

CORALS & THEIR VARIOUS FEEDING  
BEHAVIORS

Alec -

good job; see comments  
within

John

ALEC KLOMAN

DISCOVERY BAY MARINE LAB

JAMAICA, W.I.

MARCH 3, 1980.

## INTRODUCTION:

Some controversy has been raised within the past decade as to whether corals are autotrophic or heterotrophic. Those who are supporters of autotrophy (JOHANNES, COLES & KÜENZEL 1970) believe (a) that the marine zooplankton population is too sparse and too patchy to make up a sizable part of a coral's diet and (b) that the symbiotic zooxanthellae must be supporting the coral by translocation of nutrients. They speculate that corals have retained their feeding polyps merely to obtain trace nutrients, such as phosphorus, from the small numbers of zooplankton that may be caught.

Followers of the heterotrophic hypothesis (Goreau, Goreau and Yonge 1971) believe that the complex feeding polyps found on corals have evolved for other reasons than obtaining trace nutrients. They in fact point out that reef corals in the light take up inorganic phosphorus from the medium, this being a function of the zooxanthellae, not the coral.

At present, the argument is no longer concentrating on finding an "either-or" answer. As Johannes concludes in his paper (Johannes 1974) "Reef corals can obtain nourishment from zooxanthellae, zooplankton, detritus, other corals, and bacteria. The existence of several modes of nutrition in a single species implies a trophic elasticity which would enable it to cope more efficiently with varying conditions of food availability."

In following this line of thought, this paper examines the feeding behavior exhibited by 15 different scleractinian coral species found on the fore reef of Discovery Bay, Jamaica. I describe different methods by which corals capture prey items and place each coral in a 'feeding mode' category, as have Lewis and Price (1975). Each feeding mode is described.

and characterized. Experimentation with both tactile and chemical stimuli were performed as were zooplankton feeding experiments.

## II) METHODS

A) Coral collection: Various corals from various depths (all within 25 meters of the surface) were collected from the fore reef zone of Discovery Bay from February 16-27, 1980. (See Table 1 for list of corals.) The coral samples were placed in individual containers in a moving water aquarium as soon after being sampled as possible. All samples were observed and experimented with, within 2-3 days after capture. Exposure to air and handling was minimized as much as possible.

TABLE 1: CORALS COLLECTED

<i>Acropora palmata</i>	<i>Isophyllia sinuosa</i>	<i>Montastrea carmosa</i>
<i>Agaricia agaricites</i>	<i>Isophyllastrea rigida</i>	<i>Mycetophyllia danaana</i>
<i>Colpophyllia natans</i>	<i>Madracis mirabilis</i>	<i>Mussa angulosa</i>
<i>Dichocoenia stokesi</i>	<i>Meandrina meandrites</i>	<i>Porites astreoides</i>
<i>Enemilia fastigata</i>	<i>Montastrea annularis</i>	<i>P. porites</i>

B) Feeding Behavior: Of the corals collected, some were daytime feeders (had polyps open during daylight) and the others were night time feeders. Feeding experiments were therefore planned respectively for each coral according to when it was active. Live zooplankton sample were obtained mornings (0730-0830) and evenings (1630-1730) and separated in the lab into size categories (<.5mm; 1-2mm; 5-7mm; >10mm) Zooplankton from each size category were pipetted into the water surrounding each coral and resulting activity was observed under a dissecting microscope. For night time feeders, a special "Black Box" was constructed of black polyurethane plastic to keep the corals from being exposed to the overhead lab lights. In addition, a amber filter

was placed over the dissecting scope light source.

C) Mucous Transport Experiments: Using carmin dye suspended in salt water, I was able to watch mucous transport by ciliary movement. The red dye would easily get caught in mucous strands and would readily be ingested by coral polyps.

Using an ocular micrometer, particles caught in mucous strands were measured. Experiments were done with both carmin dye particles and live zooplankton.

D) Chemical Stimulation Experiments: A fairly concentrated hermit crab homogenate was made of four crabs in 30 ml of sea water. The crabs were crushed and the solution was filtered through a  $.45 \mu$  millipore filter. This crab extract was then pipetted in small amounts into water surrounding the corals and results observed under a dissecting scope.

E) Nematocytes: By means of either scalpel or 'Water Pik' pieces of tentacle were obtained from each coral. Each was examined under compound microscope and measured by ocular micrometer.

