Jane: Excellent study! Time for lots of comparing the two species and of opening doors and feeding strategies. Joe

FEEDING BEHAVIOR IN TWO SPECIES OF SEA ANEMONES AT DISCOVERY BAY, JAMAICA

by

Jayne Seymour

Dartmouth Foreign Study
in Tropical Biology

March 5, 1979

Introduction

Little is known about the feeding behavior of two common species of sea anemones which inhabit Discovery Bay, Jamaica, *Stoichactis helianthus* and *Condylactis gigantea*. These two species are very different in morphology (see fig. 1a and 1b) and colonize different microhabitats.

In the field I have noticed that *S. helianthus* is most frequently found in an exposed habitat such as the surface of coral rocks. Individuals may be either colonial of solitary. *C. gigantea* attatch their pedal disks within holes or crevices. They are usually found alone or in small groups. Experiments performed by Sebens and DeRiemer (1977) on the microhabitat preferences of these anemones confirm these observations.

Two sympatric species which show such variations in morphology and habitat are likely to have differences in feeding behavior as well. Their ability to catch certain types of prey is dependent on the physical capabilites with which their form endows them as well as the abundance of the prey in their microhabitat.

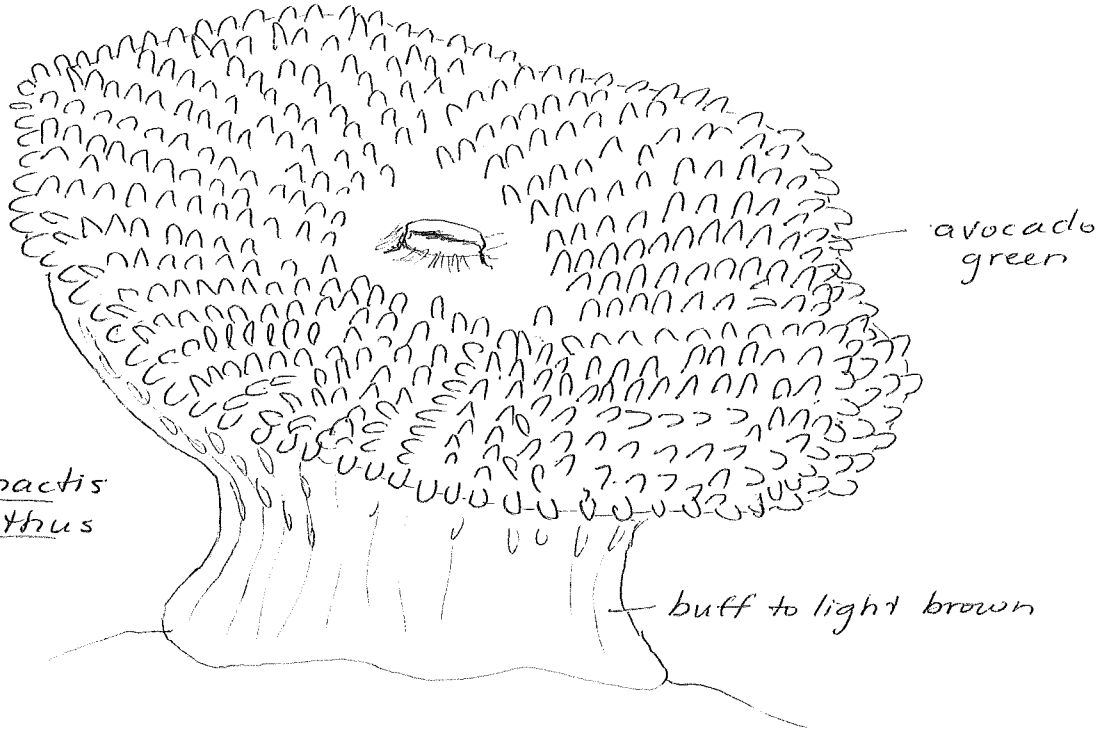


fig. 1a Stoichactis helianthus

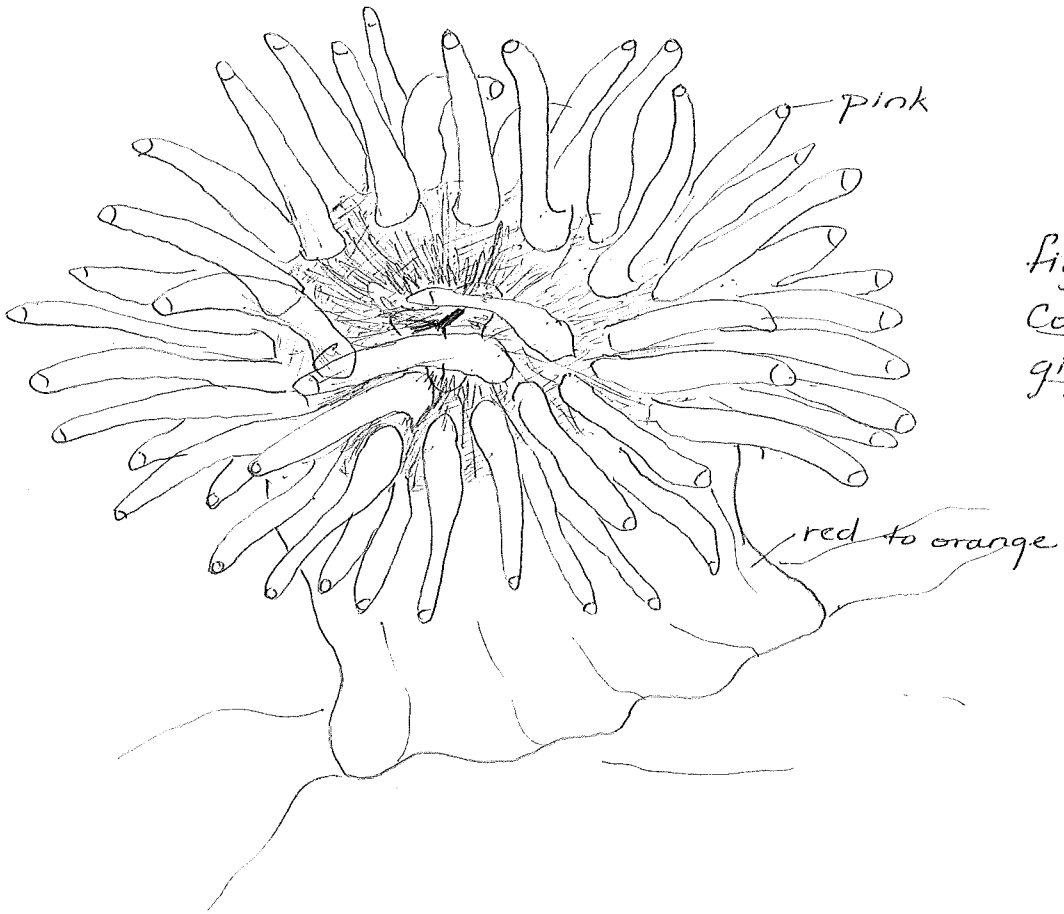


fig. 1b Condylactis gigantea

I began my study with the hypothesis that the long tentacles of C. gigantea would enable it to capture large prey. I thought it would probably not rely very much on its symbiotic zooxanthellae because their distribution in the tentacles appears patchy rather than uniformly dense. It was difficult for me to imagine what S. helianthus could capture with its stubby tentacles. I was thus lead to the hypotheses that this species was primarily a filter feeder. Due to its relatively dark green color and its location on exposed surfaces it seemed likely that it would also rely heavily on its zooxanthellae to provide it with food.

To test these hypotheses, I carried out a series of feeding experiments designed to determine the ability of each species to capture various types of prey. Based on this data I have suggested a probable natural diet for each species.

Materials and Methods

Specimens of Condylactis gigantea and Stoichactis helianthus were collected for study in the lab on several occasions. Five S. helianthus were collected from the East Back Reef by prying them loose from their substrate of dead Acropora palmata using bare hands or a diving knife. The anemones in this area were living in large ,dense colonies. There was a strong wave surge which caused the anemones to be subject to alot of buffetting. These anemones were brought back to the lab in a bucket. They were placed in glass dishes in a tank of flowing water. The next day, when they failed to anchor themselves to the glass, they were transferred to a tub with running water containing dead coral slabs.

