

Evidence of homing behavior in the coral reef mysid *Mysidium gracile*

Abstract—Mysid swarms at benthic coral reef sites disperse into the water column in the evening and reform at the exact same location the following morning, possibly reflecting homing behavior of individual mysids. To facilitate tracking of individual mysids, we radiolabeled part of a swarm of *Mysidium gracile* with the gamma-emitting radioisotope ^{65}Zn and released the labeled animals back to the focal swarm on a reef in Discovery Bay, Jamaica. We collected the focal swarm and surrounding swarms the next morning to determine the location of the labeled individuals following nighttime dispersal. Seventy-seven percent of the radiolabeled mysids returned to the same site the next day, and 13% of the labeled individuals were recovered from other nearby swarms. This recovery rate cannot be attributed to random reaggregation and suggests that mysids use a homing behavior to facilitate swarm reformation. This is the first unequivocal evidence of homing behavior in demersal zooplankton.

In Discovery Bay, Jamaica, the mysid *Mysidium gracile* is common in both back reef and fore reef habitats (Hahn and Itzkowitz 1986; Gilbert unpubl. data). During the day it occurs in swarms just off the bottom near structurally complex, three-dimensional substrata. Back reef swarms typically are found near the territories of dusky or threespot damselfish (*Stegastes fuscus* and *S. planifrons*, respectively), near a long-spined sea urchin (*Diadema antillarum*), or near both. Associations of *M. gracile* with damselfish and *Diadema* in this and other areas have been noted previously (Randall et al. 1964; Emery 1968; Hahn and Itzkowitz 1986).

In *M. gracile*, both swarming and the association with damselfish seem to provide effective defense against fish predation. Mysids in swarms have not been observed to be eaten by fish (Emery 1968; Hahn and Itzkowitz 1986), whereas those removed by a net and artificially displaced from their swarm have been attacked and eaten by wrasses (Hahn and Itzkowitz 1986). Swarming by itself may deter predation (Modlin 1990), perhaps in part because fish may have difficulty identifying and capturing individual mysids. Association with damselfish may further protect the mysids, since wrasses are potential predators of oviposited damselfish eggs and are aggressively evicted from damselfish territories (Ebersole 1977). Association with the spines of *Diadema* may also provide protection against fish predation.

In the evening, swarms of *M. gracile* break up, and individuals swim up from daytime swarm sites and disperse into the water column (M. Houlton and G. Neal unpubl. data; Chiavelli et al. unpubl. data). In 1988 in Discovery Bay, swarms in the back reef dispersed between 1800 and 1840 h, and those in the fore reef did so between 1810 and 1820 h. Observations of numerous swarm sites after dark have demonstrated the absence of all mysids from daytime swarm sites. In the early morning, swarms reform over the substrata.

In 1988 in Discovery Bay, arrival times of swarms in the back reef were between 0605 and 0625 h.

The ecological significance of the migrations of *M. gracile* from benthic substrata during the day to the water column at night probably is the same as that proposed for demersal zooplankton in general (Porter and Porter 1977). Because of their large size (1.5–6 mm) and hence potential susceptibility to visually feeding, zooplanktivorous fish, mysids may decrease predation risk by forming swarms at the bottom by day and feeding in the water column only at night. Some evidence for nocturnal feeding in *M. gracile* is the fact that gut volume of mysids in swarms is greatest early in the morning just after the mysids return from the plankton (M. Butler unpubl. data).

Swarms of *M. gracile* in Discovery Bay reappear at particular benthic sites over several successive days. This was first noted by Hahn and Itzkowitz (1986) on artificial substrata in the back reef and has been observed on natural sites in the back reef and fore reef (Houlton and Neal unpubl. data). The repeated occurrence of mysid swarms at certain sites could have two explanations. Individual mysids may be able to recognize and return to the same sites from which they dispersed the evening before. In other words, they may exhibit homing behavior. Alternatively, the mysids simply may return to any one of many, preferred benthic sites with appropriate characteristics. Two lines of indirect evidence suggest that the mysids do home (Chiavelli et al. unpubl. data). First, on successive days, swarms at given sites consisted of similar individuals with respect to body length, reproductive maturity, and pigmentation. Second, when swarms were experimentally removed from given sites, no mysids reappeared at those sites the following day. At one site, no mysids returned for five successive days.

