PILES OF TILES:

An examination of marine mysid swarm site preferences

Good discussion of your results. An area for future work to be very difficult to perform these questions.

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Abstract

Many studies have documented the schooling behavior of marine mysids, but few have examined the site selection of these demersal reef zooplankton in relation to protection from predators. This study attempts to define some of the criteria used by the mysid swarms in site selection. Artificial substrates were placed under mysid swarms to determine the effect of substrate on site selection, and the relationship between structural complexity of 3 habitats and swarm density was examined. Swarms showed no preference for dark or light substrate, and a positive correlation was found between structural heterogeneity and mysid swarm density. Based on these results and on field and lab observations, it is concluded that mysids select a site based on its structural heterogeneity and that substrate color (and its implications for camouflage) is incidental to a vertical structure.

Introduction

The schooling behavior of some types of marine crustaceans has been well documented (Emery 1968). Among these schooling species are the marine mysids (Family Mysidacea), common in tropical reef ecosystems. Steven (1961, in Hahn and Ittekowitz 1986) found that mysid swarms exhibit "a cohesiveness and ease of locomotion comparable to those of fish." Randall et. al. (1964, in Emery 1968) noted that swarms occur near large Diadema urchins for protection, while Clarke (1955, in Hahn + Ittekowitz 1986) found that swarms occur near sea anemones and Emery (1968) noted a loose commensalism between mysid swarms and territorial damselfishes (Family Pomacentridae). These reef zooplankton are demersal, dispersing from their home site to feed at night (Butler 1989), yet the degree of homesite permanence from day to day is high (Hoult and Neal 1988), indicating a strong preference for specific localities.

What criteria do mysid swarms use

when establishing a homesite? Camouflage and protection seem especially important, as planktivorous feeders abound during the day (Hoult and Neal 1988) and indeed, swarms are often difficult to see against a sandy floor. In fact, predatory attacks on intact swarms at their home sites have rarely (if ever) been recorded, indicating that the swarm's choice of microhabitat decreases predation risk.

Hoult and Neal (1988) suggest that an ideal mysid swarm microhabitat consists of a damselfish, a sandy floor, and outcropped coral. This study examines the effect of substrate color and habitat complexity on mysid swarm location in an attempt to determine the criteria used by the animals in choosing a suitable microhabitat.

Methods

The study was conducted from 26 February to 5 March at Discovery Bay on the northern Caribbean coast of Jamaica, West Indies. All observations were made on the west back reef (WBR) at 1-3 m and on the west fore reef (WFR) at 7-13 m. Observations on the WFR were made using SCUBA; those on the WBR were made using snorkelling equipment.

In each of two trials beginning two days apart, 12 mysid swarms over sandy areas were located on the back reef. Each swarm was next to a wall covered with algae, or an area otherwise protected by coral outcroppings. Two tiles (625 cm^2 and 2 cm thick) covered with black plastic were placed directly under each of four swarms. A transparent glass plate (these ranged in size from ~300-625 cm^2) was placed directly under each of four additional swarms, and the locations of the last four were noted without changing their substrates. The immediate reaction of each mysid swarm to the substrate change and

the number of swarms recurring to their homesite after 2 days were noted. In addition, the location of each swarm in relation to the artificial substrate was recorded after 2 days. A shift in location was recorded if more than half of the individuals swarmed consistently over the sandy area next to the substrate; no shift meant that more than half the swarm was consistently directly over the artificial substrate. Those swarms with no artificial substrate were omitted from the shift data, as it was difficult to detect small changes in location.

Measures of mysid swarm density were made in the WBR and at 20' and 40' in the WFR. Five 10 m transects were laid roughly parallel to and about 8 m from the reef crest on the WBR, and the # of swarms within 1m on either side of the transect line were recorded. Five such transects were laid at 20' on the WFR; they ran from end to end across a coral buttress and perpendicular through

a sand channel. Four transects were laid perpendicular to a sand channel on a coral buttress at 40' in the WFR, and five additional transects were laid parallel to and along one side of a sand channel at 40'.

Measures of structural heterogeneity were also made in each of the three areas. A link chain 9.85 m long was laid flat in a straight line over the bumps and crevices of the habitat. A measuring tape was then used to find the straight distance of the chain from end to end. This was done three times ~8 m from the reef crest on the WBR and four times at each depth on the WFR. Those measurements at 40' on the WFR were made over a coral buttress.