### III) RESULTS:

Capture of prey items by corals can be classified by three general categories: ① The primary means is tentacle capture. Nematocytes, found under the ectoderm of the tentacle, capture and hold on to prey by means of thin, and sometimes barbed, filaments which can wrap around the prey. ② A secondary method is mucous entrapment; mucous is secreted within the mouth region and spread across the coral surface by means of ciliary transport. Particulate matter becomes embedded in this mucous which can then be sucked into a polyp and ingested. ③ A third method, and one that is fairly rare in occurrence, is entrapment by mesenterial filaments. Thin filaments are extruded from the mouth, capture prey and either withdraw back into the mouth to digest the prey or digest

it outside the oral cavity.

As a general observation, corals can be placed into feeding mode categories. Each mode is determined by what primary means a coral uses to capture prey. (This categorization is adopted from Lewis and Price (1975)) There are three modes: tentacle feeders, mucous feeders and both tentacle-mucous feeders. Each are described below.

A) TENTACLE FEEDERS: Of the 15 sample corals, only three were classified as tentacle feeders - Porites astreoides, P. porites and Madracio mirabilis. This mode is characterized by relatively small polyps (under 2 mm in diameter) and a relatively high clustering of polyps (on average, 28 polyps/cm<sup>2</sup>). Polyps are open both day and night. In general, the smaller polyp size and therefore tentacle length (Porter, 1976) are adaptive to capturing smaller sized prey items. In feeding experiments, nauplii and small copepods (< 5 mm) were caught with relative ease and a high success rate. At the same time, however, larger zooplankton, in the range of 5-10 mm, was also caught and digested.

Special Remarks: P. porites: Larger zooplankton (> 1 mm) are usually caught and subdued by more than one polyp; a 10 mm Cumacean was subdued by four polyps. As prey try to escape, polyps and tentacles contract further thereby strengthening their hold on the prey. Not until the prey has stopped moving, will the polyp begin ingesting or digesting the prey. In cases where the prey is too large for ingestion within the oral cavity, mesenteric filaments are extruded and digestion occurs outside the mouth. This type of digestion is lengthy, occurring over the period of 1-1 1/2 hours.

M. mirabilis. Like the Porites spp., this coral does not seem to be limited to small prey because of its small polyp diameter. While M. mirabilis has larger polyp diameter than Porites spp. and yet has fewer polyps per square centimeter, it is as effective as Porites in capturing zooplankton. When capturing

mesenteric  
filaments

large zooplankton, many polyps participate in capturing and securing the prey, but only one polyp ingests the prey. This is different from Porites spp. where more than one polyp would help digest a large prey item.

B) MUCOUS FEEDERS: This feeding mode is best characterized by Agaricia agaricites and Seropora palmata. It should be noted that all corals produce mucus to some extent. Yet it is only in this mode, where the mucus appears to be the primary method of prey capture. This therefore implies that those species within this category have reduced or 'primitive' tentacles. Both species have very small nematocytes which when compared to nematocytes of other corals in other feeding modes might be an indicator of tentacle use; those tentacles with large nematocytes use the tentacle as a primary means of capturing food, while those with small nematocytes do not rely heavily on tentacle capture.

In experiments done with mucus, it was shown that mucus threads can capture particles smaller than 5 microns and as large as 1.2 mm. Mucus samples taken from both these corals showed large amounts of detritus, centric and pinnate diatoms and flagellated forms. No live zooplankton was observed in the mucus.

Zooplankters of various sizes were put into a container that contained mucus and was allowed to sit for one hour. Afterwards, those zooplankton found caught in the mucus were measured and found to average .18 mm in length with a standard deviation of .12 mm. Those zooplankton found free swimming outside the mucus were found to average .39 mm in length with a standard deviation of .26 mm. Clearly, the mucus is catching the smaller zooplankton and is unable to catch the larger forms.

Special Remarks: A. agaricites: This coral proved to be an enigma since I never saw it feed. It clearly is not a tentacle feeder since it appears unable to use its small tentacles

any these zoo-  
plankton are  
being eaten  
by the coral?  
are they  
sedimenting  
onto coral  
surface?

for much of anything. Zooplankters were frequently seen colliding with tentacles and always escaping. Mucous strands were seen being formed and transported about on the coral surface. Lewis and Price (1975) classified A. agarities as a mucous feeder and by a process of elimination, I have as well.

A. palmata: Lewis and Price place this coral as a mucous and tentacle feeder but I disagree. Aside from the copious amounts of mucous produced, the polyps on A. palmata are at best insensitive to the zooplankton and other organisms in the medium. Much like Agaricia, zooplankton would land on the polyps themselves and not encounter any reaction from the tentacles. Mucous feeding was observed several times. The coral surface of A. palmata is such that there are tall and short polyps. Those seen mucous feeding were always the short polyps.