In some experimental displacement studies with *M. gracile*, Hahn and Itzkowitz (1986) showed that small groups of mysids herded 2 to 6 m away from their swarms during the day usually would swim directly back to the swarm from which they were removed. Although these results certainly show that mysids have some ability to home, there is as yet no direct evidence showing that mysids that naturally disperse from their swarm site in the evening return to the same swarm site the next day. The distance that mysids disperse during the night is not known, but it is likely to be much greater than several meters.

In our study, we directly tested the hypothesis that *M. gracile* returns from the plankton in the morning to the same swarm site from which it dispersed the previous evening. We removed some individuals from a swarm in the morning, labeled them with radioactive zinc, returned them to their swarm in the afternoon, verified that the swarm dispersed at night, and then determined the radioactivity of mysids collected from the focal swarm site, as well as nearby swarm sites, the following morning. The use of trace elements to label planktonic invertebrates for dispersal studies has been

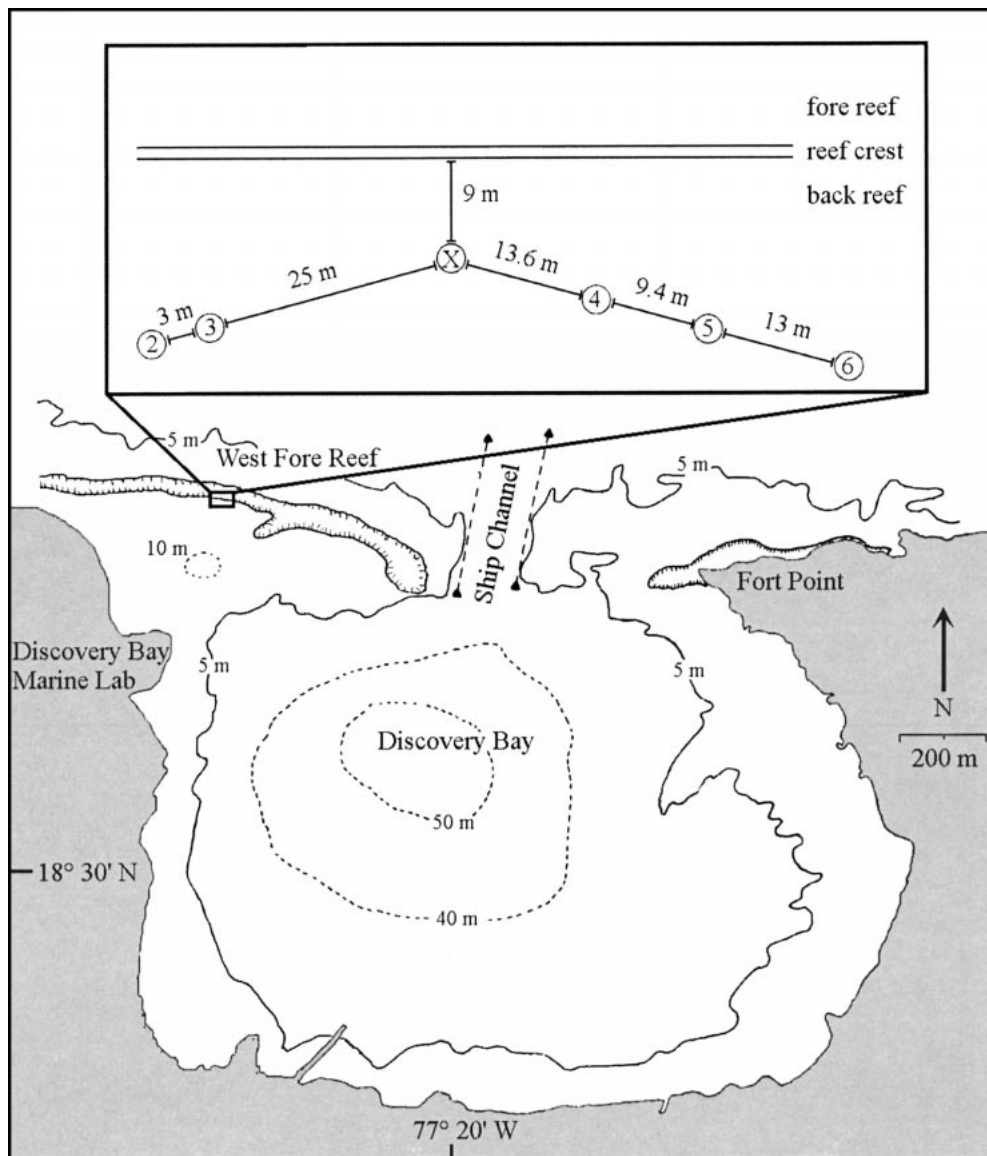


Fig. 1. Map of Discovery Bay, Jamaica ($18^{\circ}30'N$, $77^{\circ}20'W$), with inset showing locations of swarm sites. About one-half of the mysids (*Mysidium gracile*) from the focal swarm site (X) were labeled and returned to that site on 5 March 2000, and most of the mysids at this site and five nearby swarm sites (2–6) were collected for analysis on 6 March 2000.

tested in the laboratory (Levin et al. 1993; Anastasia et al. 1998), but this is the first time, to our knowledge, that the technique has been applied to a field study.

The swarms of *M. gracile* we studied were located in the shallow back reef of Discovery Bay very close to the reef crest west of the ship channel (Fig. 1). In this general area during February and March, the mean number of mysid swarms per 100 m² was estimated to be 20 in 1988 and 34 in 1990 (Hoult and Neal unpubl. data; J. Jenkins unpubl. data), and the number of mysids per swarm varied from 106 to 823 in five swarms in 1999 (Chiavelli et al. unpubl. data).

