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ASPECTS OF INTERSPECIFIC ASSOCIATIONS WITH DIADEMA

by

Dietrich Bernhard Ernst Magnus

Reprinted from the Proceedings of the German Zoological Meeting
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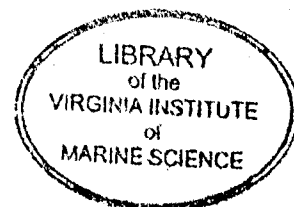
Preface
to Translation¹

This paper was translated in order to fulfill one of the language requirements for the Ph.D. degree.

An effort was made to keep the translation as literal as possible but some freedom was used in order to make the manuscript more readable. Distortion of the author's meaning may have resulted from this treatment.

This translation is intended for the use of researchers. An effort was made to make it as accurate as possible but it is likely that improvements could be made. If improvements appear desirable, it is suggested that the reader make his own translation. Constructive criticism of the manuscript would be appreciated.

¹Virginia Institute of Marine Science Translation Series No. 22



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The associations between sea urchins and numerous fishes and crabs have been known for a long time. The oldest report on a relationship between a sea urchin and a fish appears to be that of von Sarasin (1886). Nobili (1906) described the shrimp Stegopontonia commensalis as a partner with Echinothrix turcarum. Since then reports on this phenomenon have appeared from almost all of the world's seas. It must, therefore, be a widespread phenomenon. The nature of this relationship as well as its origin are still largely unknown. Most accounts are comprised of occasional observations made during cruises, or of short statements on habitat in systematic faunal works. The association has been described as a loose to firm interrelationship, respectively: protective society, symbiosis, epiokie, commensalism, or ectoparasitism. Until now no comprehensive systematic investigation or experimental analysis has been undertaken.

Pfaff (1942) found Diadema tube feet in the stomach of Diademichthys deversor, a goby living between the spines of Diadema savignyi. He was thus able to show that this fish existed at least partially as an ectoparasite. Within this family (Gobiesocidae) other species living

singly or in small groups with sea urchins may have similar relationships. There is even a close relationship in the derivation of their names, e.g. the American genera Arabaciosa, Bryssophilus, and Bryssetaeres (Jordan and Evermann, 1898). Large populations of various apogonids appear with the long-spined Diadema in addition to Aeoliscus strigatus and other urchins. They form a more or less firm community and are not associated with other fish (Abel, 1960; Hiatt and Strasburg, 1960; Klausenwitz, 1963; Lachner, 1955; Plate, 1908, 1916; Semon, 1903; Whitley, 1959).

I made three trips to the Red Sea in 1959, 1961, and 1962 to study this type of association on the coast, outer reefs, and islands in the area of Ghardaqa, Kosseir, Port Sudan, Suakin and Massauna. The relationship concerned four species of cardinal fish (Apogonidae) and one shrimp associated with Diadema setosa (Leske). Two of the fish, Paramia bipunctata Lachner and Apogon chrysotaenia Bleeker, are known as associates with sea urchins (Abel, 1960a, 1960b, 1961; Eibl-Eibesfeld, 1961; Lachner, 1955). However, Cheilodipterus lachneri Kausewitz and Archamia lineolata (Cuvier and Valenciennes) and the shrimp Saron marmoratus (Oliver)(Hippolytidae) were determined to be associates with Diadema for the first time. The investigations lasted from September to December and from March until May. Thus these interspecific relationships were investigated in different years and hours of the day, and under different conditions. Good insight into the biological and ethological prerequisites of the relationship was gained by recording environmental conditions and incidental behavioral observations. Most of the observations were made by diving, but a single shallow water location was observed with a plexiglass box. For natural observations on free animals, observations and experiments were carried out on captured animals in aquaria at the Biological Station at Ghardaqa.

The trip was made possible by the friendly assistance of the German scientific community: Mr. Hessischen, Minister for Education and Social Development, the Technical Hight School of Darmstadt, the friends at the Technical School of Darmstadt, and the University of Cairo. I would like to thank my co-workers on the trip of 1962: Mr. L. Volker; Professor H. A. F. Gohar, Director of Marine Biology at Ghardaza Station, and the co-workers at the station for their constant assistance; Dr. W. Klausewitz at the Natural Museum and Senchenberg Research Institute in Frankfurt for the identification of the fish; Professor L. B. Holthuis of Rijks Museum of Natural History in Leiden for identifying the crabs; Professor G. Cherbonnier of the Museum of Natural History in Paris for identifying the echinoderms; and Mr. E. Althaus for drawing figures 10 and 11. Miss I. Weirich drew Figs. 2, 8, and 9 which were graciously made available to me by Dr. Klausewitz from his publication (1964).