Attempts to pry C. gigantea from its substrate failed. Instead,

specimens were located which were anchored to a breakable substrate, in this case, dead Acropora cervicornis. Three were collected from the dock area. The following day, three S. helianthus and C. gigantea were collected from Columbus Park where there are many of both species anchored on easily broken pieces of A. cervicornis. Both the dock area and Columbus Park are characterized by a mild wave surge (compared to the East Back Reef). All of these anemones were kept in plastic tubs in running water on the substrate on which they were collected. Individuals which did not appear healthy (ie, were not attatched to substratum, were always bloated or had their pharynx distended) were not used in feeding trials. After two days in captivity all anemones were returned to the Bay. Two new anemones of each species were then collected from Columbus Park and kept in the lab.

Field (in situ) observations of feeding behavior were made both in the dock area and at the Mangrove area. The latter area is characterized by its border of Mangrove trees. It is sheltered from waves and turbulence. The water is very clear and is fed by freshwater springs.

Feeding behavior was observed for a variety of potential prey items in the lab and in the field, both day and night. To determine the stimuli which trigger different aspects of the feeding response, some non-living materials were used. Between each test in the lab, the anemone was allowed to resume its pre-trial posture before a new stimulus was introduced. When water became contaminated with food particles or possibly smells, it was replaced before the ~~following~~ next trial.

Reactions to the following stimuli were observed in the lab with the naked eye and/or using a dissecting microscope: carmine particles, paper towel, paper towel soaked in fish homogenate (homogenate consisted of Grey snapper mixed with a small amount of water in a blender), paper towel in motion on tentacles, nylon string, fish scent, fish homogenate mixed with carmine, live Zooplankton, crabs (found living on or under anemones), sea urchins, Ophiroids and shrimp. In the field during the day, anemones were fed fish homogenate, pieces of Grey snapper and live Beaugregories, crabs, Ophiroids, a fireworm, sea urchins. In the field during the night (7:00-7:30 and 9:00-9:30) they were fed pieces of Grey snapper and live Beaugregories. When possible I recorded the time it took for the anemone to respond, the nature of the response and whether the object was retained by the anemone or later egested.

The live Damselfish were pierced through the mouth using a safety pin. A string was tied to the pin so that I could control the fish. If the fish was enveloped by the anemone, the pin and string were left attatched to the fish. The next day I observed wherer the string was gone or whether the string was emerging from the mouth of the anemone. I could then pull on the string to see if there were any fish remains attatched to the pin.

Using a compound microscope and a dissecting microscope I observed and made drawings of mesenterial filaments extracted from the gut of both species. Carmine particles were added to observe the way in which these particles would be processed by the filaments. Observations of the surface of the pharynx and the

tentacles were also made using the compound microscope. I placed my finger on the tentacles of both species to cause them to fire their nematocysts. I then scraped my finger with a coverslip. This was then observed with a compound scope.

Results

Where field behaviour differed from behaviour in the lab it will be noted. For the sake of brevity, only one description will be given for each type of food material used, although two to four trials were performed.

I. Condylactis gigantea

1. Carmine particles. Tentacles responded immediately to tactile stimulus from particles by bending toward the mouth. The pharynx was extended to meet the tentacles. The particles didn't all stick to the tentacles. Many particles still remained on the tentacles when the feeding response was completed (1 min.) When carmine particles were placed around the mouth the particles were collected on mucus streams which were drawn into the mouth by the cilia on the extended pharynx. These cilia were observed using a compound microscope.

2. Paper towel. A piece of paper placed on or under the tentacles using forcepts had no effect in initiating a response.

3. Moving paper towel. When the same piece of paper towel was moved back and forth across the tentacles the tentacles contracted toward the mouth but the paper was not grasped. The pharynx didn't expand. The response was very brief.

4. Paper towel soaked in fish homogenate. The paper was partially rinsed off before placing it on the tentacles of the anemone. The anemone responded immediately, taking in the paper with its tentacles which shoved it into its expanded pharynx.

5. Paper towel and fish scent. I swished a piece of fish in the water at the same time I placed a piece of unsoaked paper towel on the tentacles. In less than 2 minutes the tentacles began to wave but this movement was unrelated to the position of the paper on the tentacles.

6. Nylon string. There was no response to the string until it was moved, the the pharynx was eviscerated. Tentacles contracted around the string and brought the string into the mouth. After 3 minutes the anemone began to release the string.