At 0745 h on 5 March 2000, a focal swarm of about 275 mysids was identified (Fig. 1), and its position over the substratum was marked with a weight and buoy. The swarm was just off the bottom at a depth of approximately 1 m and

was next to two dusky damselfish. At 0800 h, approximately one half of the individuals were captured with an aquarium net, gently placed into a 1.8-liter, wide-mouth, plastic jar filled with seawater, and transported to the Discovery Bay Marine Laboratory. At the same time, mysids were collected separately from a nearby swarm for the measurement of background radioactivity and transferred to a second jar.

In the laboratory, 43 control mysids from a site distant from the focal swarm were sieved with a 350- μ m mesh sieve, rinsed into two 15-ml counting tubes, and preserved with Lugol's solution. The mysids from the focal swarm site were gently transferred into a beaker with 1.5 liters of unfiltered seawater containing 37 kBq L⁻¹ (3.9×10^{-10} M) ⁶⁵Zn ($t_{1/2} = 244$ d). The ⁶⁵Zn added to the seawater was from a solution in 0.5 N Optima HCl, and the pH was buffered by

the addition of an equal volume (700 μ l) of 0.5 N NaOH. This Zn addition is within the range of oceanic Zn concentrations (Donat and Bruland 1995) and is far below concentrations at which Zn becomes toxic to crustacean zooplankton (Sunda et al. 1987). The mysids were added to the radioactive seawater within 30 min of their collection from the swarm and were exposed for 7 h. During this period, the mysids would be expected to accumulate ^{65}Zn from the dissolved phase and from ingested particles in the unfiltered seawater that might have accumulated some of the radioisotope during the exposure period (Wang and Fisher 1998); no attempt was made to differentiate the relative importance of the two uptake pathways for the mysids in this experiment.