A hand net with ~.6 mm mesh was used to capture mysids from the WBR. The samples were placed in plastic bags for transport and immediately released in an aquarium. Two groups of ~25 mysids were placed in ~~an~~ aquaria whose floors

were covered with two tiles, one covered with black and one with beige plastic. Sand was used to fill in the heterogeneous spaces left as the tiles didn't cover the entire floor. The mysids' choice of substrate was noted over several hours. For two additional groups of ~25 mysids, the tiles were placed upright to simulate a vertical structure, and the location of the swarms in relation to the tiles was recorded over several hours.

Results

When artificial substrates were first placed under the ~~my~~ sid swarms in the WBR, the swarms were disturbed only slightly retreating under a coral overhang or dispersing to within .5 m. They returned immediately ~~however~~ after the initial disturbance, with no shift in location in response to the new substrate (Table 1). After 2 days, 3 of the swarms over black substrate had shifted location slightly while 2 of those over clear glass had shifted (Table 1). There was no significant difference in ~~#~~ the frequency of shifts between swarms on the 2 types of artificial substrates. 96% of the 24 swarms studied returned to their homesite after 2 days - only one of the swarms with no artificial substrate did not return.

There is a negative relationship between depth and #swarms/20 m^2 (regression analysis, Figure 1). There was no difference ~~between~~ in ~~#swarms~~ swarm density ~~over~~ between the sand channel at 40' in the WFR and the WBR (t-test, $t = .148$, $p > .05$) (Table 2). Stratum heterogeneity also decreased with increasing depth (regression

analysis, Figure 2). The values used in the calculation were the raw distances from end to end along the substrate. To find the index of heterogeneity used in Figure 2, the total length of the chain was divided by its straight length along the substrate. ANOVAs indicated differences in both swarm density and structural complexity across the 3 habitats (Table 2).

When mysids were placed in aquaria with 2 colors of tiles, the swarms showed no preference for either substrate color. Even when the tiles were switched, the swarms remained stationary. When the swarms were placed in a tank with two tiles propped upright against each other, they moved and swarmed within 3 cm of the tiles in one of the two trials. When the tiles were moved from one side of the aquarium to the other, the swarm followed along. And when a swarm was placed in a tank with the tiles laid flat but with no sand to fill in the heterogeneous gaps between the tile edge and the aquarium wall, the mysids swarmed

the wharf pilings,

within 3 cm of the edge of the tile.

When an object (such as a hand or a notebook) lunged at the caged swarms, or even when a person walked by, the mysids reacted by polarizing and uniformly moving down toward the substrate. They returned to their original spot immediately but could be disturbed again and again. The swarms could be chased around the tank by an object from the outside, but when the object stopped moving or was removed, the swarm invariably returned to its original position.

Table 1. Responses of mysid swarms to addition of artificial substrates

substrate type	immediate reaction	location shifts*	recurrence**
black (n=8)	none	3	8
clear (n=8)	none	2	8
no substrate (n=8)	N/A (no disturbance)	unable to distinguish shifts	7

