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ZOOPLANKTON FEEDING

BY THE CARIBBEAN REEF-BUILDING CORAL

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SUMMARY

The feeding behavior and digestion rate of the Caribbean reef-building coral, *Montastrea cavernosa*, is described as well as a method for the *in situ* extraction of coral gut contents. Guts were extracted two hours after sunset from *M. cavernosa* on coral reefs in San Blas, Panamá. Zooplankton found in the guts of *M. cavernosa* include: copepods, amphipods, nemerteans, turbellarians, polychaetes, nematodes, appendicularians, salps, miscellaneous eggs, and the larvae of decapods, copepods, polychaetes, cirripedes, bryozoans, and corals. Most of the eaten plankters both by number and by weight are near bottom either demersal (truly bottom dwelling) or meroplanktonic (settling to the bottom at some time in the life cycle), and are preyed upon heavily by corals as they come up off the reef at sunset and presumably also as they settle down at dawn.

The zooplankton captured by the coral during the two hour period just after sunset contributes an average of between 1 μ g. dry weight and 75 μ g. dry weight per polyp per night on the seven nights sampled. As a cautious estimate, this amount represents between 0.2 per cent and 11 per cent of the total daily energy requirement of the coral (based on published respiration and caloric conversion rates) in this two hour feeding period alone.

Only a weak correlation exists between the amount or kind of zooplankton collected in plankton tows made just after gut extraction and the zooplankton found in the gut. There are several reasons for this: (1) the analysis of the degree of digestion of the zooplankton in the guts indicates that most of the feeding occurs at sunset, two hours before the gut sampling or plankton tow, (2) many of the zooplankton in the guts are demersal and would therefore not be captured in a net towed well above the reef, and (3) these long tentacled corals are extremely effective at capturing zooplankton that might bump into and swim away from a net.

Based on the highly variable amount of zooplankton in the guts, and the highly variable amount of zooplankton in the water, corals are probably extremely flexible in their utilization of zooplankton as a source of energy. Since most of the zooplankton in the gut comes from the reef itself, the results point to a tight recycling of nutrients and biomass within the coral reef ecosystem.

I. INTRODUCTION

Recent advances in the biology of reef-building corals are revealing the startling complexity of this group of animals. Unique from an ecological point of view is the fact that not only do hermatypic corals defy easy classification as functionally plants or animals, but also they occupy almost every trophic level of tropical marine ecosystems. Basically, they are functionally non-conformists to current concepts of taxonomic and ecological classification.

Their multi-trophic capabilities are appearing wherever new lines of investigation are initiated. Because they utilize plant products (Muscantine and Cernichiari, 1969; Trench, 1971a, b, and c; Lewis and Smith, 1971) corals must be thought of as herbivores (Odum and Odum 1956; Hand, 1959).

They are capable of eating and utilizing zooplankton (see below), and are therefore secondary consumers. They are capable of eating each other in both the adult (Lang, 1970) and the larval (see below) form, and eating carnivorous zooplankton. They are therefore tertiary consumers. Recent evidence suggests they are capable of digesting bacteria (Disalvo, 1971; Sorokin, 1972) and of absorbing glucose and free amino-acids from the water (Stephens, 1962, 1967). Some species are possibly also deposit feeders, having been observed with their mesenterial filaments extruded into reef sediments (Goreau *et al.*, 1971). The importance of their symbiotic algae in reef photosynthesis also puts them functionally as part of a primary producer unit.

It seems reasonable that each of these abilities for nutrient or calorie procurement is capable of

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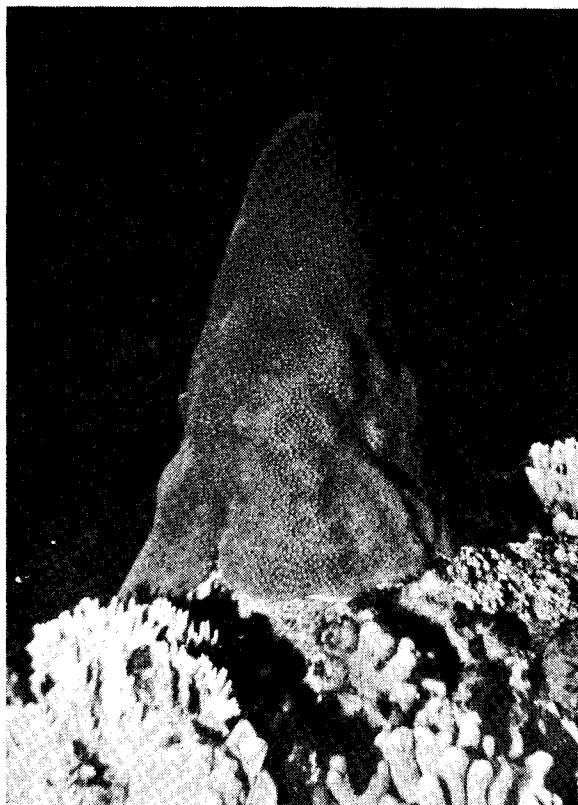


Figure 1: *Montastrea cavernosa*, massive columnar form one meter in height at 18 m depth off Salar, San Blas, Panama.

enhancing survival in the nutrient poor tropical oceans surrounding coral reefs. The question becomes what is the relative contribution of each of these (and other) methods, and does the contribution change or remain constant in different localities and at different times? Finally, do these methods account reasonably well for the overall energy-metabolic requirements of the coral?