The Ecology and Ethology of Diadema setosa

These active sea urchins prefer open shady areas in shallow water at the base of coral reefs (Fig. 1). Because of intense intraspecific competition, a great part of the population is forced to occupy relatively open, poorly suited areas. The urchins apparently seek to avoid contact with the upper, living part of the coral reef. On the other hand, they climb structures such as wharf pilings and pier posts, often upwards to the water surface on nightly feeding migrations. Soft sediments lacking hard particles and meadows of sea grass are systematically avoided.

The shoalest habitats are on coasts protected from surf, the lee side of coral reefs, or in tidal pools on wide reef flats in the lower water zone, namely in the northern Red Sea about 50 cm below the mean water line. The main habitat extends from there to a depth of six meters.

In localities where surfs and swells are strong, Diadema is generally missing. However, it can endure strong currents and tides. It shows little sensitivity to water turbidity. In the harbor bay of Suakin it's many spines are covered with algae and silt flocculent. The animal continually cleanses itself by crossing several adjacent spines and straightening them from within outward, rubbing the adjacent sides of the spines. Therefore, I did not succeed in individually marking them with irridescient material, strings or colored paint. The spines are so extraordinarily mobile that all marks and even filaments tied tightly around the body were quickly stripped off.

One could not avoid frequent puncture wounds while marking or conducting other experiments. The sea urchins defended themselves against handling with lively spine movements. The effect of such punctures has often been over-exaggerated. The wound indeed burns violently for a few minutes, like that imparted by a stinging nettle, but more from the penetration of sea water than from the work of the poison. The poison, however, does cause swelling of the external squamous epithelium and consequently much capillary breakdown.

During the day, the sea urchins are inactive and hardly change position. In the evening, within a few minutes after sunset, they simultaneously leave their resting areas and travel around during the night. They move, at most, only a few meters from their resting places and feed on the algae of the hard bottom and the upper-most layer of substrate. The return to the resting place does not occur as simultaneously as evening departure. It begins with the first morning light and is finished 20 minutes later. The urchins apparently perceive the resting place by an optical stimulus and seem to prefer horizontally protruding structures. The greatest speed of the animal on firm ground amounts to 1.3 cm per second at 29 C.

On flat, small underground structures one occasionally happens on mass concentrations. The animals apparently mutually perceive the stimulus and congregate at it.

Associations with Diadema

Paramia bipunctata

This fish is the most frequent associate of Diadema setosa in the Red Sea (Fig. 2). The species is apparently identical with that observed by Abel (1960a, 1960b) and called Cheilodipterus novemstriatus (Ruppel). The fish are usually located in loose assemblages averaging 40-60 animals beside or over small groups of sea urchins. The size of the single assemblage is variable and changes from day to day when individuals from neighboring schools exchange position. It is not the sea urchin but the fish that sets the standards for the association. In midday the fish prefer to assemble in very shallow water over sea urchins that lie in the shade. Sea urchins in different locations are preferred under different conditions. The whole association is adapted to areas which are more or less undisturbed by tides or change in direction of the current (Fig. 6). Individual fish often change their position by a quick advance when they are feeding on planktonic animals. The fish apparently feed entirely on plankton. They never skim over the substratum or about the sea urchin spines.

Close approach of large fishes or humans causes the fish to move closer together and along side of the sea urchin spines and finally between them (Fig. 1, 3, 5, and 7). The amount of flight behavior is directly related to the location of the sea urchin. When the sea urchin is situated in the open, most of the fish leave it as soon as an aggressor

reaches the longest spines (20-25 cm long). The fish flee partly to other sea urchins and partly to the soft bottom surfaces beyond. But if the sea urchin is protected by a cleft or hole, the fish remain near it and squeeze themselves between the bases of the spines (Fig. 3). In this position, parallel to the spines, their dark longitudinal stripes, corresponding with the spines, take on morphological importance.

