The Ecology and Life History of the commensal shrimp *Gnathophylloides mineri* (Schmitt) and its urchin host, *Tripneustes ventricosus* (George + George).

Mark and Bruce —
An excellent study! You've really advanced knowledge on this system. A well integrated attack and some clear-cut, exciting results.

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ABSTRACT: The relationship of the commensal shrimp Gnathophylloides mineri (Schmitt) with its urchin host Tripneustes ventricosus (George + George) was studied at Discovery Bay, Jamaica from February 12 - March 2, 1980. The behavior of the shrimp and interactions with its host were studied through observation and experimentation. Evidence was found for: the ability of the shrimp to change coloration in order to increase crypticity, the use of chemical cues in locating hosts, intraspecific agonistic behavior between shrimp, and migration of shrimp from one host to another in natural and laboratory conditions.

INTRODUCTION: Commensalism of the shrimp Gnathophylloides mineri (Schmitt 1933) with certain echinoderms, notably the urchin Tripneustes has been documented in Barbados (Lewis 1956, 1958), in Puerto Rico and the Virgin Islands (Schmitt 1933), and in Hawaii (Castro 1971), although the ecology of these commensal shrimp has received little attention. One study (Steve Hufford - Dartmouth Foreign Study Program 1979) looked at the substrate and host preferences, and found that the shrimp preferred the dark-colored Tripneustes* as a host over other urchins, such as Diadema, Lytechinus, or white-colored Tripneustes. However, a number of

*Hufford cites T. esculentus (Leske) as the host species, although T. ventricosus (George + George 1979) is more likely to have been the shrimp's host in his study here at Discovery Bay.

interesting questions have surfaced in light of this preliminary study.

What cues (chemical, visual) are the shrimp using to locate their preferred host? What are the natural densities of the shrimp on their host, and how is overcrowding dealt with by the shrimp, i.e. are they territorial or intraspecifically agonistic? Are there preferred attachment sites on the host? Do these preferred sites change over the course of the day? How do the shrimp feed - are they demersal or do they remain on the host at all times? Finally, what benefits do the shrimp gain from their host, and how does the urchin react to the presence of shrimp?

Our study has attempted to provide insight into these questions through experimentation and observation of the shrimp and their hosts both in their natural habitat and in the laboratory.

Study Organism: Gnathophylloides mineri is a small shrimp 6-7 mm body length, with large claws up to 5 mm in length. The shrimp is white except for a dark lateral stripe on each side which is the same color as the podia of its host - as a result, this white and black shrimp is virtually indistinguishable as it clings to the longer spines of Tripneustes ventricosus, claws held outward in defense. The commensal shrimp gains the advantages of a well-protected resting spot, as well as a possible food source.

METHODS + OBSERVATIONS:

I. Urchin Census: In order to determine the natural densities of shrimp, as well as to acquire a pool of experimental organisms, a census and collection of shrimp from 100 T. ventricosus was made. Urchins were collected from the East Back Reef Thalassia beds from Feb. 23 to Feb 29. Each urchin collected was searched for shrimp by both researchers for about 10-15 minutes each. The number, sex, and position of each shrimp was noted, and the shrimp were collected and brought back to the lab for use in experiments. The urchin was then measured and marked by denuding a small patch of spines on the aboral end to prevent overlap of hosts censused, after which the urchin was replaced. A few things should be noted about the censusing procedure: 1) Sex of the shrimp is fairly easily determined macroscopically using the lateral stripe and claw comparisons outlined by Lewis (1956). 2) The position on the urchin was designated either as oral surface, aboral surface, or middle, the latter being a 4 cm wide band encircling the widest part of the urchin. The aboral surface consists of everything above the middle band, and the oral surface is everything below. Position was further pinpointed as ambulacral or interambulacral zones, the interface between these zones or the edge of the mouth (oral edge) 3) The vast majority of our censusing was done from a boat anchored over the Thalassia beds. As a result, transport of urchins and the possibility of damaging or losing shrimp was kept to a minimum. Also, both researchers looked at each urchin, again improving the efficiency of finding these cryptic shrimp. 4) Finally, when the experimentation was complete, the body length (not including claws) of 25♂ and 25♀ shrimp were recorded to check for size dimorphism between sexes.