7. Fish scent. Response varied from nothing to tentacles waving, expanding and extending pharynx and bloating of column. One individual was observed to place tentacles in its mouth.

8. Fish homegenate mixed with carmine. Tentacles respond immediately by curling up around homegenate and moving twoards the mouth. By the time the tentacle had reached the mouth the pharynx was extended. The tentacles were placed in the mouth. mucus strands appeared and homogenate that wasn't on the tentacles was drawn into the mouth over the extended pharynx.

9. Live zooplankton. Five small pipettes full of water containing live zooplankton were dropped on the surface of the anemone, both on the tentacles and the area around the mouth. No response was elicited by the zooplankton. However, when a peice of detritus in the sample hit a tentacle, it caused the tentacle to contract and enter the mouth.

10. Sea urchin (Diadema antillarum). The tactile stimulus caused the tentacles initially to draw in the sea urchin. Soon the anemone attempted to reject the sea urchin by expanding its tentacles and letting them droop down so the urchin would fall off.

11. Brittle stars (Ophiroids). Two species of Ophiuroids were tested in the field, Ophiocoma echinata (brown with large thick spines) and Ophioderma cinereum (grey and smooth). When O. cinereum was placed on the edge of the tentacles, it was able to escape in 2 minutes. When placed in the center of the anemone the brittle star seemed unable to escape; tentacles were well coiled around it. Yet in 6 minutes the Ophiroid was free. This seemed to have occurred because the anemone let it go. When O. echinata was placed on the edge of the tentacles it escaped easily. When placed in the center of the anemone it was rapidly engulfed by tentacles. It finally escaped, covered with mucus after having lost the tips of three legs. When this weakened brittle star was then given to another anemone, the anemone at first grasped it with its tentacles, but made no attempt to ingest it. The star remained on the tentacles for at least 30 minutes, After $2\frac{1}{2}$ hours it was gone.

12. Xanthid crabs. Anemones were unable to entrap these crabs although apparent attempts were made. When a dead crab was used, it was ingested. Several hours later, the crab was found next to the anemone, fully intact but covered with mucus.

13. Fish, dead and alive. Although C. gigantea would readily take small pieces of fish in the lab, it was ineffective at holding this type of prey in the field. When pieces of fish were brushed against the tentacles, they immediately contracted and were placed into the expanded pharynx. However, the fish was easily pulled away. When the fish was left on the tentacles for about 30 seconds, it became more difficult to pull away. Numerous trials

with live Beaugregories demonstrated that the tentacles were unable to grasp and hold a live fish.

14. Shrimp (Gonodactylus). The anemones were incapable of holding on to this strong crustacean.

II. Stoichactis helianthus

1. Carmine particles. When carmine particles are placed on the tentacles there is no observalbe immediate reaction. Soon, mucus is secreted from the tentacles at the site of the carmine particles. The particles are entrapped by the mucus but no further response is seen. When the particles were placed around the mouth (fully closed) there was no response and no mucus was seen. However if the particles were placed on an open mouth or a pharynx which had already expanded in response to a previous stimulus, the particles were collected on mucus strands which were drawn into the mouth. Examination of a piece of the pharynx with a compound microscope revealed that its surface was covered with beating cilia. Lack of motion of particles adhered to mucus on the tentacles indicates that their surfaces are not ciliated.

2. Paper towel. There was no response to either a still or a moving paper towel.

3. Paper towel and fish scent. Motion of paper on tentacles was continued while a piece of fish was swished in the water. After 3 minutes there was no respone directed to the paper, but the pharynx began to expand.

4. Paper towel soaked in homogenate. The paper began to stick to the tentacles as soon as it touched them, indicating that the nematocysts had been stimulated to fire by the combined

tactile and chemical stimulus. The pharynx expanded as the tentacles engulfed the paper and the oral disk rolled up to meet the pharynx. The paper was ingested and retained for at least an hour.

5. Nylon string. There was no response until the string was moved. Rubbing the string against the tentacles elicited a slow contraction of the oral disk. In 1 minute the mouth was open. By 7 minutes the pharynx had expanded to meet the string which was transferred to the mouth from the tentacles. At 9 minutes the string was drawn half way into the mouth. Eleven minutes later the anemone had rejected the string.

6. Fish scent. The anemone responded in about 3 minutes after I began to swish the piece of fish through the water. The pharynx was slowly distended. Some contraction of the oral disk was observed. The column became bloated.