Shortly before sunset, i.e., before the sea urchins become active, the association quickly dissolves as the fish inconspicuously disperse from the sea urchin and lie tightly over the bottom upon the loose smooth sediments. The fish remain separate, either slowly swimming around or fixed in position and facing into the current. At least 20-30 minutes after dawn, they assemble about one meter over the sand flats to form small groups and return to the Diadema.

Their behavior of remaining close to the bottom while resting, prevents the fish from inhabiting shallow waters which become turbid in moderate wave undulations. Diadema, however, can inhabit these areas (Fig. 4). Near Ghardaqa Station, on the small coastal reef which is protected from a strong surf by a long outer reef, and in similar places in the Red Sea, the Diadema-P. bipunctata relationship occurs frequently. The relationship occurs only on the rare open protected areas of the coast, and is completely absent in other areas, although sea urchins frequently occur there. Conversely P. bipunctata groups are occasionally found in places where Diadema is absent or the fish may be in the vicinity of the sea urchins but not associated with them. I observed, for example, a large school (of P. bipunctata) on the flat patch of reef off Shab Abu Sadaf near Ghardaqa in a depth of about 1.50 meters. It was located within a spacious hole in a dead Acropora coral with many side openings.

There were no sea urchins in the vicinity. Small groups of P. bipunctata were commonly located at angles between the iron supports of the station pier at Ghardaqa in 1-2 meters of water. They had no contact with the Diadema or with the sessile sea urchins on the bottom.

Trap Experiments on Paramia bipunctata

I employed two types of traps which were similar to sea urchins. To the wooden bases of these traps were fastened lead discs 4 cm in diameter. The first type consisted of 100 spines and was made of wire rods. Each spine was 1 mm in diameter and 25 cm long. The second type had 50 spines and was made of wooden rods. Each spine was 3 mm in diameter and 18 cm long. The wire traps were black while the wooden traps were either black, red, or white. Herbst (1962) constructed a miniature reef almost entirely of Galaxea fascicularis close to the Ghardaqa Station. It lay in three meters of water, had surface dimensions of 6 x 8 meters, and was about one meter high. A sea-grass meadow was situated in the middle of the circular clay-sand bottom of 25-30 meters diameter (Fig. 4a, 4b). This reef held about 300 Diadema and at least 2,000 P. bipunctata.

The trap acted as a small sessile Diadema to which a medium-sized group of fish was attracted. The fish sought places between the spines as they did in their sea urchin shelter. In most cases they immediately distributed themselves over the trap. When a sea urchin (associated with fish) was carefully removed, the fish remained near the trap and used it as a sea urchin. A disturbance caused the entire school, or the greatest part of it, to shift from between the trap spines to behind it (Fig. 5).

The experiment was successful with traps of the two types, also with the different colored traps; however, best results were obtained with the wire spined traps.

I left a trap in a favorable place next to the small reef for over eight weeks. By the end of this time, it was densely covered with algae, polychaete tubes, and sponges; and during the entire time, it had sheltered a group of P. bipunctata.

About 12 meters from the Galaxea reef in two meters of water on a sandy-clay bottom, stood an old barrel with a large opening in its under side. Fifteen Diadema lived in the barrel and a large group of P. bipunctata were associated with it daily (Fig. 4a). The fish were located in the shaded part of the barrel, over the barrel, and beside the barrel. They could be dispersed with a small stick. This allowed me to adjust the fish to different traps and Diadema to different ecological conditions, while I stood about one meter from the barrel. In the barrel, the fish always formed small groups around the individual traps. The majority of the fish preferred the stouter wire-structured traps to the wooden traps or even to the living sea urchins.

In another experiment, I placed beside the barrel, a retiform fruit basket constructed of date palm bars and weighted with iron. It, at once, drew a large group of fish, and the fish remained in the half shade of its interior. Even in midday they stood as in a pergola (Fig. 6).

Plate (1908) proved, in the Gulf of Suez, that one can capture a Diadema society, by slipping a sea urchin in a bucket and then lifting the bucket from the water. I have repeatedly been successful in capturing fish for aquarium studies with a wire-spine trap placed in a bucket (Fig. 7). In the aquarium the fish lined up facing the trap no differently than

they do in the wild and also invariably preferred the wire trap to the sea urchin.