At the end of the exposure period, all mysids were actively swimming. They were gently collected with a 350- μ m mesh sieve and resuspended in 1 liter of unfiltered and unlabeled seawater. Twenty-eight of the radiolabeled mysids were transferred to a 2-liter bowl through which seawater flowed and were kept overnight in the laboratory to estimate the desorption of ^{65}Zn label from the mysids to be released back to the reef. The remaining 115 mysids were transported back to the focal swarm from which they had been removed and released into this swarm at 1600 h. Upon returning to the laboratory, six labeled mysids were removed from the flow-through bowl, rinsed into a counting tube, and preserved with Lugol's solution. These mysids were used to indicate the initial amount of the ^{65}Zn on mysids released to the reef. At 2215 h that evening, the focal swarm site was examined. No mysids were detected, showing that the swarm had completely dispersed.

At 0800 h the next day (6 March), the focal swarm site was reexamined, and a swarm was observed in exactly the same place it had been the day before. As many mysids as possible were collected from the swarm with an aquarium net, placed in a 1.8-liter jar, and transported to the laboratory. There, the mysids were collected on a 350- μ m mesh sieve, transferred with tweezers to eight separate counting tubes, and preserved with Lugol's solution before determination of ^{65}Zn activity. Sufficient numbers of mysids (at least 16) were pooled into each counting tube to assure statistically significant radioactive counts. At the same time, the labeled mysids that had been kept overnight in running seawater in the laboratory were similarly placed in a counting tube and preserved.

After the mysids at the focal swarm site were collected, five nearby swarms of mysids were located and mapped (Fig. 1). Mysids from each swarm were collected with an aquarium net, placed in separate 1.8-liter jars, transported to the laboratory, and placed in counting tubes.

The radioactivity of the samples was measured with an LKB Compugamma gamma counter equipped with a large well NaI (TI) detector. The gamma emissions of the samples were counted at 1,115 keV for 10 min to ensure sufficient counts and propagated counting errors <3%. All counts were related to a ^{65}Zn standard. Radioactivity measurements are expressed as disintegrations min^{-1} (dpm). After measuring the ^{65}Zn in the samples, the preserved mysids were removed from the counting tubes and enumerated in glass petri dishes. The lengths of the focal swarm mysids were measured from the eyes to the base of the uropod endopodites

Table 1. Radioactivity and counts of mysids (*Mysidium gracile*) from the focal swarm and five surrounding swarms collected on 6 March 2000. The number of labeled mysids in each swarm was estimated from the total radioactivity by assuming 883 dpm labeled mysid $^{-1}$.

Sample	DPM	Total mysids	Number of labeled mysids
Focal swarm	77,667	274	88
Swarm 2	33	102	0
Swarm 3	856	105	1
Swarm 4	7,044	150	8
Swarm 5	756	180	1
Swarm 6	3,933	250	4

to the nearest 0.5 mm with a dissecting microscope equipped with an ocular micrometer.

The radioactivity and mysid counts of the samples are given in Table 1. The mysids collected before the experiment showed no radioactivity, as expected. The radiolabeled mysids that remained in the laboratory flow-through tank for 18 h showed a 29% decline in ^{65}Zn radioactivity from 1,243 to 883 dpm mysid $^{-1}$; these mysids had a mean length ± 1 SD of 4.52 ± 0.57 mm. The 274 mysids collected from the focal swarm site had a mean length ± 1 SD of 4.47 ± 0.76 mm. Each of the eight focal swarm tubes contained enough ^{65}Zn to give a strong, unequivocal radioactive signal, with the entire focal swarm containing 77,667 dpm.

To estimate the number of radiolabeled mysids that returned to the focal swarm site on 6 March, we assumed that the radioactivity of the mysids held overnight in the laboratory was comparable to that of the released mysids. From the laboratory mysids, we calculated a radioactive label of 883 dpm mysid $^{-1}$. By dividing the total radioactivity collected at the focal swarm on 6 March by this value, we obtained an estimate of 88 radiolabeled mysids in the focal swarm, or 77% of the 115 radiolabeled mysids originally released.