One hundred urchins of the normal, dark variety were sampled. These urchins have darkly pigmented tube feet and pedicellaria, and white spines, producing a "salt and pepper" pattern. A somewhat rare color morph of the same species lacks the darkly pigmented tube feet and pedicellaria, and appears entirely white. These pigmentless "albino" Tripneustes provided insight into the cryptic ability of the shrimp. Seven of these albino urchins were found, sized + censused.

Results of Census:

TOTAL URCHINS SAMPLED: 100 regular, 7 albino

MEAN URCHIN SIZE: 10.4 cm S.D. = .99 (N = 95)

TOTAL # SHRIMP FOUND: 113

MEAN # SHRIMP/URCHIN = 1.1, S.D. = 1.35

SEX RATIO (N=92) = 40 ♂, 51 ♀, 4 immature

POSITION:

ORAL END: 82%

ABORAL END: 9% N = 113 shrimp

MIDDLE: 5%

UNKNOWN: 4%

DISTRIBUTION:

| No. of shrimp | No. of regular urchins | No. of albino urchins |
|---|---|---|
| 0 | 38 | 3 |
| 1 | 39 | 1 |
| 2 | 13 | 2 |
| 3 | 7 | 1 |
| 4 | 1 | 0 |
| >4 | 2 / N=100 | 0 / N = 7 |

SHRIMP SIZES:

| | ♂ | ♀ | N |
|---|---|---|---|
| MEAN BODY LENGTH (mm): | 5.8 mm | 6.9 mm | 25 |
| S.D.: | .48 | .51 | 25 |

DISCUSSION of CENSUS RESULTS:

1) The density of shrimp on urchins does not follow a normal distribution, but rather is skewed toward none or one shrimp per urchin. The maximum number of shrimp found on a single urchin was 10, a rare example. The sex ratio of the shrimp censused was 5:9, with ♀'s more abundant.

2) Shrimp dramatically preferred the oral surface of the urchin to other localities (82%). A strong preference was also noted for an attachment site along the interface between the ambulacral and interambulacral region (i.e., these sectors with and without tube feet). It should be noted that this is where the longest spines on the urchin occur, and would presumably offer the shrimp the optimum clinging sites since these spines are most comparable to shrimp body sizes and would offer the best protection. Shrimp avoided the ambulacral regions with tube feet (only 3 shrimp found there); perhaps the tube feet interfered with the shrimps' clinging or feeding.

3) Body length measurements indicate a very highly significant ($P < .001$) dimorphism between sexes, the females being longer than males.

4) A final note concerning the albino urchins censused.

On seven albino urchins sampled, 7 totally white shrimp were found. These shrimp lacked the normally dark brown lateral stripe and were entirely white on the sides. This discovery implied either the existence of "albino" white shrimp which selectively choose a similarly colored urchin host (no white shrimp were found on black urchins), or else the ability of the shrimp to change their color to adapt to their host's coloration in order to become more cryptic. This discovery led to the following experiment.

II COLOR CHANGE EXPERIMENT: To test the ability of the shrimp to change color, three regular (striped) shrimp were placed on an albino urchin, and three white shrimp were placed on a regular (dark) urchin and left for 4 1/2 days. The urchins, of course, were isolated in separate holding tanks. The experiment was later repeated with five shrimp on each urchin.

Results: The results of this experiment indicate that at least some shrimp have the ability to change their color from white to dark and vice versa, depending upon their substrate color. For the first trial (3 shrimp/urchin) two of the shrimp on each urchin had changed color to match their host within 2 days, while the third shrimp on each urchin showed only slight color change after 4 days. For the second trial (with 5 shrimp/urchin), only one of the dark shrimp on the light urchin changed completely, while the other four dark shrimp lightened noticeably, but retained some semblance of a darkened lateral stripe. On the dark urchin, three white shrimp darkened to match their host, while two shrimp remained entirely white.

Discussion: Apparently some shrimp have the ability to lighten and darken their pigmentation while others do not, or for some reason, do not in the laboratory. If the shrimp could not change color, one might expect a specific host preference depending on the color of the shrimp, i.e. white shrimp should choose white hosts and dark shrimp should choose dark. A later experiment conducted along this vein demonstrated that such host-specific selection between dark and albino urchins was not occurring. This might lend support to the possibility of capture and lab conditions creating an unfavorable environment for color change. It might be possible that it is energetically expensive for the shrimp to change color, and they might not do so under possibly stressful lab conditions.