Cheilodipterus lachneri

I often observed single or several young individuals of Cheilodipterus lachneri associated with P. bipunctata (Fig. 8). As long as the two species are united in the association, they remarkably resemble each other in behavior, size, color, and shape. However, C. lachneri lacks the small dark mark on the dorsal side of the base of the tail and the lateral spot on the base of the tail appears to be larger. They apparently spend only their juvenile period with P. bipunctata, sharing the protection that a school gives to its members. The adults are considerably larger and live alone (Klausewitz, personal communication).

Apogon chrysotaenia

I can confirm Abel's (1960a, 1960b) details on the behavior of Apogon chrysotaenia with Diadema. The fish live in nearly the same habitat as P. bipunctata. However, they are not as abundant and do not form schools as large as the latter. Their resting and feeding behavior is similar to that of P. bipunctata, only they appear to be less strongly bound to rock bottom areas and are less shy. A group often maintains itself over or beside a Diadema and in case of danger a few members flee between the spines but most disperse.

Archamia lineolata

I was able to observe two large schools of these fish for several weeks on a small Galaxea reef near Ghardaqa (Fig. 9). The fish were almost transparent except for their large irridescent blue eyes and were remarkably stationary. They were found only over and beside Diadema, situated in flattened depressions protected from water currents. Their behavior towards the sea urchins was like that of P. bipunctata. They reacted similarly to the traps and could be caught with the pail trap. They formed schools in the aquarium and did not mingle with the schools of P. bipunctata.

Saron marmoratus

In the harbor of the city of Suakin, Diadema hides on most days in the cracks and depressions of the decaying walls of the wharf with only the tips of their spines protruding (Fig. 3). At least every fourth sea urchin of the population is associated with the sexually dimorphic shrimp Saron marmoratus (Fig. 10). Frequently 2-5 shrimp of different sex and age live together with a sea urchin. During the day, the shrimp remain in the entrance of the depression with their heads directed outward (Fig. 11). After sunset, the sea urchins leave their haunts and the shrimp accompany them, always maintaining themselves near the long spines of the sea urchin (Fig. 12). Both sea urchin and shrimp graze on epiphytes covering the hard bottom during the night and return to their caves in the morning. When the sea urchin was removed, the shrimp fled to a fissure in the wall. When the sea urchin was moved, the shrimp followed it. The shrimp were never without the protection of the sea urchin when outside of the cave.

I was also able to observe a relationship of the shrimp and sea urchin in Ghardaqa. However, there are still many unanswered questions concerning this facultative and very close partnership.

Summary

The daily active, loose association of cardinal fish Paramia bipunctata, Apogon chrysotaenia, and Archamia lineolata with Diadema as well as the association of P. bipunctata with juvenile Cheilodipterus lachneri permits the fishes to widen their niches. They are able to inhabit areas which would not be habitable without the sea urchins. The sea urchin functions as a hard bottom structure element to conceal the fish from diurnally active enemies (tangible hiding places in the terms of Abel), and as a feeding area providing a place to lie and wait for food organisms conducted to the localities by water currents. The fish are apparently successful in locating Diadema which are not in contact with coral polyps and are close to resting areas, depressions in the substrate. To fulfill the function of a feeding station, the sea urchin must be in a food conducting current and in an area where the fish can advance in order to capture the food. It must further offer the entire school sufficient space and allow its members to have optical contact. As long as the remaining biological demands can be satisfied and an appropriate depression in the substrate is located nearby, the Diadema fulfills the conditions for a feeding place and protective area for the association. However, the results of the field investigations and the trap experiments were not optimal because the observations were not continuous. The sea urchin itself gained little from the association. The fish did not clean the sea urchin, thus there is no cause to call the relationship symbiotic.

Also, in the association of the shrimp Saron marmoratus with Diadema, the shrimp obtains all the benefits from the relationship because they as nocturnal grazers are able to enlarge their feeding habitat under the protection of the sea urchin, which is equivalent to a moving place of refuge.