The radioactivities measured in the five nearby swarms also were converted to numbers of radiolabeled mysids with the 883 dpm mysid $^{-1}$ conversion factor. Radioactivity equivalent to 14 radiolabeled mysids was found in the five surrounding swarms sampled on 6 March; one radiolabeled mysid was found in swarm 3, eight in swarm 4, one in swarm 5, and four or five in swarm 6 (Table 1). The distribution of radiolabeled mysids between the six swarms is shown in Fig. 2. In all, approximately 90% of the labeled mysids released were recovered the next day.

Our study clearly demonstrates that most of the mysids in the swarm on 6 March returned to the same swarm site from which they dispersed on the evening of 5 March. The 77% return, although high, may actually be an underestimate. Our calculations are based on the assumption that the radiolabeled mysids that were held in the laboratory overnight were an accurate proxy for the radiolabeled mysids released back to the focal swarm site. The control mysids were allowed to swim in a flow-through tank to mimic natural conditions, and the measured desorption (29%) is close to the level of ^{65}Zn desorption measured by Wang and Fisher (1998) with

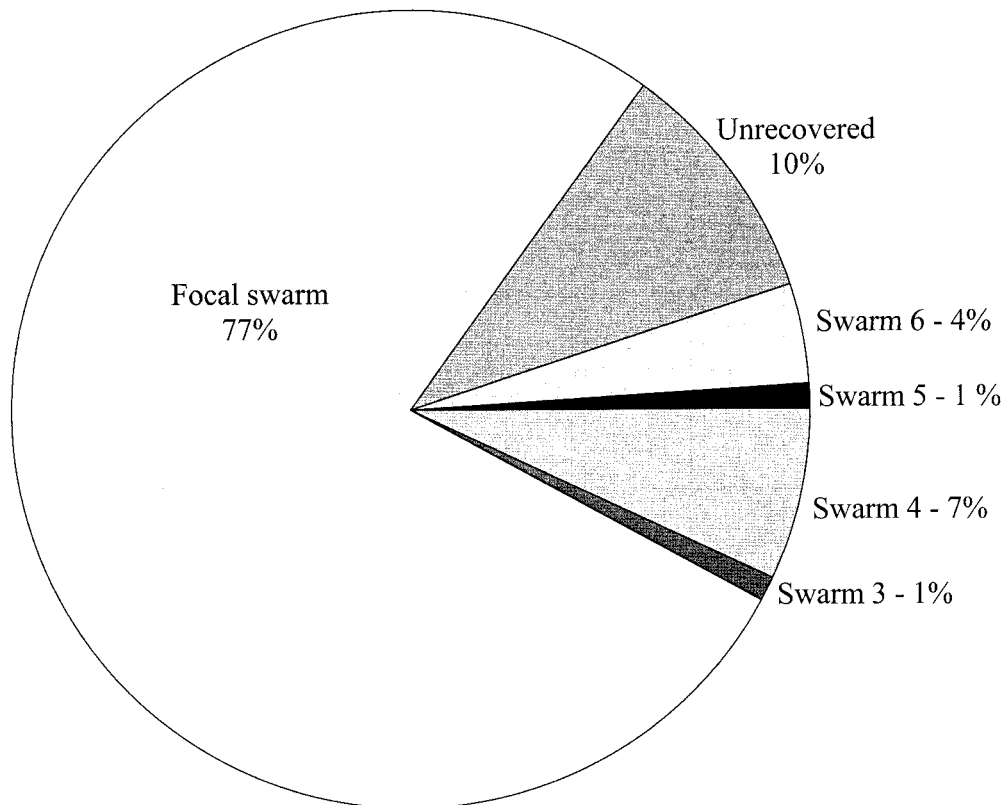


Fig. 2. Location of the radiolabeled mysids collected on 6 March 2000 following nighttime dispersal into the water column. A negligible amount of radioactivity was collected in swarm 2.

marine copepods. However, it is possible that more ^{65}Zn desorbed from the released mysids, since these mysids were exposed to more turbulent flow conditions and probably were more active than the contained individuals. If more of the ^{65}Zn was lost from the released mysids than we estimated, our calculation of the percent of labeled mysids recovered would be an underestimate. Additionally, we were unable to collect every single mysid in the focal swarm on 6 March, and some of the mysids that managed to escape capture may have been labeled. This would also lead to an underestimate of the return rate.