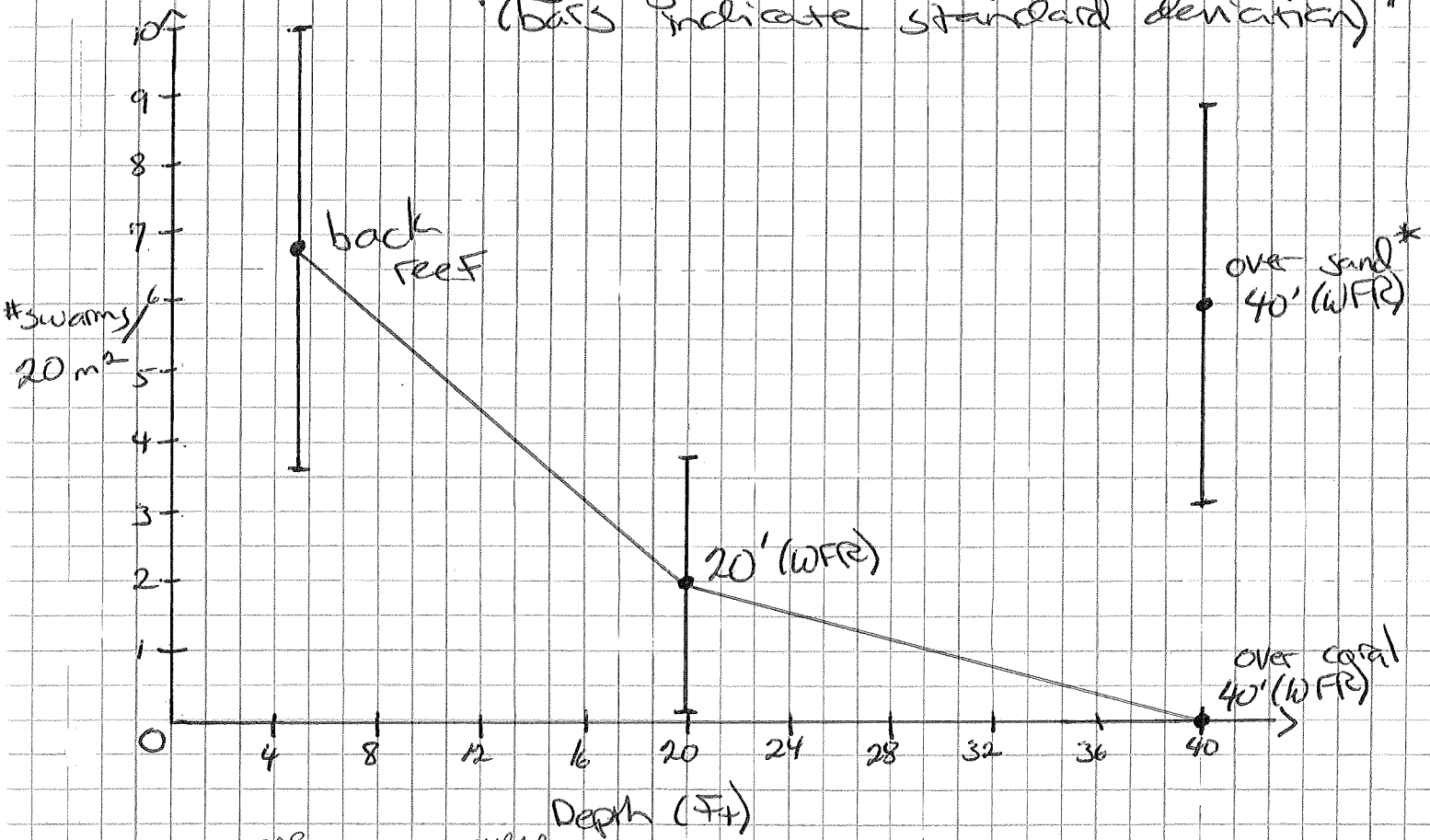
**measures swarms present after 2 days
*swarms "shifting" in location after 2 days ($x^2 = 3.5$, $p > .05$)

Table 2. Relationships of swarm density and structural homogeneity across depths

	back reef	20 ft (WFR)	40 ft (WFR) over coral	40 ft (WFR) over sand	ANOVA result
# swarms / $20m^2$	$\bar{x} = 6.8 \pm 3.2$ (5) □	$\bar{x} = 2.0 \pm 1.9$ (5)	$\bar{x} = 0 \pm 0$ (4)	$\bar{x} = 6.0 \pm 2.9$ (5) □	$p < .01$* LSD = 1.9
structural heterogeneity**	$\bar{x} = 537.7 \pm 31.1$ (3)	$\bar{x} = 675.0 \pm 71.41$ (4)	$\bar{x} = 785.5 \pm 31.1$ (4)	not performed	$p < .01$ LSD = 49.3

*result does not include data over sand channel at 40 ft.
**values given are actual end-to-end lengths of chain when stretched over substrate (in cm)
□ a t-test showed no significant difference between these 2 values ($t = .48$, $p > .05$)

Figure 1. Depth v. mysid swarms at 3 different depths (regression analysis, r = .778, p < .01) (bars indicate standard deviation)



* these data were not used in statistical analysis

Discussion

Mysid swarms do not shift location when an artificial substrate is placed over their natural sandy substrate. There are several possible explanations for this behavior. First, the mysids may not be able to detect the difference in substrates. This is extremely unlikely, as the compound eyes of these crustaceans should enable them to distinguish light from dark (Barnes 1987). Further, I noted a coordinated response of all individuals in a swarm to movement around an aquarium containing mysids in the lab, indicating that mysids have a relatively complex sense of sight. ¶ A second explanation for the mysids' failure to respond to artificial substrates lies in the fact that my criterion for a positive response was a change in location. Perhaps the homing instinct of the animals is so strong that a more disturbing change than simply a substrate substitution must occur to result in a location shift. This explanation is also unlikely, as some small location shifts occurred over two days on