We do not yet have the information to answer these questions. In this paper, however, I will attempt to make qualitative and cautious quantitative estimates of one of these methods, feeding on zooplankton, and its potential contribution in meeting the daily energy requirements of the Caribbean coral *Montastrea cavernosa* (Linnaeus) (Fig. 1). Its feeding behavior will be described as well as the first evidence for actual zooplankton feeding.

II. MATERIALS

All experiments reported here were conducted on Ulacsucun Reef (9 deg. 32' 48" N; 78 deg. 58'

42" W), a semi-protected area behind the San Blas Islands on the Atlantic coast of Panama. The San Blas reefs are amongst the richest in the Caribbean in terms of both the number of coral species present and the high abundance of living coral on the reef (Porter, 1972a). There exist at least 49 hermatypic and 16 ahermatypic scleractinian coral species (Porter, 1972b), roughly 95 per cent of those described from the Caribbean region as a whole. Constructional coral reefs can be found between the surface and 40 metres where the bottom grades into a sand-mud bottom.

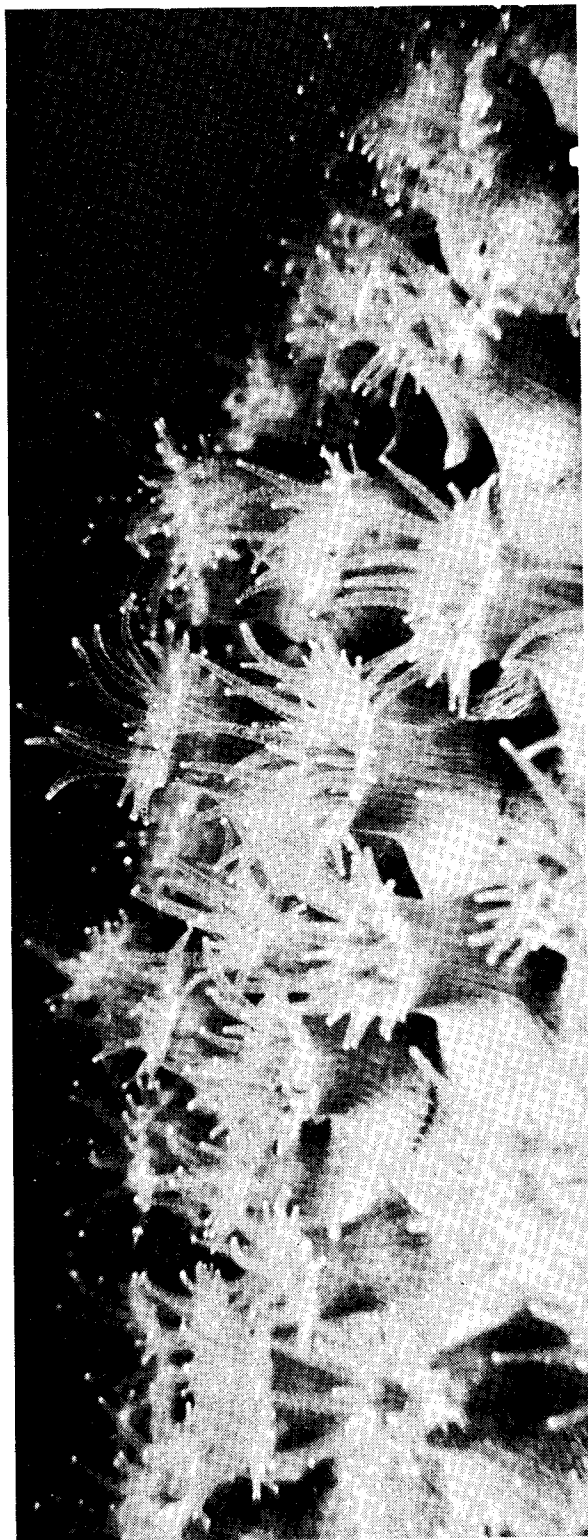
The Caribbean scleractinian coral species vary considerably in both their skeletal and soft-part morphology. *Montastrea cavernosa* was chosen for the zooplankton feeding studies because it has many large, distinct polyps with long tentacles (Fig. 2). Laboratory and field observations have shown it to be extremely effective at capturing zooplankton artificially attracted near it by lights at night, and it seemed a reasonable candidate on the basis of its long tentacles alone. Gut sampling to be described below, was made more efficient by the large number of polyps on each head, each discrete polyp being a distinct sample. Numerous small heads of *M. cavernosa* are common in San Blas, negating the necessity to use the same head twice during different experiments. *M. cavernosa* is easily kept in the laboratory under flowing seawater conditions.

M. cavernosa is an important reef-builder found from the Atlantic coast of Africa (Gravier, 1909) to the Caribbean. In San Blas, it has at least two polymorphic forms (Lehman and Porter, 1973), a large polyped form (polyps 0.92 cm. in diameter; expanded tentacle length usually 2 x's the polyp diameter), and a small polyped form (polyps 0.48 cm. in diameter; tentacle length 0.75 x's the polyp diameter). The experiments and observations described here were done exclusively on the long tentacled form (Fig. 2) unless otherwise noted.

III. METHODS

Montastrea cavernosa was observed under a variety of natural and laboratory conditions. Underwater observations were made with SCUBA both day and night at different depths to determine its feeding behavior and daily activity pattern. Small colonies between four and ten cm. in diameter were collected from between one to five metres on Ulacsucun Reef and without exposure to air transferred to a 300 litre glass aquarium for observation. The corals were placed back on the reef after observations where they could be collected again if necessary. Corals were handled in this way for over a year without visibly deleterious effects.