III Host-location tests: In order to gain insight into the mechanism of host location, a simple T-maze was constructed which offered the shrimp a choice between two directions with only chemical cues to use. This was accomplished by creating two holding tanks in which urchins could be placed, and having the water flow from these tanks converge on the shrimp from two directions. Since the shrimp could not see into either of the holding tanks, its decision on which direction to choose must be made without visual cues. Currents flowing from each of the holding tanks carried chemical cues from the organisms placed in them to the shrimp.

In theory, therefore, this T-maze eliminates the visual cues which might be responsible for host selection, and presents the shrimp with a choice between two different chemical "tastes".

Three different experiments were run: i) between Tripneustes and seawater, ii) between Tripneustes and Diadema, and iii) between seawater and a group of 12 shrimp to test for intraspecific aggregation. After each group of 10 test shrimp the positions of the organisms in the holding tanks were reversed to nullify possible differences in lighting or flow rates.

Results:

i) Tripneustes vs. seawater:

| | ♂ | ♀ | TOTAL |
|---|---|---|---|
| URCHIN | 20 | 10 | 30 |
| SEAWATER | 3 | 2 | 5 |
| NO CHOICE | 2 | 3 | 5 |
| TOTAL | 25 | 15 | N= 40 |

ii) Tripneustes vs. Diadema:

| | ♂ | ♀ | TOTAL |
|---|---|---|---|
| Tripneustes | 4 | 7 | 11 |
| Diadema | 3 | 4 | 7 |
| No choice | 0 | 2 | 2 |
| TOTAL | 7 | 13 | N= 20 |

iii) Shrimp aggregation vs. Seawater.

| | ♂ | ♀ | TOTAL |
|---|---|---|---|
| Shrimp: | 6 | 2 | 8 |
| Seawater | 4 | 7 | 11 |
| No Choice | 1 | 0 | 1 |
| TOTAL | 11 | 9 | N= 20 |

<u>Discussion</u>: The urchin vs. seawater test indicates that shrimp are able to use chemical cues to some extent to locate a host urchin. It is interesting, however, that although shrimp chose the urchin-side of the T-maze 75% of the time, only rarely did they actually find their way to the urchin in the holding tank, which required swimming up in the water column to a 2 cm dia. opening. This suggests that chemical cues alone are possibly not sufficient for shrimp to locate hosts by, but perhaps require visual cues as well. It is possible, for instance, that chemical cues are used to bring the shrimp within visual range of the host, after which visual cues are used to make contact. It is also possible that oversaturation of the water near the urchin prevented location by swamping shrimp's receptors. A reluctance to swim up in the water column may have contributed to the shrimp's inability to get to the host.

It is also interesting that shrimp chose Diadema nearly as often as Tripneustes. It is possible that the shrimp may not be chemo-locating for Tripneustes-specific chemicals, but respond to some sort of generalized urchin pheromone, although it is also likely that the shrimp may have been stressed by testing them previously in the seawater vs. Tripneustes trial, and perhaps did not perform optimally.

Finally, no preference for the water containing the 12 shrimp over seawater was observed. This suggests that under these conditions in the lab, the shrimp did not tend to aggregate as a result of species-specific pheromones. Some mechanism for aggregation of the shrimp for reproductive purposes must be functioning in nature, although this was not demonstrated in this test. The sexual behavior of these shrimp remains a prospect for future study.

IV <u>RECRUITMENT & MIGRATION</u>: In order to test the rate of recruitment of shrimp by urchins, we removed all shrimp from two white and two dark urchins and placed them in the EBR Thalassia beds in an enclosure made of wire mesh. The enclosure was checked each day and the urchins carefully inspected.

After 3 days one pigmented shrimp was found on a white urchin. A day later two more dark shrimp were found on one of the dark urchins. What does this mean? Either shrimp are migrating from other urchins, or there is an abundance of pelagic shrimp in need of a host. The latter is doubtful, since availability of hosts does not seem to be limiting (38% of urchins sampled had no shrimp). It is possible that the shrimp leave the urchin at night like many benthic invertebrates in order to feed. In this way new hosts might be taken.