both control (clear) and black substrates. It has been suggested (Hahn and Itzkowitz 1986) that mysids swarm in one location until they are severely disturbed; these artificial substrates may not have ranked as large enough disturbance to result in a move. A third explanation is concerned with the intrinsic value of camouflage in predator protection. The mysids may be able to detect the substrate change, but do not respond because their relationship to the substrate is not one of camouflage. Wittman (1977, as cited in O'Brien and Witz 1988) suggests that swarming and camouflage are at opposite ends of a predator protection spectrum. Thus swarming in itself may provide enough protection for the mysids. This explanation is also unlikely, as the combined effects of swarming and the camouflage that mysids clearly get from the sandy substrate would be expected to afford more protection than either one alone. In addition, the facts that mysids are so cryptic against a sandy floor with suspended sand particles, and that

they are most often found in these areas (Hoult and Neal 1983) suggest that the sandy substrates do offer camouflage to the mysid swarms. A final explanation for the lack of mysid response to artificial substrates is that while the color of the substrate is important to microhabitat selection, the physical structure of the microhabitat is even more important. This explanation seems most likely, and it is supported by my casual observations of mysid swarm distribution. While the majority of swarms in the back reef are found over sandy substrates next to coral outcroppings, occasionally swarms are found in depressions in coral covered with dark colored algae or over low algal covered corals. The common thread is a crevice or shelf: something the swarm can retreat under or into when approached.

Thus both substrate type and physical structure of microhabitat probably play a role in mysid site selection. Mysid swarms were attracted to a vertical structure

 (but, in only 1 trial?)

placed in an aquarium, indicating a strong preference for structural complexity. Along with the lack of response to artificial substrate, this suggests ~~tha~~ a hierarchy of criteria in site selection: structure may be more important than substrate type.

The suggestion of a commensalistic relationship between damselfish/Diadema and mysids (Emery 1968) is neither supported nor refuted by my data. Certainly the relationship as hypothesized is a useful one for the mysids, who may receive protection from the territorial damselfish or the urchin's spines, but it is extremely unlikely that presence of a damselfish or urchin is a prerequisite for site selection by mysids. Hahn and Itzkowitz (1986), in their census of swarm locations, found that 17.5% of the swarms they located occurred in areas with neither a damselfish nor a Diadema, indicating that the relationship is not obligate for the mysids. Further, it seems (from qualitative observations) that a mysid swarm would derive more protection

from crowding into a cave or crevice than from hiding near a fish or within the spines of an urchin. And in fact, the avoidance responses I observed when trapping mysids were predominantly crowding responses, either under a shelf or into a cave; no swarm sought protection directly from an associated urchin or damselfish.

There were both more mysid swarms and more structural heterogeneity at shallower depths. From this data, one can infer a positive correlation between structural complexity and mysid swarm density. Given that mysids prefer structural complexity when choosing a homesite, it seems likely that the lower heterogeneity of the deeper habitats is the main reason for this correlation. In other words, there are fewer available vertical outcroppings at deeper depths, thus there are fewer swarms at these depths. The swarms were much larger at 40 ft., indicating further that the number of available microhabitats at this depth is low. The most prominent and

complex vertical outcroppings at 40 ft tended to occur mainly next to sand channels, hence the greater mysid density along sand channels. In this case, the combination of a sandy substrate and a large coral outcropping is the probable result of selection for vertical substrate in an area where vertical substrate is scarce. In other areas at this depth, there were sandy ~~areas~~ spots where mysids would have been cryptic, but there were no large coral outcroppings.

In conclusion, it appears that mysid swarms employ a hierarchy of criteria when selecting a microhabitat. First, they look for structural complexity in the form of a shelf or cave in which to take refuge. Substrate type may or may not be considered. Further study on the predation risk of mysids on different substrates could determine if substrate actually protects the animals from predation. The nature of the proposed commensalism between mysids,

damselfish, and sea urchins should also be studied. Do mysids require a damselfish or an urchin to establish a homesite? And does the presence of either actually reduce predation?

Perhaps all 3 simply seek the same type of microhabitat.

While it is clear that mysids show a preference for certain sites, little is known about the mechanism of this selection. Perhaps light plays a role in site selection. Bainbridge and Waterman (1958) showed that mysids respond to polarized light by swimming at right angles to it: perhaps light orientation plays a role in finding a suitable homesite. In an asymmetrically lit aquarium, two separate mysid swarms (at different times) stayed in one corner of the aquarium while those in a more evenly lit tank formed separate swarms spread out over the tank, indicating a possible preference for certain light conditions. Another possibility is that mysids can detect current

flow around a structure, and that this plays a role in site selection. Both these possibilities are supported by experiments by O'Brien (1989), who showed swarm-wide behavioral responses to changes in current and light conditions.

Another missing link in the puzzle of mysid site selection is the mechanism used by the animals in returning to the homesite from day to day. Possible mechanisms for this homing behavior are several: they may orient visually, chemically, or magnetically by the points of the compass.

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