To determine the effectiveness of feeding, *M.*



cavernosa colonies were placed in the aquarium in the laboratory at night and fed concentrated suspensions of zooplankton. The zooplankton was collected in shallow water tows made over neighbouring reefs several minutes before feeding observations were begun.

An *in vitro* feeding experiment was also conducted to provide a base line for interpreting the degree of digestion of the plankton extracted from the gut in later experiments. Coral colonies were brought into the lab and maintained in filtered sea water for 24 hours prior to feeding. After sunset, when the tentacles of the coral were fully expanded, the head was transferred to a small glass bowl without exposure to air and after a half hour acclimation period a concentrated suspension of newly hatched and adult brine shrimp with some unhatched eggs poured in gently; the coral was allowed to feed for five minutes. The brine shrimp were rinsed away with filtered seawater and the head transferred into a large tank. The contents from ten randomly chosen polyps were extracted with a No. 13 Gauge Yale Hypodermic Syringe (needle diameter 2 mm.). The blunted needle was inserted into the gastrovascular cavity of each polyp through its mouth and the contents of the stomach were slowly extracted until the column wall and the oral disc collapsed over the skeleton (Fig. 3). This produced between one and two ml. of gut contents which were then injected into separate Vacutainer test tubes. These had been injected with five ml. of seawater formalin to stop the digestion and preserve the sample; the resulting volume represented a 5-10 per cent formalin solution. As a check for contamination, control aliquots of similar volume were collected from the water immediately in front of the extracted polyp to detect any external zooplankton which might be sucked into the gut from the outside during the gut extraction. Sampling of polyps and surrounding water was repeated at intervals up to two hours after the feeding pulse.

In situ collections of gut contents were made on seven nights at 8.30 P.M. (approximately two hours after sunset) which several all-day and all-night net tows had established as near the peak of plankton density in the San Blas. This nocturnal plankton abundance maximum appears to be similar at several other shallow water Caribbean localities as well (Kuenzel, 1972; Glynn, in press). An *M. cavernosa* head was rapidly located at approximately 10-13 m. on the reef and immediately tapped firmly to close the polyps and thereby pre-

Figure 2: *Montastrea cavernosa* expanded at 8.00 P.M. for nocturnal feeding. Each polyp is roughly one centimeter in diameter with tentacles one to two times this in length. (San Blas, Panamá).

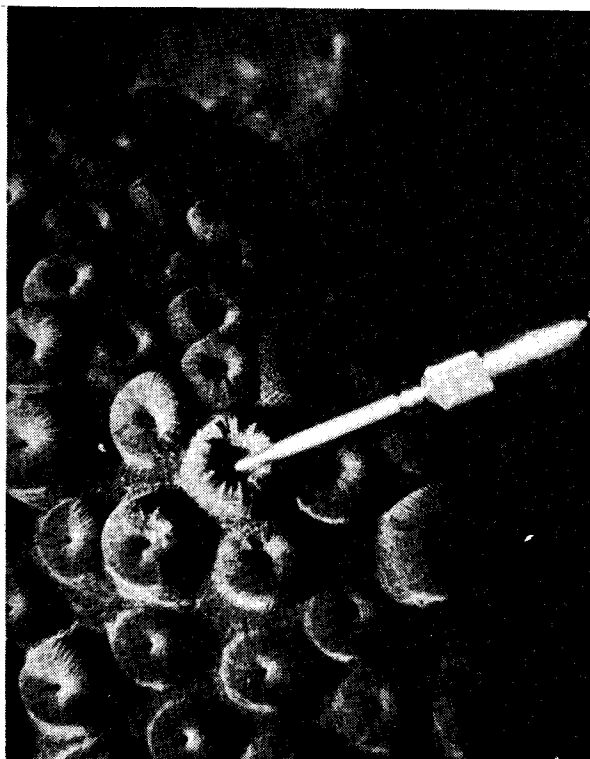


Figure 3: *Montastrea cavernosa* heads were tapped to make them close fully and the gut contents removed with a hypodermic syringe. Note that the column wall and the oral disc collapse over the skeleton after the contents have been removed.

vent gut enrichment by zooplankters attracted to the lights. Gut contents were then extracted from approximately 100 polyps randomly chosen from the entire surface of the head. At the same time, an equal number of controls were syringed from the shell of water one to two cm. around the head. Afterward, a plankton tow was made in the vicinity of the sampled head to collect the zooplankton from this region. The net was 0.5 m. in diameter, had a 2.0 m. long sock, was made of 160 μ mesh nylon, and was equipped with a Harvey flow-meter which recorded directly the volume of water passing through the net. It was pushed for 33 m. parallel to the 13 m. depth contour about one metre above the bottom, and passed directly over the sampled coral head. The divers shined their lights back and forth rapidly to minimize the enrichment of the tow with plankton attracted to the light. Finally, a 13 m. vertical plankton haul was taken above the sample reef. One day collection was made at 1.00 P.M. on a specimen whose polyps were not expanded for feeding.

The samples were stained with 1 per cent aqueous Eosin-Y, a non-specific stain for animal tissue other than chitin, and Alcian Blue, a stain for mucus. The samples were individually filtered onto 1.2 μ pore Millipore filters under five mm. Hg vacuum, and without rinsing or drying, transferred to glass slides. The gridded, 25 mm. diame-

ter filters were aligned on a drop of polyvinyl lactophenol, an embedding resin that does not require dehydrated specimens, two more drops pipetted on top, and a thin cover slip of similar diameter added. It was found that any sort of drying or dehydrating destroyed the already partially digested zooplankters beyond recognition. The edges of the mount were sealed with clear nail polish. The prepared filters cleared unpredictably. Where large amounts of mucus were present, the samples were filtered a drop at a time, often with a change of filters if clogging occurred.