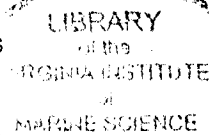
Discussion

O. Kinne - Hamburg/Helgoland: What did you observe the fish eating? Did they feed between the spines of the sea urchin or must they leave their refuge in order to feed? What are the enemies of the fish, namely from whom do they seek to protect themselves?

Magnus: They are predators that feed on crustaceans, polychaetes, other invertebrates, fish fry and small fish, and on such items that are brought to the feeding post by the water currents. Through the stomach analyses of Hiatt and Strasburg (1960) on cardinal fish in the Marshall Islands we are well informed. My investigations (concerning metamorphosis and similar biology) produced a similar picture. Most of the members of the fish association stand motionless above or beside the sea urchin, near the outer half of the protective spines and only occasionally do members pass between the spines. In case of alarm, the entire school first withdraws among the spines. Food quest and consumption normally takes place, therefore, in a narrow range around the sea urchin. Their enemies are diurnally active predatory fishes. I have not been able to establish specific enemies.

F. Schaller - Braunschweig: Have you employed two-dimensional traps resembling sea urchins? How do the fish respond to these?

Magnus: No, I have only used three dimensional traps. The results of



the preceding free water observations pointed out that the fish reacted not to an optical pattern but to a thigmotactic stimulus. I think they would perhaps swim to a two-dimensional model but would not recognize it as a qualified feeding station. However, one should still carry out such an experiment.

Riedl-Wien: Our colleague, Mr. Magnus, has again conducted a very convincing piece of research in an area of under-sea experimentation which has received little attention. His methods can be followed by us and provide numerous and direct answers for those not acquainted with salt-water investigations.

This association calls one's attention to the relationship of Leptomysis mediterranea G. Sars with Anemonia sulcata (Pennant) which still awaits investigation. Swarms of mysids, from 20 to over 500 individuals, normally stay over large specimens of the anemone. Obviously the shrimp are protected by the anemone. During the day, one can capture such a mysid swarm by substituting a floating block for the anemone and later return the swarm to its own anemone. When deprived of its own anemone, the swarm seeks an alternative. During the night, the swarm leaves the anemone and becomes pelagic. At daybreak, it returns to the anemone.

The alternation of habitat (day-night rhythms) is well-known for the group but the existence of so specific a relationship between shrimp and sea anemone is new. Future investigators should study the alteration between the pelagic-benthic habitats and the development of the specialized relationships.

FIGURES

- Fig. 1. Paramia bipunctata schools are found with Diadema on the reef border in the shade. When the fish are disturbed they move, as a group, between the spines of the Diadema. Ghardaqa, small Galaxea reef in three meters of water.
- Fig. 2. Paramia bipunctata after formalin preparation.
- Fig. 3. P. bipunctata school seeks protection at the bases of the spines of a concealed Diadema when it is greatly alarmed. Suakin harbor wall in one meter of water. a and b: successive phases in flight behavior.
- Fig. 4a. Study area at Ghardaqa. Depth lines are for mean water depth in Sept.-Oct.; current direction is wind dependent. Diadema which are found in less than one meter of water, at the base of the station pier and on solitary rocks, are always free of fish (waves reach the bottom in these areas). Below the one meter line associations are numerous: pier, Galaxea reef, and around a barrel. b: Profile of the height of the Galaxea reef (3a is increased three times), SHW = Spring tide high water, SNW = Spring tide low water.
- Fig. 5. P. bipunctata school directed toward current among the wire spines of the trap (length of spines 25 cm). Sand bottom in two meters of water.

- Fig. 6. P. bipunctata school directed toward the current in the submerged fruit basket. Ghardaqa. 2 meters of water.
- Fig. 7. P. bipunctata school nearby and among the wire spines of a trap in a bucket. Ghardaqa Galaxea reef, 2.5 meters of water.
- Fig. 8. Cheilodipterus lachneri. After formalin preparation.
- Fig. 9. Archamia lineolata. After formalin preparation.
- Fig. 10. Saron marmoratus female from a colored photograph.
- Fig. 11. Diadema and Saron marmoratus male side by side in resting place in a hole in the wharf wall at Suakin during the day.
- Fig. 12. Diadema and S. marmoratus male and female grazing together at night. Suakin in one meter of water. Flashlight photograph.

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