7. Fish homogenate mixed with carmine particles. Tentacles respond by contracting and forming a pit into which the homogenate settles. By 30 seconds the pharynx begins to expand rapidly. The oral disk folds around the homogenate and bends over towards the mouth. The expanded pharynx comes in contact with the homogenate which is drawn into the mouth on mucus strands by cilia action. This is difficult to observe becouse the expanded pharynx and the folded over oral disk cover the homogenate.

8. Live zooplankton. Several pipettes full of water containing live zooplankton were placed on the oral disk. No response of any kind was observed over several minutes. On many other instances in subsequent observations, live zooplankton were seen swimming

on the surface of the oral disk, apparently unnoticed by the anemone.

9. Xanthid crabs. These crabs were found living under almost every C. helianthus examined in the field. They were frequently observed perched on top of the anemone. When a crab was placed on an anemone in the field or in the lab, they usually were able to move about freely without being stung by nematocysts. If I moved the crab across the tentacles, the anemone usually contracted, but the crab was always able to walk off the anemone. Apparently the crab was either not being very much affected by the nematocysts of the crab did not stimulate the anemone to fire its nematocysts. The latter was shown to be the case when homogenate was added to an anemone on which a crab was perched. The oral disk rapidly began to curl up. The crab tried to move off the anemone but had suddenly begun to be held by the nematocysts. The crab was thus unable to escape. However, the crab was later egested, covered with mucus but alive.

10. Sea urchins (Diadema antillarum). The urchins were readily enfolded by the oral disk. After the urchins were finally expelled (15-30 min.) they were covered with mucus.

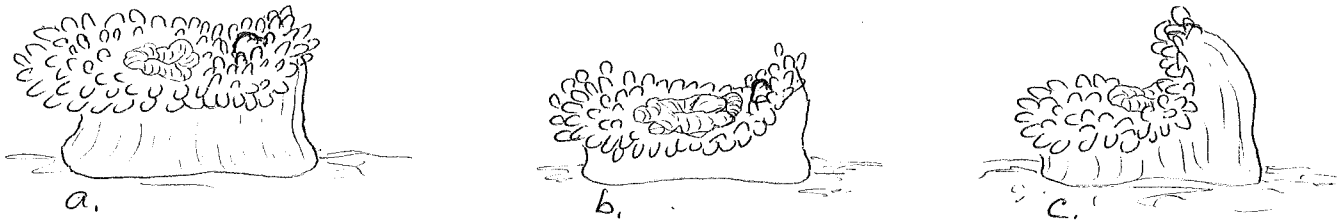
11. Brittle stars (Ophiroids). The same two species were used as with C. gigantea. S. helianthus was successful at capturing both types. The O. echinata were more easily engulfed because or their flexibility. Alot of mucus was observed to be excreted around this species. The O. cinereum were more difficult to capture because their smooth surface made them harder to grasp. In addition this brittle star stiffens up its arms when it is threatened. The made it difficult for the anemones to assume their ball-shaped

feeding configuration. (See fig.3) Two and one half hours later there anemones were checked to see if they had retained their prey by feeling them for any hard contents. No anemone was found to contain a brittle star.

12. Fish, dead and alive. Fish pieces were readily taken under all conditions. The response was rapid. The tentacles held the food while the oral disk rolled up to meet the expanding pharynx, into which the food was drawn. The anemone was highly successful at capturing live Damselfish. The fish had only to brush the surface of the anemone to become stuck to the tentacles. The more it struggled, the more tightly it was held. Soon after contact with the anemone, all movement of the fish aside from breathing stopped. This was before the oral disk had engulfed the fish. This suggests that the nematocysts may contain some kind of a neurotoxin. To test the strength of the anemone's grip I attempted to pull the fish away. On contact, the fish were held about three times more strongly than the fish that C. gigantea had been allowed to hold for 1 minute. The strength of the grip increased with time. If I pulled hard enough, I could tell that the tentacles were ripping off the anemone rather than coming off the fish.

