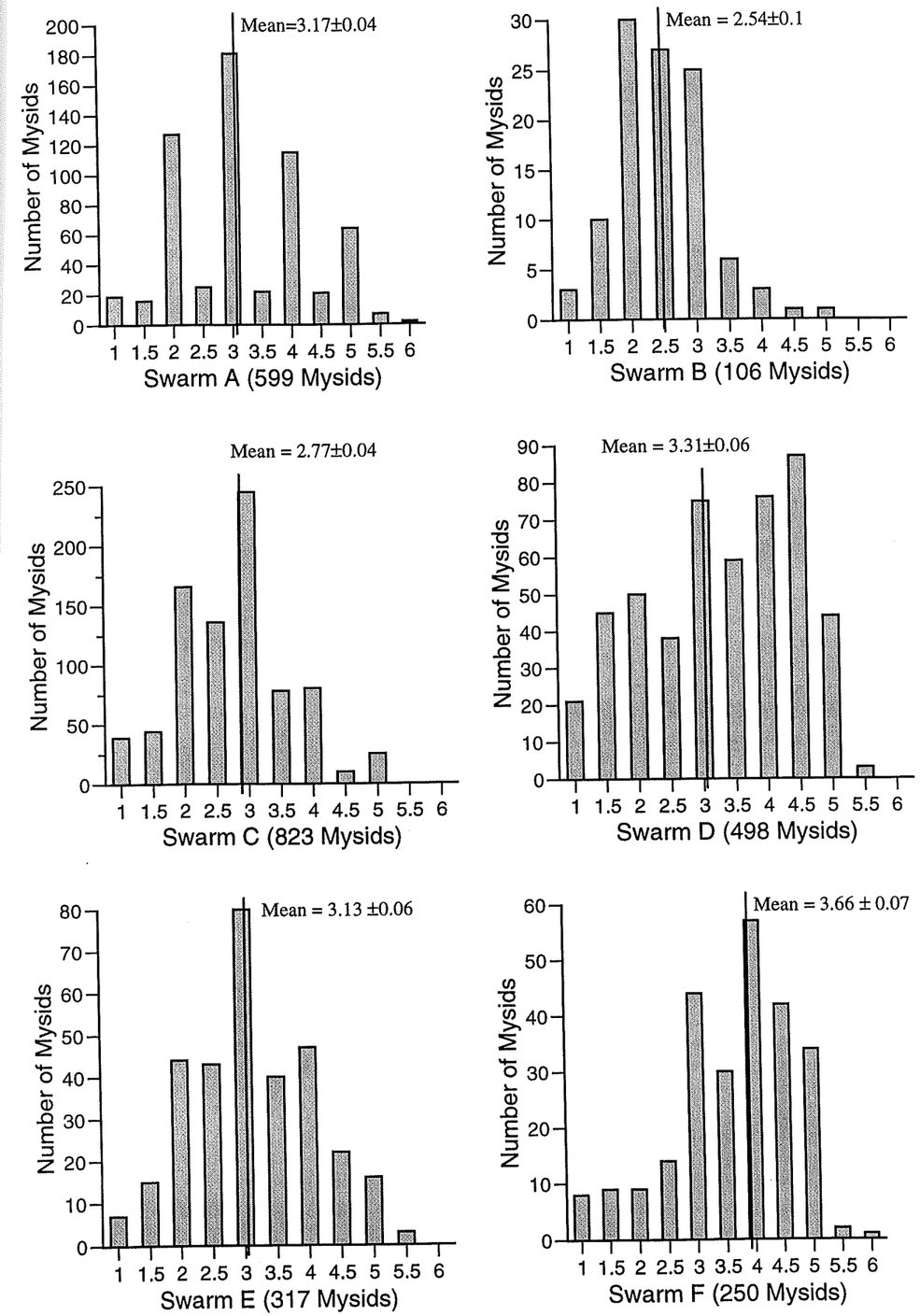

Fig. 1. Frequency distributions of mysid lengths found in entire swarms collected on the backreef of Discovery Bay.

Table 2. Mean lengths of mysids in six swarms collected in their entirety on the backreef at Discovery Bay, Jamaica. Schools with similar symbols indicate that they are not significantly different in mean length size using experimental-wise multiple comparisons.

	School	Total Mysids	Mean Length (mm)
■	A	599	3.17 ± 0.04
✹	B	106	2.54 ± 0.1
✹	C	823	2.77 ± 0.04
■ ◆	D	498	3.31 ± 0.5
◆	E	317	3.13 ± 0.06
	F	250	3.66 ± 0.07

DISCUSSION

Red mysids were found in the four swarms where we had dyed and returned mysids, suggesting that mysids may be homing. However, we found (1) similarly colored red mysids in randomly collected swarms, and (2) mysids seemed to readily change color from white to red and back again. Consequently, we cannot attribute finding red mysids to homing behavior.

Swarms were not found in the locations where we had collected the entire swarm the previous morning. This provides strong indirect evidence for homing. If mysids were not homing and instead were selecting a place to return at random each morning, we would expect to find that a given area would have a swarm there the following morning. This is the first evidence that mysid individuals may return to home sites. Thus far, no one has studied how far mysids may travel during their night dispersals.

In order to determine if mysids are indeed homing, a study using a UV dye instead of a color dye to mark individual mysids may provide better information. A blacklight could then be used to determine whether individuals are indeed returning back to the same group each morning after they disperse. Future studies could also address the question as to why mysids change color during the day, and if this change follows a regular cycle.

Regarding lengths of individual mysids within the swarm, we found that swarms are not dominated by individuals of one particular size, contrary to Butler (1989) and Deem (1998). Deem's result that as group size increased, mean size of individual mysids increased may be explained by differences in sampling method. We sampled the entire group while Deem only took a subsample of each group, perhaps skewing his results because of non-random spatial distributions of different sized individuals within swarms. We found a large range of mysid sizes within a given swarm. Although not quantified, different life stages were also found in each swarm. This suggests that mysid swarms are made up of several generations of individuals. This hypothesis would be further supported if mysids are shown to home and always return to the same swarm.

Modlin (1990) found that *M. columbiae* swarms are also made up of different sized individuals that are vertically stratified within the swarm. Smaller individuals were found at the top of the swarm while largest individuals were at the bottom of the swarm. Future studies could assess whether such vertical stratification also occurs in *M. gracile*.

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