C) TENTACLE / MUCOUS FEEDERS: This category comprised a majority of the corals collected: Colpophylia natans, Dichrocnia stokesi, Eusmilia fastigata, Isophylia sinuosa, Isophyllastrea rigida, Meandrina meandrites, Montastrea annularis, M. cavernosa, Mycetophylia danaana, and Mussa angulosa. These corals are characterized by a mucous feeding mode during the day and a tentacle feeding mode at night. The feeding polyps of these species are larger in diameter and generally spaced farther apart than those corals in other feeding modes. With this increase in size comes an inability to successfully capture small prey by means of tentacle capture. In most cases, nauplii would be able 'duck' in and out of tentacle range and escape capture. Only the larger, and slower forms of organisms were caught by tentacle capture.

Mucous feeding, which was a primary feeding mode in the daytime, also occurred at night. It appeared as though the tentacles acted as signaling devices to the mouth, telling the mouth when and where to suck in mucous strands. These strands would sometimes get caught around a tentacle, therefore triggering the tentacle much

Did you try this?

filtrate of a ?

the same way a zooplankton would and ingestion would follow. During the day, ingestion of mucus was induced chemically by using a crab homogenate which caused extension of <sup>the</sup> oral region, opening of <sup>the</sup> mouth which caused inward flow of mucus and in some cases tentacle extension. (See part D of Results for more information concerning chemical stimulation.)

Special Remarks: C. natans This coral is characteristic of many in this feeding mode and therefore useful as an example. Colpophyllia is structured such that it has many ridges or septa running along the coral surface. A cross section view is drawn in Figure 1. When carmin dye is injected into these

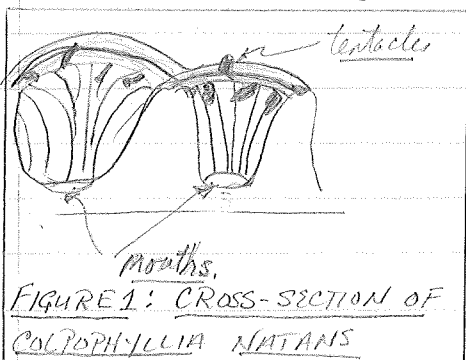


FIGURE 1: CROSS-SECTION OF COLPOPHYLLIA NATANS

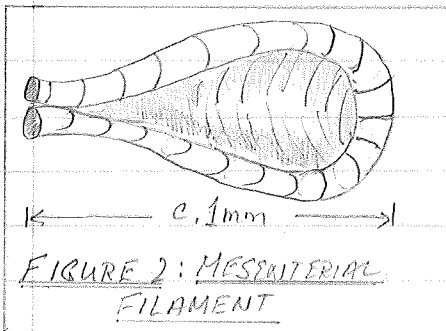
cavities, the particles are swept up towards the top of the septa. In all corals tested, there was this same general pattern of movement away from the mouth region towards the interpolyp spaces. (See part E of Results for more information concerning ciliary movement.) The dye particles get trapped in mucus filaments which lie

on the upper half of the septa. These filaments stay on the septa until the tentacles are triggered by the mucus's presence, at which point the mouth opens and sucks in a large strand of mucus.

As mentioned previously, the tentacles are so widely spaced, relatively speaking, on many of these corals, that many of the small zooplankton ( $< 2\text{mm}$ ) escape. However, large zooplankton are readily caught and ingested. Once the tentacle has secured its prey, the mouth will open towards that tentacle, envelop the prey and take it from the tentacle. In cooperation, the tentacle will bend towards the mouth and help place the prey securely inside the oral cavity.

M. meandrites and E. fastigata: Both these corals are similar to C. natans but have an additional characteristic that is worth while to point out. In both corals, you will find along the tops of the septa mesenterial filaments that originate

from the mouth. A rough sketch of one of these filaments is given in Figure 2 below. These filaments are interesting in that they may provide additional means of nutritive intake for these corals. Several possibilities exist: ① As mentioned before in the case with P. porites, these mesenterial filaments may be digesting the mucous strands outside the oral cavity. In effect, one mouth becomes many mouths. ② Due to the 'loop-like' nature of the filaments, mucous strands or balls may get caught within the loop and be pulled down into the mouth and digested there. (These mesenterial filaments slide up and down the septa, between the coral ectoderm and calcareous skeleton.) ③ In much the same way that tentacles act as signaling devices for the mouth, mesenterial filaments may be doing the same thing only in places where tentacles can't reach, namely the ridge tops of the septa.



As to which of these three possibilities is correct, no one seems to be sure. Mention of these filaments in the literature is rare and by many authors regarded as insignificant. Yet, over the period of 8 days, I saw in three separate occasions, mesenterial filaments at work, which suggests to me that they play more of a role in coral digestion than

some people are willing to admit. In fact, these filaments provide an interesting solution to the paradox of ciliary movement of mucous, a subject that will be dealt with in the Discussion Section.