13. Shrimp (Gonodactylus). The shrimp fought harder than any other prey item tested. As soon as the shrimp touched it , the anemone began to curl up. When the shrimp broke free from the first place it was held, it swam into the other side of the oral disk and became even more firmly embedded in the tentacles than before. The anemone rolled up into a ball around the shrimp whose struggles could be seen from the outside. Eventually, the

fig. 2 S. helianthus consuming a piece of fish



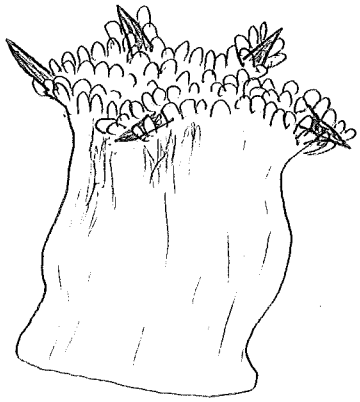


fig. 3 S. helianthus enveloping Ophioderma cinereum

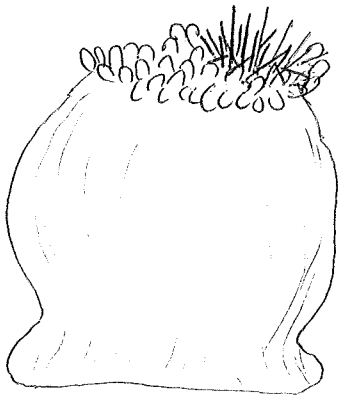


fig. 4 S. helianthus enveloping Diadema antillarum

fig. 5 Condylactis gigantea consuming a piece of fish.

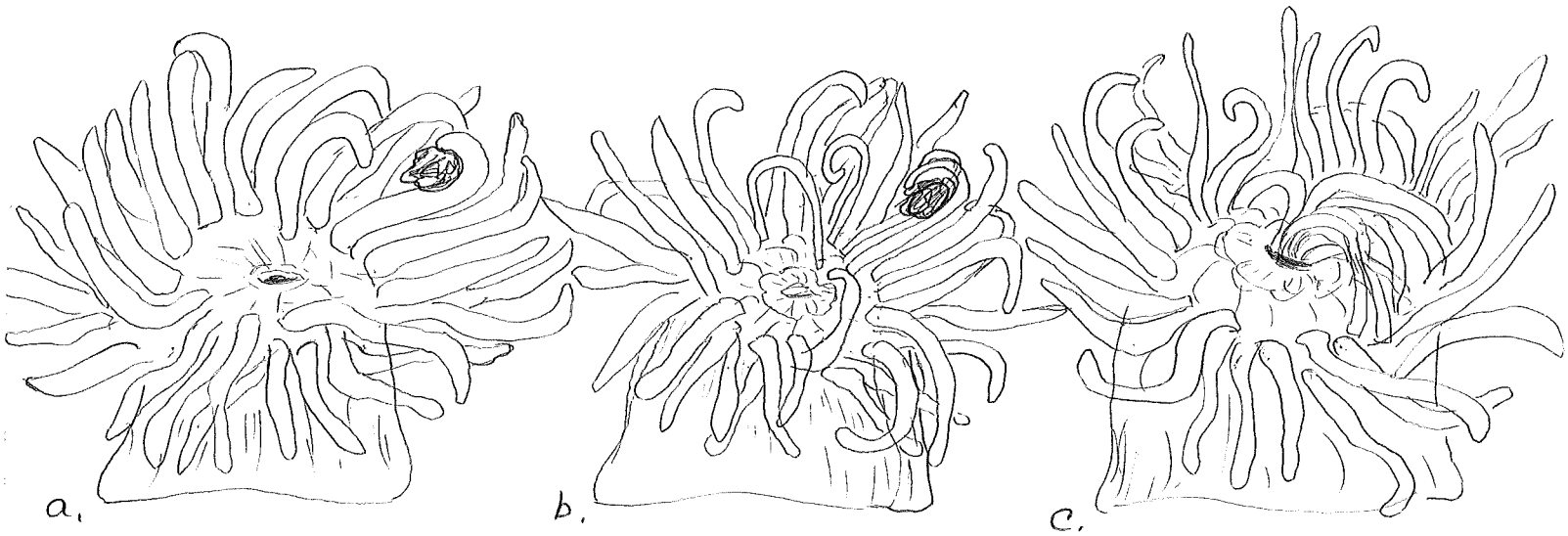


fig. 6 Unfired nematocysts (similar in both species)

fig. 7 Fired nematocysts from S. helianthus

fig. 8 zooxanthellae (same in both species)