In order to test for any dimersal behavior, we equipped two urchins with 3 shrimp each and placed them in an enclosure during the day. We later went and retrieved the urchins that night at 10 PM and inspected them for shrimp. We found that all six shrimp were inhabiting the same urchin at 10PM.

This experiment lends partial support to the idea that some shrimp leave their host at night (before 10 PM) and inhabit new hosts. However, the reasons why the shrimp leave their host are still unknown; perhaps seeking of mates or simply moving to a "superior" urchin. The dimersal behavior of these shrimp is not nearly understood and warrants further study.

V SHRIMP OBSERVATIONS: The content of this section comes from observations we made during the course of our experiments and some periods of formal observation.

A topic of interest to us was the urchin's reaction to the shrimp. It is apparent that the urchin is accustomed to the presence of the shrimp. The most prominent urchin defense against such an organism would be the pedicellaria, which do not bother the shrimp to any noticeable degree.

Similarly, the podia do not directly bother the shrimp, but the random brushing of the podia against the shrimp during the podia's usual movement does disturb the shrimp to the extent that the shrimp will not stay long in the ambulacral regions. The podia do not exhibit direct aggression.

The spines, on the other hand, will give the shrimp limited trouble. The spine reacts to the shrimp in one of two ways; either it does not react at all, or it senses and treats it as a piece of foreign matter. In the latter case, the urchin's spine swings in a circular motion in an effort to rub the shrimp off. In the face of this pressure, the shrimp may shift position, and eventually the spine habituates and ceases to react aggressively toward the shrimp.

A second topic of interest was the activity of the shrimp. One big question was feeding activity. Through observation, it is apparent that shrimp feed off material on the spines. However, the mandibles of the shrimp observed were moving so fast that it was difficult to see exactly what occurs during feeding. It is clear that either the last leg set before the mandibles, or a specialized set of mandible arms has small pinchers which the shrimp scraps over the surface of the spine from underneath the body up the spine and into the mouth.

Movement of the shrimp over the surface of the urchin is governed by feeding. The shrimp moves from spine to spine, pausing to feed. It was also observed that the shrimp would move toward the anus when the urchin was defecating, suggesting that the shrimp may also feed off fecal material but actual feeding was not observed.

Shrimp that are not feeding remain sedentary, sitting quietly on a spine. While resting like this they maintain territories which they will defend against intruders. If another shrimp (usually a feeding shrimp that is moving) comes too close, the resident shrimp will pinch at him to drive him off. Often pinching is not even required. Moving shrimp instinctively know they are intruding and without any signs of aggression from the resident they will put out a burst of speed to remove themselves from the territory and any possible retribution. When placed together in artificial containers, shrimp commonly fight and attempt to space themselves.

Finally, through the course of our experiments enough information was gathered to detect several stages in the life history of the shrimp. Females examined under disecting scope were found to carry 2 to 4 eggs. Apparently, a large investment in a small clutch is the rule, rather than the production of thousands of smaller eggs. The eggs probably develop on the urchin. This stage is inferred from the presence of larva on some of the urchins we checked. No direct evidence is available. The adults probably spend their entire lives on the urchin and go through molts. We found the shed skins from molts the shrimp went through. Like other crustaceans, the shrimp probably have several molts in their lifetime. Thus, the entire life history of the shrimp is probably dependent on the urchins.

VI Density/Migration: The effects of increasing density of shrimp on an urchin was examined by placing a small urchin (6 cm diameter) in a glass bowl and then adding shrimp by tens every half hour until 50 shrimp had been added. The effects of each addition were recorded. After all 50 were on, another small urchin (7 cm diameter) was added to the bowl. The second urchin was devoid of shrimp. After five hours, the second urchin was checked to see if any migration occurred between it and the "loaded" urchin. Similar experiments were preformed for 40, 30, 20, 10 and 5 shrimps.

Results: The first 10 shrimps added for the density experiment distributed without much trouble on the urchin. Most went to the oral surface and middle zone of the urchin. After 20 shrimp had been added, effects of crowding appeared. Half of the shrimps tried to locate on the oral surface. There was considerable fighting and bumping of shrimp in competition for space there. The other half was mostly located in the middle zone. Many shrimp found relatively secure locations and set territories which they defended vigorously.