M. angulosa: This coral specimen as well as some others in this category (Sorphyllia sinuosa, Sorphyllastrea rigida and Mycitophyllia danaana) all exhibit slow, slink-like movement. Reactions to zooplankton and mucous filaments are slow and time consuming. Such reactions provide a neat contrast to the smaller and very quick polyps on species such as P. porites and M. mirabilis.

The next three sections consider various general observations as they relate to each of the three feeding modes as a whole. Part D deals with tentacle feeding and the responses of tentacles to both chemical and tactile stimulation. Part E is based in part on observation and in part from a paper that concerns ciliary movement and the paradox of this ciliary movement. Finally, Part F concerns those majority of corals which are both mucous + tentacle feeders.

D) TENTACLE FEEDING: Those polyps which use tentacles to capture prey go through what can be called a 'preparatory phase.' (Lewis and Trice call it "preparatory feeding posture") When food is sensed to be near-by, there is an extension of the polyps and tentacles; the oral disc expands and begins to produce mucous. When the prey is caught, a general contraction occurs. Two things are of interest: By what means do polyps "sense" near-by foods and by what stimuli do polyps contract? Goreau et al (1971) state that corals have a perceptible chemotactic sense and are able to detect low concentrations of glycine, alanine and phenylalanine. In my experiments with crab extract, I was able to elicit two types of reactions: ① opening and eversion of the stomodeum and ② opening and eversion of stomodeum along with extension of the tentacles. Results of experiments are in Table 3. Out of the 12 corals tested, 10 reacted in one way or another which strongly suggests that most coral polyps have a chemotactic sense.

The second question, 'what causes contraction,' is answered simply by observing feeding by polyps. Any sort of movement, whether by a zooplankton or a metal prodding rod, will cause the tentacle and polyp to contract. Usually, the stronger the force the farther the contraction.

E) MUCOUS TRANSPORT: There is no one polyp shape or form but for my purposes in this section it is allowable to consider a generalized polyp form because in dealing with ciliary

TABLE 2: CORAL POLYP MEASUREMENTS

SPECIES NAME	AVERAGE POLYP DIAMETER (MM)	AVERAGE NUMBER OF POLYPS / CM <sup>2</sup>	NUMBER OF TENTACLES PER POLYP	FEEDING MODE
ACOROPORA PALMATA	~1	29.8	12	MUCOUS
AGARICIA AGARICITES	1.3	15.5	IRREGULAR	MUCOUS
COLPOPHYLLIA NATANS	IRREGULAR	<1	IRREGULAR	TEN. & MUCOUS
DICHOCDENIA STOKESI	3.4	2.5	IRREGULAR	TEN. & MUCOUS
EUSMILIA FASTIGATA	IRREGULAR	<1	IRREGULAR	TEN. & MUCOUS
ISOPHYLLIA SINUOSA	3.5	<1	IRREGULAR	TEN. & MUCOUS
ISOPHYLLASTREA RIGIDA	IRREGULAR	<1	IRREGULAR	TEN. & MUCOUS
MADRACIS MIRABILIS	1.96	19	IRREGULAR	TENTACLE
MEANDRINA MEANDRITES	IRREGULAR	~1	IRREGULAR	TEN. & MUCOUS
MONTASTREA ANNULARIS	1.5	9	IRREGULAR	TEN. & MUCOUS
M. CAVERNOSA	3.7	2.5	IRREGULAR	TEN. & MUCOUS
MYCETOPHYLLIA DANAANA	IRREGULAR	<1	IRREGULAR	TEN. & MUCOUS
MUSSA ANGULOSA	IRREGULAR	<1	IRREGULAR	TEN. & MUCOUS
PORITES ASTREOIDES	1	37	12	TENTACLE
P. PORITIS	1.3	29.5	12	TENTACLE

- POLYP DIAMETER: A line of length from base of tentacles, across mouth region, to base of tentacle on far side.
- IRREGULAR: In the case of polyp diameter, irregular means polyp sizes varied so much that an average would be meaningless. The same is true with # of tentacles in that each polyp would have a wide range of tentacles that an average would be meaningless.