Control and experimental filters were scanned at 35 X magnification, and most organized structures, remnants of coral polyps, zooplankton, and mucal blobs were examined at higher power (100 X to 200 X), with a few squares examined under oil immersion. Everything that had been ingested by a polyp was measured and classified taxonomically as accurately as possible with a note on its state of digestion. The dimensions were used to estimate the organism's volume and by further extrapolation, its caloric content (Johannes *et al.*, 1970; Cummins and Wuycheck, 1971).

Plankton tows were split using a Riggs plan-kton splitter. Generally 0.125 of the tow was counted, representing approximately 0.83 m³ of reef water. The tow plankton was stained with Eosin-Y, Alum-Cochineal, and Alcian Blue so that crusta-

ceans stained red, forms without exo-skeletons turned purple, and mucus stained blue. The plankton was counted and measured on a gridded Sedgwick-Rafter counting cell under 35x to 200x magnification.

IV. RESULTS

Montastrea cavernosa is a voracious carnivore. From the field and tank observations, it seems reasonable that it is one of the most effective zooplankton feeders in the Caribbean. As with many other coral species in the Caribbean, *M. cavernosa* is most commonly expanded at night (Fig. 2) and closed during the day (Fig. 4; Table I). Occasionally it can be observed expanded during the day as well (Fig. 5). During the day in San Blas, approximately 5 per cent of the *M. cavernosa* heads are partially or fully expanded. These colonies have a number of things in common: (1) they are generally the short-polyped morph (Fig. 5), (2) they are generally the ones in more shaded or protected parts of the reef, (3) they are usually the same ones expanded day after day, regardless of cloud cover,

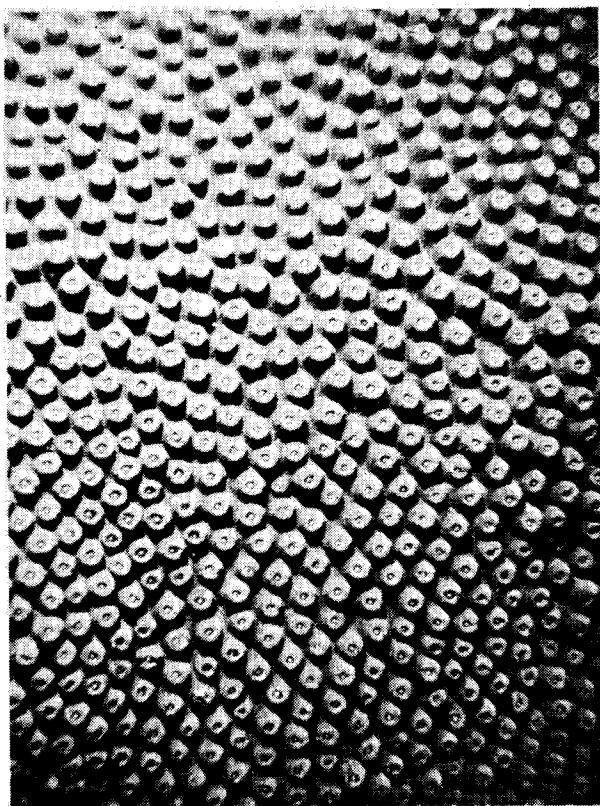


Figure 4: *Montastrea cavernosa* at 11.00 A.M. contracted during the day. Note, however, several polyps partially open in the bottom center of the photograph.

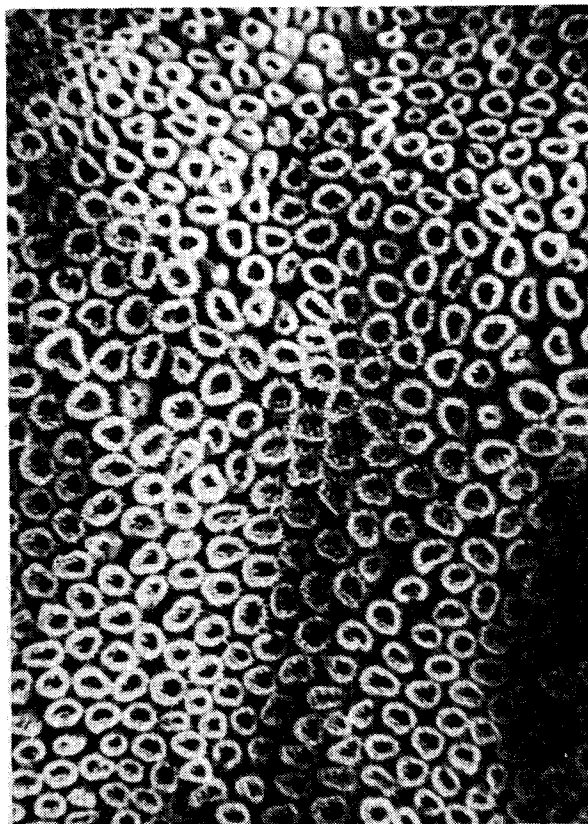


Figure 5: Small polyped morph of *Montastrea cavernosa* at 11.00 A.M. fully expanded. Note the several states of contraction in several of the polyps near the centre and top of the photograph.

and (4) they are expanded at night as well. These therefore represent a segment of the population which is constantly expanded. The other coral species listed in Table I vary considerably in their similarity to this pattern and generalizations are difficult and perhaps misleading to make. There is also some variation in individual *M. cavernosa* heads from day to day in the extent of tentacle expansion and also in the relative extension of different polyps on the same head (Figs. 4 and 5). In Fig. 4, several polyps in the bottom centre of the photograph can be seen to be partially expanded while the others are more tightly closed. Even in the pictured "closed" position, however, the slit of the mouth will remain open unless disturbed by mechanical or chemical stimuli of a noxious nature. When the mouth slit is open, the polyp sustains a pumping motion by expanding and contracting the oral sphincter. Under the microscope, fine particles of carmine could be seen sucked into and exhaled gently from the gastric cavity.