After 30 shrimp had been added, fighting broke out in the middle zone as well. Even more intense fighting broke out on the oral surface as some of the most recent additions tried to settle there.

With 40 shrimp on the urchin the anal surface began to get colonized fully. Shrimp were still trying to get on the oral surface, adding to the density and confusion there. The overflow went up the sides.

After all 50 shrimp had been added, fighting occurred in all regions, particularly the heavily contended oral and middle zones. The anal zone was still moderately serene. No shrimp were excluded from the urchin. There were occasional attempts to settle in ambulacral regions, but shrimp would rarely stay more than 3 to 5 seconds before moving.

Results for the migration experiments are as follows.

| Number of shrimp on loaded urchin | Number that transferred |
| --- | --- |
| 50 | 9 |

| | |
|---|---|
| 40 | 5 |
| 30 | 1 |
| 20 | 0 |
| 10 | 0 |
| 5 | 0 |

Discussion: There were several interesting things that occurred as density increased. Shrimp that had territories would leave them at much less provocation than what would normally be required to make a shrimp relinquish a territory. This fact may add to the general observation that there is a lot greater movement of individual shrimp under crowded conditions than when conditions were normal.

Somewhat curiously, the behavior of the urchin did not change at any point during the experiment. With so many shrimp one might expect some kind of response, perhaps a cleaning response. The interaction between urchin and shrimp must be fairly tight to not elicit any change in behavior on the part of the urchin.

It is also curious that at the same time so much fighting is occurring on the oral surface, and the middle zone, the anal zone is still relatively free for colonization. This fact underscores the preference of the shrimp for the lower half of the urchin. The significance of this preference is not clear, but it could be to facilitate feeding or for protection. This experiment also confirms some other previously noted trends. Still no shrimp would colonize the ambulacral regions and there was a noticable preference for the stiff spines between the ambulacral and interambulacral regions.

The fact that no shrimp were excluded from the urchin even at such high densities suggests that there is a strong urge to stay on the urchin despite frequent conflicts that must be energetically demanding and stressful. The results of the migration experiments also suggests that this urge to remain with the original host is present though at ~~higher~~ the highest densities migration will occur.

VII Diel Movement: To study diel movement, we set up 3 urchins with one shrimp apiece in the same tank, allowing one and a half hours for the shrimp to acclimate and find their desired positions. We then began recording the position of each shrimp every hour from 12pm to 12am. Thus, a diel activity pattern could be tested with 6 hours each of day and night. The experiment was performed in this time slot to coincide with any internal clocks that might be present rather than simulating a dark period in the middle of the day. To insure dark conditions in the lab between 6pm and 12am, black garbage bags were placed over the experimental apparatus.

Results: Movement of the shrimp on the urchin is more common than ~~on~~ one would expect. At the end of each hour, the shrimp was usually in a new position. On only 5 occasions out of 36 recordings did the shrimp appear to be in the same position as an hour before. The movement was random in nature. No pattern emerged whereby the shrimp would all move to one locale on the urchin at a particular time. However, there was, as noted before, a preference for the bottom half of the urchin.

Discussion: The discovery that the shrimp move around a lot came as a surprise. It was assumed that with the territoriality displayed by the shrimp, the shrimp would move very little and instead defend a "home" territory. This experiment was performed because of the possibility of a general movement to one surface or the other as day/night conditions changed. This movement might be rooted in feeding activity and it was hoped that if any movement did occur it would give us a clue to the nature of that feeding activity. At the time this experiment was run, no information had been obtained on feeding behavior. No general movement pattern emerged, but the reason for the random movement was discovered later when observations of feeding behavior were made.

It turned out that movement was dictated primarily by feeding, but not ~~in~~ an organized manner manifested in a set diel movement pattern. The process of feeding involves the movement of the shrimp from spine to spine in search for food. This carries the shrimp to new positions on the urchin every hour. Only resting (non-feeding) shrimp stay in the same spot and maintain territories.

VIII <u>Albino shrimp / host preference test</u> : The objective of this experiment was to determine if the "albino" shrimp we found would have a preference for albino <u>Tripneustes</u> over regular <u>Tripneustes</u>. The impetus for this experiment came from a students' discovery last year that regularly pigmented shrimp would show a preference for regularly colored

*Tripneustes* over an albino *Tripneustes*. We wanted to determine if the opposite preference was exhibited by the albino shrimp.