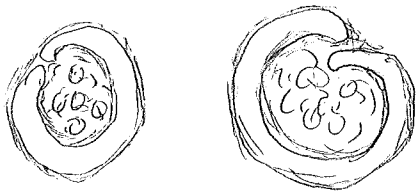


fig. 9 surface of mesenterial filament
(C. gigantea)

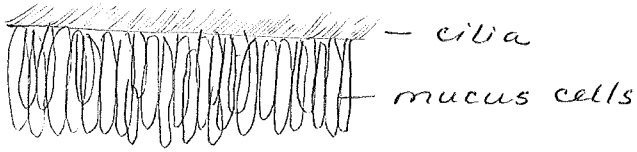


fig. 10 Mesenterial filament from S. helianthus channeling carmine particles along groove via mucus and ciliary action

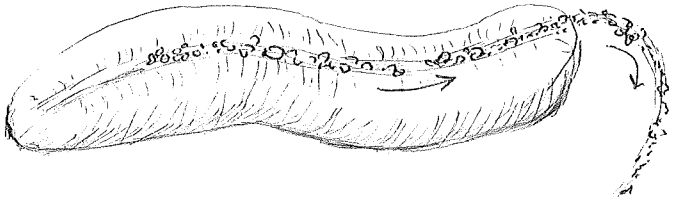


fig. 11 Mesenterial filaments
(found in both species)

anemone released the shrimp.

14. Fireworm (polychaete). This encounter was observed when I accidentally caused a fireworm to fall on top of an anemone. The anemone made no attempt at any kind of a feeding response. The worm slowly moved off the anemone leaving a trail of bristles. Soon after the fireworm had left, the anemone released its pedal disk from the substratum.

III. Synthesis: Generalized feeding responses. (See figs. 2&5)

1. Condylactis gigantea. Contact between food particle and tentacle is followed by immediate contraction of the tentacles. Tentacles wrap around the prey item and draw it to the mouth. As they do so, they contract in diameter and become darker in color. The pharynx begins to expand shortly after the food has contacted the tentacles. The pharynx expands much less than in S.helianthus. The tentacles involved are then placed in the mouth where they remain for 1 to 2 minutes. Meanwhile, the column of the anemone becomes inflated.

2. Stoichactis helianthus. Upon contact with a food item the area immediately in the vicinity forms a depression which surrounds the lower half of the particle. Meanwhile the pharynx begins to expand, expecially in the direction of the trapped food particle. The oral disk then begins to roll up over the food. If the food item does not struggle and is not large, only half of the disk will curl up. If the prey is large and/or struggling, the entire disk will roll up to form a ball shape.

Discusion

The results show that tactile stimulation is probably more

important than chemical in promoting a full feeding response. There seems to be a threshold level of tactile stimulation that is required. Neither a paper towel nor zooplankton were adequate whereas a nylon string and carmine particles (for C. gigantea only) were.

Tentacle waving in response to chemical stimuli in C. gigantea increases the likelihood that it will encounter food. Pharynx evisceration is not as important because the tentacles are able to put the food particle into the mouth. In S. helianthus it is more important for the pharynx to be well expanded because the tentacles are less agile at putting to food into the mouth.

It is adaptive for the anemones to have these threshold levels and differential responses. A high threshold for a chemical trigger to feeding behavior prevents the anemone from reacting to the many smells around it produced by potential prey which may never venture near enough to be captured. Likewise, the anemone's response to touch is carefully tuned so that the anemone doesn't waste energy trying to feed on every piece of detritus or sand that lands on its tentacles. The anemone seems capable of assessing the evidence that the stimulus it is receiving is likely to represent an edible object. For instance, both species readily responded to the paper soaked in homogenate while ignoring the paper when it was not directly associated with a chemical cue. However the anemones do seem incapable of making a distinction between edible and non-edible prey since they will attempt to engulf such animals as brittle stars which they are apparently incapable of digesting.

A strict interpretation of the results of this experiment

can go no further than indicating the feeding capabilities of S. helianthus and C. gigantea. However, the data make it possible to speculate as to the natural diet of these two anemones.