M. cavernosa was observed during the day by

Table I Expansion Periods of Caribbean Corals

Species	Diurnal Activity ^a	Nocturnal Activity ^b	Colony Form	Polyp Size
<i>Stephanocoenia michelinii</i>	1	1	massive	medium
<i>Madracis decactis</i>	2	1	columnar	small
<i>Madracis mirabilis</i>	1	1	ramose	small
<i>Acropora palmata</i>	1	1	palmate	small
<i>Acropora cervicornis</i>	1	1	ramose	small
<i>Acropora prolifera</i>	1	1	ramose	small
<i>Agaricia agaricites</i>	4	1	plating	small
<i>Agaricia lamarcki</i>	4	1	plating	small
<i>Siderastrea siderea</i>	4	1	nodose	medium
<i>Siderastrea radians</i>	5	1	nodose	medium
<i>Porites asteroides</i>	2	1	nodose	small
<i>Porites furcata</i>	1	1	ramose	small
<i>Favia fragum</i>	5	1	nodose	medium
<i>Diploria clivosa</i>	3	1	encrust.	medium
<i>Diploria strigosa</i>	4	1	nodose	medium
<i>Diploria labyrinthiformis</i>	4	1	massive	medium
<i>Manacina areolata</i>	5	1	nodose	medium
<i>Colpophyllia natans</i>	5	1	massive	medium
<i>Montastrea annularis</i>	4	1	massive	medium
<i>Montastrea cavernosa</i>	4	1	massive	large
<i>Meandrina meandrites</i>	5	1	nodose	large
<i>Dichocoenia stokesii</i>	5	1	nodose	medium
<i>Mussa angulosa</i>	5	1	nodose	large
<i>Scolymia lacera</i>	5	1	solitary	large
<i>Scolymia cubensis</i>	4	1	solitary	large
<i>Isophyllia sinuosa</i>	5	1	plating	large
<i>Isophyllastrea rigida</i>	5	1	nodose	large
<i>Mycetophyllia lamarckiana</i>	5	1	plating	large
<i>Eusmilia fastigiata</i>	2	1	ramose	large
<i>Millepora</i> spp.	1	1	ramose	small

(1) Most fully expanded (2) most partially expanded (3) ten percent or fewer fully expanded (4) ten percent or fewer partially expanded (5) most colonies contracted.

a) Observations at 11:00 A.M. on 50 different days, August, 1971 to July, 1972, Islas San Blas, Panama.

b) Observations at 8:30 P.M. on 30 nights, August, 1971 to July, 1972, Islas San Blas, Panama.

sitting in front of a colony and watching for polyp closure of the expanded polyps as a sign of food capture. No closure was observed, but occasionally a tentacle could be seen to twitch onto the mouth, and straighten out within 5 to 10 seconds.

These observations were repeated on the reef at night using SCUBA and 88,000 candlepower flashlights. The lights were trained onto the coral head and the interaction between the coral and the artificially attracted zooplankton observed. The *M. cavernosa* ate every visible zooplankton that collided with it and occasionally individual tentacles could be seen to follow after and intercept a moving zooplankton. All zooplankters visible to us were eaten: copepods, mysids, crab zoea, ostracods, isopods, and other crustaceans, chaetognaths, appendicularians, nematodes, nemerteans, polychaetes, small medusae, salps, and even a tiny ctenophore. The coral avoided nothing, missed nothing, and regurgitated nothing during our observation periods. Twice during observations in the glass tanks, an extremely fast shrimp was seen to evade capture after tentacle contact by reversing his swimming direction to directly away from *M. cavernosa*. Also a 1 mm. long isopod (unidentified) was observed to walk imperviously in the troughs between the necks of the expanded polyps without visible harm or attempted capture. Well over 200 zooplankton captures were observed with lights on the reef at night and over 120 in the tanks at night. Normally, the zooplankton encounters a tentacle and is immediately wrapped in its tip. The tentacle is then drawn toward the mouth, the prey either wiped or transferred into the mouth, and the tentacle returned to feeding position in less than 15 seconds. The polyps never contract fully during feeding, making this tentacle capture response defy the kind of photographic time-lapse analysis successfully employed elsewhere (Johannes and Tepley in press). If, however, there is some disturbance or the zooplankton is very large and active, after ingestion, full polyp closure may ensue. Further, if two tentacles from neighboring polyps capture the same zooplankton, and initiate a tug-of-war over it, closure of both polyps may ensue, with the first tentacle to contact the zooplankton usually retaining the prey.

Observations under a microscope in the lab indicated that the tentacle twitching seen in the field during the day time and also at night were probably the capture of zooplankton too small to be seen with the unaided eye. Copepods as small as 0.1 mm. could be seen through the microscope to be captured and ingested in this manner. The whole operation gave the impression of an elephant eating a peanut.