To test the host preference of the albino shrimp, two urchins were placed in a plastic tub together. One urchin was regularly colored. The other was albino. A single albino shrimp was then introduced to the tub and recordings were made of which urchin it was on at 10 seconds, one minute and three minutes after introduction. Only two albino shrimp were available for experimentation. The test was run 10 times for each shrimp. To advoid any bias in lighting, swimming direction etc., the relative position of the urchins was switched after 10 trials.

Results: At the end of twenty trials, the shrimp chose each urchin 10 times, showing no preference for one over the other. Also, no shrimp ever transferred from one urchin to the other once it landed on one urchin indicating again a lack of preference. It should be noted to advoid questions that each shrimp would land on both urchins in equal frequencies. It was not a case where one shrimp picked the same urchin 10 times and the other shrimp picked the opposite urchin 10 times.

Discussion: A possible reason for the lack of preference shown by these shrimp may be: the ability to change color proved earlier (section II). This ability would remove any pressure on the shrimp to choose an urchin which it "matched" and would be camoflaged against. The shrimp is essentially free to choose any urchin available and then change color accordingly.

Another variable that could be at work here is chemical cues which we have proved to be important (section III). Perhaps, last year's discovered preference of regularly pigmented shrimp for regular Tripneustes was based on chemical cues and not color differences as suggested. Our lack of preference could be attributed to the lack of chemical difference between our two urchins.

There is the possibility of some urchins having more chemical "appeal" that others. This has been suggested by our findings of very high numbers of shrimp on some urchins (6, 7, and 10 shrimp). There was no visible difference between those urchins and any others. It is also suggested by the transfer of the shrimp in the ~~migration~~ dispersal study (section IV) to one urchin.

In regards to this experiment, choice by the albino shrimp was determined by which urchin it noticed first, regardless of color. Had more time and shrimp been available, tests with these same urchins and regularly colored shrimp might have cleared some of the uncertainty involved here. In any event, the chemical appeal of individual urchins merits further study.

GENERAL DISCUSSION: Quite a lot has been contributed to the knowledge of the ecology of these commensal shrimp and their hosts, even though a number of new questions have been raised. To summarize the main findings of this study, we found

1) shrimp migrate from one host to another, probably during the evening. The reason for such migration is unclear, although some indications have been provided by our study, eg:

2) Because shrimp prefer certain specific locations on their host (eg Oral end, interambulacra/ambulacral interface spines), there are a limited number of preferred attachment sites on each urchin.

3) Competition for these preferred resting spots was observed as aggressive encounters between shrimp, which resulted in the displacement of ~~my~~ the subordinate shrimp. This displacement caused by aggression was evidenced by our overcrowding experiment.

4) Shrimp probably use chemical cues as well as visual cues in locating hosts. Both the recruitment and migration experiments indicate that shrimp migration is probably occurring at night, which is perhaps supported by the fact that chemical cues would be necessary in order to locate hosts at night.

5) Some urchins may be preferred over other urchins; this might be explained by stronger chemical signals being released by a particular urchin, thus attracting more migrating shrimp (examples are the one urchin censused with 10 shrimp on it, and the one urchin during the migration experiment which collected all 6 shrimp placed

within the enclosure). It is also possible that shrimp may be migrating to urchins ~~in~~ which represent a superior food source, which might happen, for instance, if one urchin were defecating. Our observations have suggested some feeding taking place on feces of the urchins.

6) Once a shrimp has migrated to a particular host, it can change color to match its substrate, eg in the case of albino urchins. This ability to change color correlates with the shrimp's lack of a preference of one color host or another.

Some questions which warrant further study:

1) Are there chemical differences between urchins of the same color? Why are these shrimp leaving their hosts in favor of other urchins?
2) What is the food that is available on the spines, and how important is this source for the shrimp?
3) Is aggregation occurring with the shrimp? How do sexes get together?
4) Can shrimp change color under dark lighting conditions, or is vision necessary?
5) Are the shrimp palatable to fish or other predators?
6) Does the entire life cycle of the shrimp occur on the urchin as suggested by this study?

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