TABLE 3: RESULTS OF CHEMICAL STIMULATION

OPENING AND EVERSION OF STOMODEUM	OPENING + EVERSION OF STOMODEUM, EXTENSION OF TENTACLES
MADRACIS MIRABILIS	MONTASTREA CAVERNOSA
DICHOCDENIA STOKESI	ISOPHYLLASTREA RIGIDA (TENTACLES ONLY)
MYCETOPHYLLIA DANAANA	MUSSA ANGULOSA
PORITES PORITES	MONTASTREA ANNULARIS
PORITES ASTREOIDES	COLPOPHYLLIA NATANS

NO REACTION

ISOPHYLLIA SINUOSA

AGARICIA AGARICITES

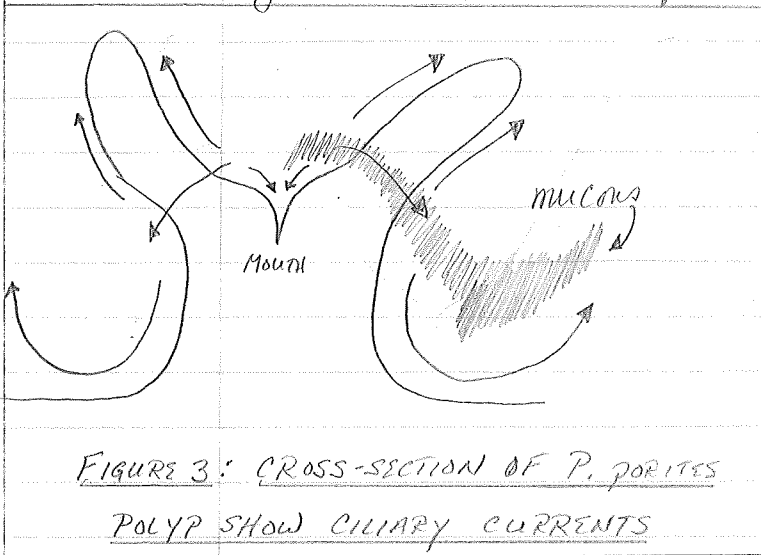
NOT TESTED

EUSMILIA FASTIGATA

ACOROPORA PALMATA

Time of stimulation?

movement, all sorts of generalizations can be made. Consider a Porites porites feeding polyp, a cross-section of which is drawn in Figure 3. (Figure taken from Lewis & Price (1976)) By suspending a



solution of carmin dye particles in the water near the coral, ciliary movements are easily seen. In all the corals tested, the same basic patterns hold true. Currents flow away from the oral cavity, either out along the tentacles or between them. Near the mouth, cilia beat towards the mouth but this is a small proportion of the overall ciliary movement. Particles that get caught in inter-polyp spaces usually get caught in mucous

filaments and are threaded off the coral. Obviously mucous will go wherever the cilia move it and in all cases this is away from the mouth. It is clear, therefore, that the purpose of the cilia is to transport mucous all over the coral surface.

F) MUCOUS & TENTACLE FEEDING: An interesting question to be asked with these corals is "Can the tentacle feeding mode which regularly occurs at night be induced to occur during the day?" A question like this has some significance which will be discussed in the Discussion section. Of the corals tested with the crab Homurgaster, the mucous-tentacle feeders that opened during the day were: Mycitophyllia danaana, Isophyllostrea rigida, Mussa angulosa, Dichocoenia stokesi, Colpophyllia natans, Montastrea cavernosa.

#### IV) DISCUSSION:

One reasonable place to start discussing coral feeding behavior is with what there is in the water to eat. It is well documented, both by papers and my experience trying to collect zooplankton, that zooplankton are not abundant. Demersal zooplankton keep a low profile during the day and emerge after sunset to migrate up the water column. Therefore during the day, most zooplankton are to be found near the ocean floor, while at night abundancy levels would be highest at some depth between the surface and the bottom.

Another food source thought to be utilized by corals is suspended particulate matter. This food source is estimated to be much more abundant and reliable than zooplankton. Marshall (1972) has shown that the amount of fine suspended organic particulate matter in the waters of Eniwetok Atoll was between one to two orders of magnitude greater than what could be collected by the finest sampling nets. Since zooplankton is in such small quantities, suspended particulate matter might make up a large portion of food resources.

DOM?

To my knowledge, no one has come up with any other potential food resources corals might be using. The problem that is posed to coral polyps is this: "What is the most efficient way to capture <sup>these</sup> seemingly sparse resources?" The answer to this question appears to be one of three things.

Those corals that limit themselves strictly to tentacle capture generally have their polyps open day and night and therefore feed around the clock. Their smaller polyp diameters enables them to successfully catch the smaller organisms that can more easily escape from the larger polyped corals. Yet by no means are these corals restricted to small prey; larger prey are caught as well.

Then there are the mucous feeders, which tend to feed primarily by ingestion of mucous filaments. These corals also feed

day and night, like the tentacle feeders, but appears to be catching smaller prey items. Mucous nets can catch microscopic particles (1-100  $\mu$ ) (Lewis, 1977) as well as macroscopic particles and zooplankton under 1.2 mm. This suggests that some sort of resource partitioning is occurring; tentacle feeders concentrate on larger particles while mucous feeders concentrate on smaller particles. In a medium where potential zooplankton availability is low, partitioning resources this way would make a great deal of sense.