The brine shrimp experiment is summarized in Fig. 6. Six intact brine shrimp were found in the

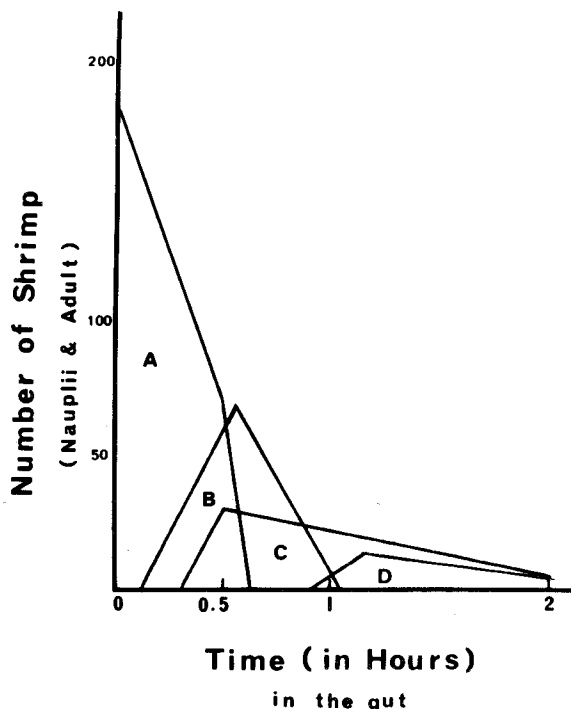


Figure 6: The total number of brine shrimp (*Artemia salina*) in each digestive state (see text for a description of the states) extracted from the gut of *Montastrea cavernosa* after a five minute feeding period.

control samples from just in front of the head, all just after the first rinse following the five minute feeding pulse. These shrimps, however, were completely undigested and clearly distinguishable from all gut plankton. In the brine shrimp experiment, therefore, the controls served mainly to test the effectiveness of the rinsing process. After the final wash, no fresh shrimp were present in any of the subsequent control samples, indicating that the rinsing had been complete and no further feeding was taking place during the following period. All of the shrimps from the gut showed some degree of digestion which depended on the age and size of the shrimp and the amount of time in the gut. Digestive states were determined arbitrarily by morphological changes. State A shrimp are intact, the only sign of digestion being the agglutination of the setae of legs and swimming antennae. State B shrimps have the setae reduced to half their normal length and some disruption of the body wall. State C shrimps have blurred body walls, no setae, and swimming antennae reduced to stumps. The only distinguishable character left in state D shrimps is the black, granular eye; stain is no longer picked up by the body wall, which is highly fragmented. The rate of digestion is morphologically specific: nauplii enter the D state and become unrecog-

nizeable after one hour in the gut, adults remain recognizable until two to three hours, and highly culticularized eggs remain distinguishable for more than two to three hours. It seems reasonable that this differential digestion rate applies to zooplankton under natural feeding conditions as well.

Obviously, as digestion proceeds, the brine shrimp becomes less and less identifiable. There is also some weak evidence that the remaining carapace of a state D digestion shrimp is evicted from the stomach cavity; state D digestion bodies began appearing in the control samples taken near the head two hours after feeding. Empty skeletons were also seen rejected in the feeding experiments of Nicholls (cited in Yonge, 1930a). Likewise, Nicholls found in his pulse-chase feeding experiments with shark red corpuscles that counting became difficult after two to three hours of digestion since these cells became less identifiable and were also evicted. These two facts could explain the reduction in the total number of shrimp observed in the later digestion stages.

Table II lists the number and kinds of partially digested zooplankters removed from the *M. cavernosa* guts. Several of these are shown in Fig. 7a through c. Occasionally algal filaments were found in the gut and also in the controls. The algae from the gut and control were always indistinguishable, neither showing any disruption or digestion. Since the samples were taken at 8.00 P.M., these represent a sample of the prey population on which *M. cavernosa* had been feeding for two hours since sunset. The prey is clearly highly diverse. At least eight phyla are represented by these counts, and considering that almost all the phyla represented on a reef have at least one member with planktonic larvae the taxonomic diversity of prey is certainly greater than shown here. Further, it is difficult to make any generalizations about prey size. The feeding response described above is probably limited to zooplankton between 0.01 and 2.5 times the diameter of the polyp, but throughout the microscopic examination of the stomach contents, concentrated blobs of red or blue staining material could be seen in the thin strands of mucus taken from the gut. These may have been smaller plankton or bacteria more easily obtained by mucus feeding. In addition, since *cavernosa* is capable of responding to dissolved micro-organics in concentrations of less than 10^{-3} M (Lehman and Porter, 1973), absorption of dissolved, colloidal, or particulate organics can not be discounted either in its feeding capabilities.

On the nights of most active feeding, the plankton is not randomly distributed between the polyps (Table III), having a χ^2 level of fit to Poisson distribution of $p < 0.001$. The head is slightly over-represented by polyps without any plankters in them and by polyps with more than two plan-

Table II. Gut Zooplankton: Taxonomic Composition, Summary for all Guts.

Taxon	Number of individuals
Planktonic Adults	
Copepods	110
Appendicularians	2
Salps	1
Planktonic Larvae (Must Settle)	
Protozoas	3
Zoeas	66
Polychaetes	1
Cyphonautes	1
Planulae (agariciid)	1
Others	6
Demersal Adults	
Nereids	7
Polychaetes	9
Amphipods	4
Nematodes	4
Nemertean	5
Turbellarians	2
Isopods	2
Demersal larvae	
Decapods	104
Egg masses	2
(Plant material: Filamentous algae, <i>Zostera</i> ?)	