The return rate we observed is too high to be consistent with the idea that mysids that have dispersed into the water column at night simply descend to the substratum in the morning and move to the nearest suitable swarm site. For example, if there were, on average, 200 mysids per swarm and 10 swarms per 100 m^2 —both low estimates according to previous observations (*see above*), there would be about 2,000 mysids per 100 m^2 area. If the mysids over a given 100 m^2 area remained and actively or passively dispersed within this area at night, a random return to the benthic sites in the morning should lead to only about 20 or 10% of the individuals returning to the same site they occupied the previous day. The number returning to the same site in this scenario would change as dispersal distance increased or decreased. Unfortunately, the distances mysids move from their daytime sites at night are still unknown. A chi-square good-

ness-of-fit test confirmed that the distribution of returning labeled mysids was highly nonrandom ($P < 0.0001$).

Although the mysids in our study showed a high degree of homing after nocturnal dispersal, it was clear that some mysids in the focal swarm did not home precisely. About 13% of the labeled mysids were recovered at four nearby sites (Table 1, Fig. 2) and so returned only close to the site where they were the previous day. The remaining 10% of the labeled mysids may have returned to sites even farther away, been consumed by predators, or simply been among those mysids that escaped capture on the morning of 6 March. Alternatively, we may have unknowingly recovered all of the labeled mysids if more ^{65}Zn desorbed from the released mysids, as discussed above. Our finding of extensive but not complete homing is consistent with the removal experiments conducted in this area the previous year and described by Chiavelli et al. (unpubl. data). When mysid swarms were completely removed from sites, no mysids returned to those sites the next day. Some mysids did return to the sites in subsequent days. The results of our study suggest that these mysids probably came from nearby sites.

To our knowledge, only one other study has marked and measured the return of mysids to specific swarm sites on successive days. Wittmann (1976) considered the diel pattern of swarm movements and disintegration in *Leptomysis* in the Adriatic Sea. He reported that surviving mysids labeled by paint showed a daily return of 0 to 93%, but he neglected

to indicate whether mysids were returned to their original swarms and whether they were allowed time to acclimatize before nocturnal swarm shifts. During a 16-d observational period, swarms generally returned to the same sites on successive days; however, it is not clear whether these swarms completely dispersed and reformed or showed only diel shifts in their positions. Marked specimens were often found in surrounding swarms, leading Wittmann to conclude that swarm reformation is governed more by precise habitat preferences than by homing of individual mysids. The lack of detail provided by Wittmann makes it difficult to compare our results to his, but the return rate we measured does fall within his reported range.

The ecological significance of homing in *M. gracile* is not known. Perhaps it facilitates a very rapid reformation of swarms at suitable sites early in the morning. Without homing, individual mysids might have to spend considerable time aggregating into swarms of sufficient size to provide defense against fish while also locating sites where there are either damselfish or sea urchins for additional defense against these predators. During this time, the mysids might be very vulnerable. The mechanism by which *M. gracile* homes also is not known. Perhaps it recognizes home sites using visual cues. Alternatively, like larger benthic crustaceans (Lohmann et al. 1995), it may use a magnetic compass sense to home. Although many invertebrate taxa show diel shifts in distribution from benthic substrata to the water column (Ohlhorst 1982), we know of no demersal zooplankton other than *M. gracile* that has been shown to exhibit homing behavior to particular sites. This trait may require very advanced sensory mechanisms, and it may be selected for only when it leads to a pronounced reduction in predation risk.

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