A combination of both feeding modes would certainly be adaptive because of the increased potential food availability. Not only do these corals catch small particles during the day in their mucous nets, but also catch zooplankton as they migrate up and down the water column at sundown and sunrise. Exactly two-thirds of the corals collected <sup>in this project</sup> followed this feeding mode, which can certainly be used as evidence in arguing that the mucous-tentacle feeding mode is more efficient in terms of food caught than the two other feeding modes.

In fact, even these mucous-tentacle feeders can open up their polyps to feed by tentacle during the day. If a large number of zooplankters happen to drift by, it seems as though many of these corals will respond to chemical stimuli by opening & extending their mouths and sometimes even extrude their tentacles. In other words, these corals are trying to make the best of the situation in which they live.

An interesting problem arises when considering the ciliary movements which transport mucous filaments on the coral surface. As pointed out earlier, the basic trend of these currents is to carry mucous away from the mouth. If, however, corals are to be deriving nutritive value from particles caught in the mucous, it seems paradoxical that mucous is moving away from the mouth instead of towards the mouth. From the drawing on page 11, one can see that a small percentage of cilia create

current directed towards the mouth. In many cases, this small current can not overcome outwardly directed currents and as a result the mucous threads never make it into a polyp mouth.

One conclusion that can sensibly be made here is that mucous is not primarily to be used as a substance which is later to be digested. Perhaps its major role is to keep the coral surface free from detritus and sediment that is always settling on corals. It has been documented that layers of detritus or sediments greatly decrease the ability of the zooxanthellae to photosynthesize and this in turn affects the coral host. (See Rogers, 1974) Such a hypothesis has interesting implications. If, for example, mucous feeding occurred only seldomly, which appears to be the case in Agaricia agaricites, one might expect Agaricia spp. to have higher numbers of zooxanthellae to help offset the small amounts of nutrition being supplied by the mucous. A hypothetical case or example might be helpful. (See Figure 4)

If we assume that total energy needs were the same for different corals, (certainly an unwarranted assumption)

FIGURE 4: HYPOTHETICAL ENERGY BUDGET

FEEDING MODE	% ENERGY SUPPLIED BY POLYPS	% ENERGY SUPPLIED BY ZOOXANTHELLAE	TOTAL ENERGY
TENTACLE	X	100 - X	100%
MUCOUS	Y	100 - Y	100%

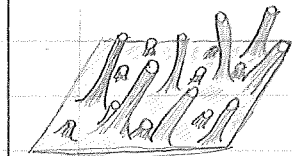
and if we assume that X and Y are equal, then one would expect that the percentage of energy supplied by the zooxanthellae would be equal in both cases as well. However, if as I have suggested, the percentage of energy supplied by mucous feeding (Y) was less than (X), the balance would have to be made up by additional zooxanthellae.

Of the corals in the mucous feeding mode, this might very well be the case with A. agaricites. However, A. palmata seems to have evolved a polyp morphology that is adaptive to taking more of an advantage from mucous. The surface of

A. palmata has both tall and short polyps, as shown in Figure 5.

FIGURE 5: ACROPORA PALMATA

CORAL SURFACE



Many of the short polyps lie flush with the coral surface. If a film of mucus covers the coral surface, these short polyps will always be 'embedded' in mucus and will be

able to suck mucus in just by opening the polyp mouth. As pointed out on page 6, this was seen happening many times.

Another means of digesting more mucus than what comes through the mouth, is the use of mesenteric filaments found on Eusmilia fastigata and Meandrina meandrites. (see pages 7-8)

My final print is an attempt to assess the differing capture rates of tentacles on different species of corals. One method of doing this is to repeat the feeding experiments done by Lewis and Price (1975) which was to count zooplankton before and after coral feeding. Those corals with high numbers of zooplankton left over were assumed to have a low capture rate while those with a low number of zooplankton had a high capture rate.