Table III Gut Zooplankton: Number of Plankters per Polyp

Date	Number of polyps sampled	Number of Plankters			
		0	1-2	3-7	8-20
Night:					
July 19	64	59	5	0	0
26	93	73	19	1	0
30	97	58	33	6	0
31	92	43	29	15	5
Aug. 1	75	72	3	0	0
26	49	29	18	2	0
Day:					
Aug. 19	70	65	5	0	0

ters in them. This is not surprising. Although the polyps were sampled completely randomly from all parts of the head, a random distribution of the contents would be expected only if the probability of each polyp's capturing plankton were equal. This seems unlikely, however, since the polyps on the top of the head as well as those on the up-current side are more likely to be encountering drifting zooplankton. Because of the large number of samples and controls taken each time, it was not possible to identify the exact position on the head from which it came, although this will be desirable in future studies.

As a test for possible enrichment, the gut contents of several polyps feeding on zooplankton artificially attracted to them by light were taken ten minutes after they began feeding on this plankton (the total length of time needed to complete the normal gut extraction process was also ten minutes) to compare with normal, not obviously enriched gut contents. The enriched gut contents differ in several striking ways from the normal contents. As many as 100 zooplankters are found in these guts, never that many are found in the normal ones. The majority of the zooplankton from the enriched guts are also completely undigested. What digestion is visible never proceeds beyond a state A degradation; no A specimens were found in the normal gut contents. These enriched guts also contain a number of zooplankton such as crab megalopa not found in any of the normal guts. Finally, there is an extraordinary bias for eyed forms with almost 90 per cent of the enriched plankters having eyes as opposed to 50 per cent or fewer in the normally extracted guts. The control sample from in front of the head rarely showed any zooplankton in them, and when they did, the plankters are completely undigested and easily distinguishable from gut plankton. It therefore seems possible to rule out gut enrichment since from the point of view of both taxonomic composition and distribution of digestive states, enriched guts would be very different from those encountered normally.

It seems useful to divide the plankton into true planktonic forms and near bottom forms, either demersal (truly bottom dwelling) or meroplanktonic (settling to the bottom at some time in the life cycle). This is an operational division justified by the disparate origins and value of the zooplankton to the coral. A majority both by number and by weight of the gut zooplankton is coming up from the reef itself (Table II). Most of the zooplankton eaten by the coral is also nocturnal, coming from the reef at sunset, and returning before sunrise. This well documented planktonic pattern has been shown to cause a quantitative and qualitative shift in the zooplankton community over several Caribbean reefs (Kuenzel, 1972; Glynn, in press; personal observations). For the demersal zooplankton, one of the most dangerous times is when it begins to rise off the reef bottom. The likelihood of being eaten on the way up by either corals or crepuscular fish is very high. Strong evidence from the distribution of digestion states among the various forms supports this idea. Within the demersal forms, more than 90 per cent of them were in state C or D, indicating that by far the majority of feeding on this group had taken place between one and two hours before the sampling began, *i.e.* just after sunset. In the truly planktonic forms, however, such as copepods, the plankters are more evenly divided between states B, C, and D, indicating a

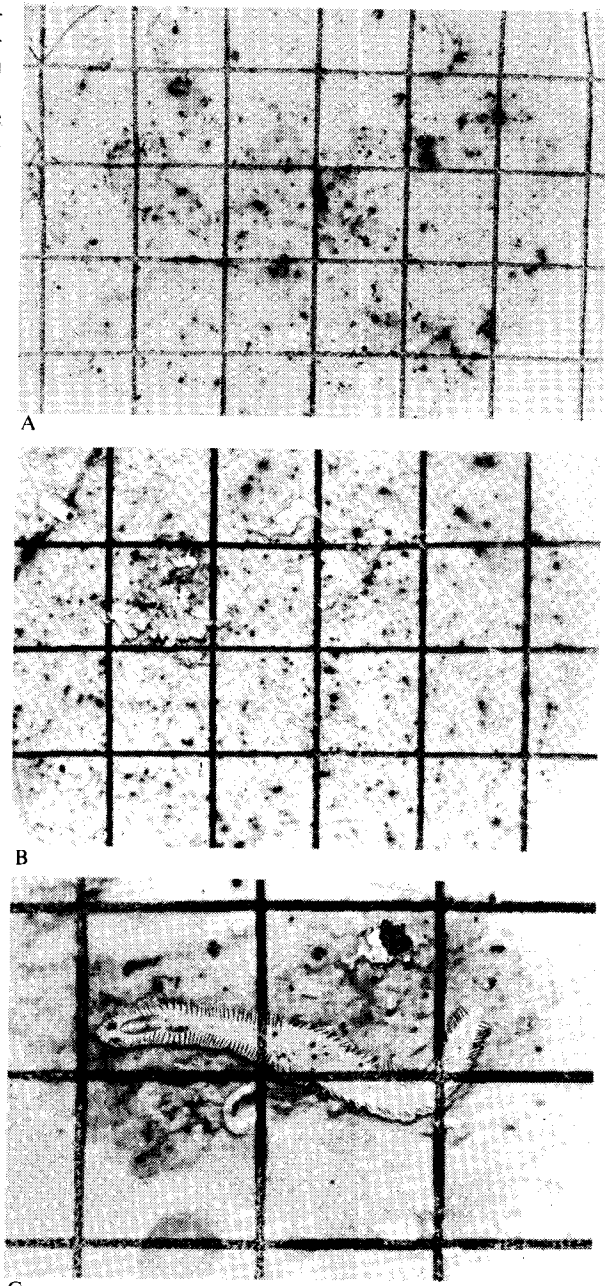


Figure 7: Gut contents from natural populations of *M. cavernosa* two hours after sunset filtered onto gridded Millipore filters. Each grid square is 3.33 mm on a side. (A) Note the prominent eye in the well digested crustacean in row 1, column 2 in the top left; also the well digested polychaete at the intersection of rows 2 and 3 with column 1 and a very highly digested one in row 1, column 3; (C) partially digested polychaete, note the jaws and setae clearly visible through the highly digested body.