It is likely that C. gigantea does not rely at all on large prey. It is difficult to imagine that it could even trap a very small or weak fish. Small fish were sometimes seen among its tentacles in the field and the anemone made no attempt at capture. The sensitivity of the tentacles to small pieces of detritus and carmine particles indicates that this anemone would be effective at utilizing detrital matter floating in the water. In spite of the negative results for zooplankton in feeding trials, there is still the possibility that they are included in the diet. Sebens and DeRiemer (1977) report that C. gigantea does feed on zooplankton. It's long tentacles which are constantly in motion and have a large surface to volume ratio seem well designed to maximize contact with suspended particles.

An organism which feeds on small, low-energy units of food would have to gather each unit in a way that expends little energy. Each feeding response of C. gigantea to a small particle requires only that the tentacle which contacts the food bend into the mouth. It is not necessary for the pharynx to be greatly expanded nor for the oral disk to contort to feed. Although its nematocysts may be inadequate for trapping large prey, they may aid in immobilizing small prey as well as deterring potential predators. The latter may prove to be their most important function.

C. gigantea may also rely heavily on its zooxanthellae for food. Out of 14 species of Anthozoans examined in one study,

C. gigantea was found to have the second highest density of zooxanthellae. (Sebens and DeRiemer, 1977)

S. helianthus probably relies on infrequent captures of large prey. According to Hyman (1940) many anemones have adopted this strategy and can survive for long periods without food. This anemone is relatively poorly adapted as a suspensing feeder. Since it primarily colonizes exposed areas and is almost always found with its oral disk nearly parallel to the water surface, alot of debris would have the opportunity to collect on the anemone's surface. This continual rain of debris seems to have deadened its response to light tactile stimulation. Therfore, particles in suspension are incapable of eliciting a feeding response.

S. helianthus' feeding mechanism is inefficient for collecting small particles for food. To feed it must expend a relatively large amount of energy to eviscerate and extend its pharynx as well as rolling up at least half of its oral disk. This would seem to involve a far greater energy expense than curling up one tentacle. On the other hand, S. helianthus' "high cost" feeding mechanism has been shown to be superior for entrapping large prey. The anemone can well afford to expend alot of energy if it will gain an entire fish in the process.

Since S. helianthus is ineffective at removing detritus which collects on its surface, it depends on Xanthid crabs to perform this task. It is interesting to note that the only area where S. helianthus was not observed to have symbiotic crabs was the East Back Reef. Here the wave action would be sufficient to clear all debris from the anemone's surface. The Anemones have come to ignore the crabs

as a stimulus to feeding. (This is certainly no loss since the anemones apparently cannot digest through the crab's exoskeleton). The crab gains shelter and a source of food from the relationship. In addition to cleaning the anemones, crabs may also act as a lure for the anemone's prey. A fish or other animal which tries to capture the crab may blunder into the anemone and be caught.

The findings of this study not only contradict my original hypotheses, they contradict evidence presented by Sebens and DeReimer (1977). These two workers report observations on zooplankton feeding by both C. gigantea and S. helianthus. They also cite earlier studies which state that these two anemones both consume gastropods and echinoids. However the latter is of questionable accuracy since it dates to the 18th and 19th centuries. It is possible that the anemones were not observed long enough after they had engulfed the prey to see whether the food was retained or expelled.

Long-term field observations may be necessary to confirm my extrapolation from feeding capabilities to feeding habits. Since anemones may feed only rarely on large prey and it may be difficult to make observations on feeding with respect to very small prey, definitive results will not be easy to obtain.

How about a gut content analysis of field specimens?

LITERATURE CITED

Hyman, H.L. The Invertebrates protozoa through Ctenophora. McGraw Hill: New York and London. 1940, pp. 566-599.

Sebens, K.P. and DeReimer, K. 1977. Diel cycles of Expansion and Contraction in coral reef Anthozoans. Marine Biol. 43:247-256.

RELATED ARTICLES

Johannes, R.E., S.L. Coles and N.T. Kuenzel. 1970. The role of zooplankton in the nutrition of some scleractinian corals. Limnol. Oceanogr. 15:579-586.

McFarlane, I.S. 1970. Control of preparatory feeding behavior in the sea anemone Taelia felina. J. Exp. Bio. 53:211-220.

Williams, R.B. 1972. Chemical control of feeding behavior in the sea anemone Deadumene luciae (Verrill) Comp. Biochem. Physiol. 41A:361-371.