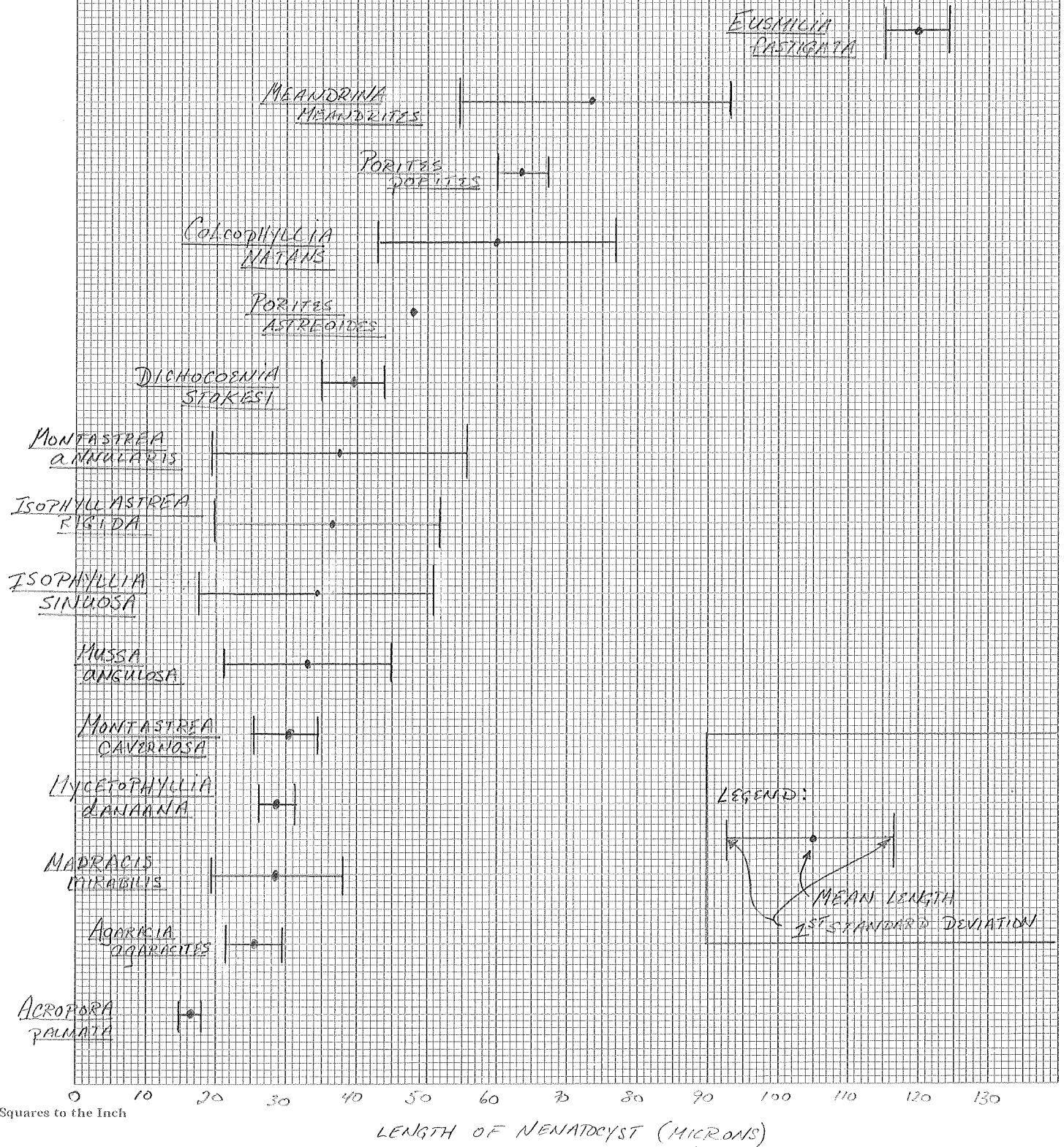
What I have done is to look at the length of nematocytes found in various tentacles. A correlation between nematocyte length and capture rate obviously assumes that the two are somehow connected and I don't think this is too far fetched: a long filament can wrap around prey items many times thus insuring a good grasp whereas a shorter filament can wrap around a prey item fewer times and have less of a hold.

The results are found in Figure 6. There are some interesting points that appear to back up the hypothesis that increasing length of nematocytes confers greater capture rate.

- a) The corals found on the bottom end of the scale, namely A. palmata and Agaricia agaricites, are what I've called mucus feeders. (ie. they don't use their

This belongs  
in "Prepareds"  
section

FIGURE 6: NEMATOCYST LENGTHS.



tentacles.) If these corals rely on mucus and not their tentacles to capture prey, one would almost guess that they would have smaller tentacles and smaller nematocytes.

- b) The three corals at the upper end of the scale, Eusmilia fastigata, Meandrinia meandrites and Porites porites, are those corals that I would rate having the highest success rate of prey capture. I base this totally on my observations of coral feeding and have no quantitative evidence to support it.
- c) The corals found in between the corals mentioned in (a) and (b) are corals that have neither great success nor poor success capturing prey. They comprise a grey area from which nothing qualitative can be drawn without substantial quantitative data.

Drawings of the various nematocytes are found at the end of the paper.

#### V) CONCLUSION & AREAS OF FURTHER INTEREST

This paper contains observations and results of experiments done on 15 different species of stony corals found on the fore reefs of Discovery Bay. It describes three basic feeding behaviors and suggests that these behaviors are an attempt at partitioning sparse food resources. Tentacle feeding and mucous feeding are examined with particular emphasis on answering the question "How is each method specifically adapted to dealing with the resource it is trying to capture?" For the tentacle feeders, chemical stimuli from nearby organisms put the feeding polyp into a preparatory phase which might increase the likelihood of capturing the organism. For the mucous feeders, the physical nature of the mucus itself and its ability to retain small particulate matter is in itself adaptive. Mucous is capturing "food" particles that are smaller and far more abundant than zooplankton.

In doing all of this, this paper has raised more questions

than have been answered. What follows below are four areas of future investigation, two of which stem directly from evidence in this paper, and two of which are of general interest.

- ① If my hypothesis about the paradox of ciliary movement on mucous feeders is correct, one would expect to find more zooxanthellae per unit area <sup>in mucous feeders</sup> than in other corals. Is this so? Can any basic trends concerning zooxanthellae/unit area be made about various corals at differing depths?
- ② Is the hypothesis of nematocyst length and capture rate being some how related correct? Simple feeding experiments would begin to answer this question.
- ③ Do polyp morphologies vary with increasing depth? Does one feeding mode begin to predominate as others diminish?
- ④ Do various coralline structures reflect respective feeding modes? If not, what could be the possible explanation for such diverse shapes and forms?

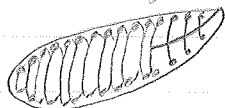
Good

-19-

# NEMATOCYST SKETCHES

(lengths given are averages)

① Agaricia agaricites



← 25.4  $\mu$  →

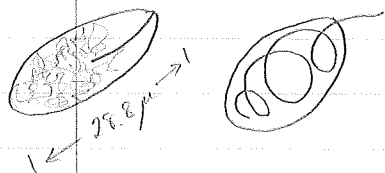
② Acropora palmata



← 16.8  $\mu$  →

- could see no filament

③ Madracis mirabilis



← 28.8  $\mu$  →

④ Porites astreoides



← 48  $\mu$  →

⑤ Mussa anguloba



← 33.1  $\mu$  →

⑥ Montastrea annularis



← 37.4  $\mu$  →

⑦ Isophyllastrea rigida



← 36.2  $\mu$  →

ALSO Montastrea cavernosa  
( $\bar{x}$  = 30.2  $\mu$ )

⑧ Dichocoenia stokesi



← 39.4  $\mu$  →

⑨ Meandrinha meandrius



← 73.7  $\mu$  →

ALSO Colpophyllia natans  
( $\bar{x}$  = 60  $\mu$ )

⑩ Mycetophyllia danaana



← 28.8  $\mu$  →

ALSO Eusmilia fastigata  
( $\bar{x}$  = 120  $\mu$ )

## REFERENCES

- ① Goreau T.F., Goreau, N.I., and Yonge C.M.; "Reef Corals: Autotrophs or Heterotrophs?" Biol. Bull. Mar. Biol. Lab. Woods Hole (1971) 141(2): 247-260
- ② Johannes R.E. "Sources of Nutritional Energy for Reef Corals," Proc. of 2<sup>ND</sup> Internat'l Coral Reef Sym. Oct. 1974
- ③ Johannes R.E., Coles S.L., Keenzel, N.T. "The Role of Zooplankton in the Nutrition of some Scleractinian Corals," Limnol. & Oceanog. vol. 15, no. 4 pp. 579-586.
- ④ Lewis, J.B. "Suspension Feeding in Atlantic Reef Corals, and the Importance of Suspended Particulate Matter as a Food Source." Proc. of 3<sup>RD</sup> Internat'l Coral Reef Sym. May 1977.
- ⑤ Lewis, J.B. & Price, W.S. "Feeding Mechanisms and Feeding Strategies of Atlantic Reef Corals." J. Zool., London (1975) pp. 527-544.
- ⑥ ———, "Patterns of Ciliary Currents in Atlantic Reef Corals and their Functional Significance" J. Zool., London. (1976) 178: 77-89.
- ⑦ Marshall, N., Parrish, J., Ball, M.L. "A Technique for Collection of Particulate Organic Matter in situ." Mar. Biol. (1972) 12(3): 194-195.
- ⑧ Porter, J.W. "Autotrophy, Heterotrophy and Resource Partitioning in Caribbean Reef Building Corals," American Nat'l list Sept-Oct. 1976.
- ⑨ Rogers, C.S. "A Comparison of the Metabolic Rates of Stressed and Unstressed Colonies of Agaricia agaricites" OTS Project done at DBML (1974).