Table IV Gut Zooplankton: Percent of Daily Energy Requirement of the Caribbean coral *Montastrea cavernosa* met by zooplankton during two hours of feeding from 6 P.M. to 8 P.M.*

Date	Number of polyps sampled ^a	Total μ g dry wt. in the gut ^b	Value in calories ^c	Daily Energy Requirement in calories ^d	Per Cent of D.E.R. met
July 19	64	48	0.3	224	0.1
26	93	528	2.9	326	0.9
30	97	4533	24.9	340	7.3
31	92	6785	37.3	322	11.6
Aug. 1	75	56	0.3	263	0.1
26	49	163	0.9	172	0.5
Daytime	—	—	—	—	—
Aug. 19	70	36	0.2	245	0.1

- a) The average area of one polyp is one cm².
 b) Gut zooplankton's weight is determined by extrapolating from the average weight of taxonomically similar non-digested specimen of the same volume.
 c) Caloric content is based on caloric conversion tables for zooplankton (Cummins & Wuycheck, 1971).
 d) Calculated assuming a respiration rate of 1.10 mg O₂ cm⁻² day⁻¹; and a conversion rate of 3.5 cal/mg O₂ (Brody, 1945).

* Note added in proof: The values shown in the last column of Table IV are based on whole organism (coral plus zooxanthellae) respiration rates. Whatever portion of the measured respiration rate is due to the zooxanthellae should be added on to these values — if 50 per cent of the respiration is due to the algae, these values would double. Further, since plankton peaks in abundance at the surface once at sunset and once at dawn, this suggests two vertical migrations per night by the zooplankton on the reef. This means that the bottom-dwelling plankton might pass the coral-crevice interface four times in one night with a concomitant increase in the likelihood of being eaten. The values reported above are for the first two hours of feeding only (first rise of plankton from the reef).

more constant catching rate. It will be valuable to perform the gut extraction just after dawn to see if there is a similar feeding pulse as the demersal plankton settles down on the reef for the day.

Extremely cautious extrapolation from the gut plankton content to its potential caloric value to the coral is possible. The difficulties in extrapolating are very apparent. First, these contents represent only two hours of feeding; second many of the softer bodied and smaller forms may have been digested before the sampling took place; third the conversion from zooplankton weight to its caloric value assumes full digestion by the coral; fourth the weight of the zooplankton is itself only an estimate based on the volume of the plankters; and finally the caloric need of the coral is only an extrapolation from published respiration rates for Caribbean corals (Johannes *et al.*, 1970; Wells and Wells, 1971).

Table IV gives the total μ g. dry weight of zooplankton in the guts of the polyps for each of the experimental nights. What per cent this contributes to the daily energy requirement of the coral depends on the respiration rate. The consumption of 1 mg. O₂ corresponds to the release of approximately 3.5 cal. (Brody, 1945), and 1 mg. dry weight of zooplankton contains approximately 5.5 cal. (Comita and Schindler, 1963). The respiration rate for *Montastrea annularis*, the Caribbean congener of *M. cavernosa*, is 1.10 mg. O₂ cm⁻² day⁻¹ (Johannes *et al.*, 1970). This is reasonable in the light of additional work on coelenterates (Altman and Dittmer, 1964) and assuming a similar rate for *M. cavernosa*, the plankton counted from the guts after two hours of feeding at night accounts for between 0.2 per cent and 10 per cent of the daily energy requirement of the coral. Further information is needed on a precise determination of the

Table V Tow Zooplankton: Tow Contents^a for two Horizontal Tows and one Vertical Haul made just after Gut Sampling in the same locality vs. Gut Contents

Taxon	July 30 Vertical Haul from 13 m	July 30 Horizontal Tow at 13 m	July 31 Horizontal Tow at 13 m	Total Gut Contents
Adult Pelagic				
Ostracods	18	5	2	0
Chaetognaths	41	6	5	0
Appendicularia	28	2	7	1
Gymnosomes	128	6	10	0
Copepods	3579	1067	1109	110
Adult Demersal				
Nemerteans	2	3	3	5
Nematodes	23	9	7	4
Mysids	0	5	20	0
Amphipods	0	7	25	4
Polychaetes	8	9	59	16
Larvae-Juvenile				
Polychaetes	15	0	2	1
Zoeas	23	6	18	66
Decapods	28	26	46	104
Nauplii	110	33	30	0

a) Concentrations of zooplankton in the tows and haul are expressed in number of individuals/m³. Tows, haul, and gut contents were taken on Ulacsun Reef, San Blas, Panama, July-August, 1972.

respiration rate of *M. cavernosa* and its symbionts and the daily variation in this rate before a reasonable energy budget analysis can be worked up.

The amount of plankton in the gut varies considerably from night to night, correlating weakly with the phase of the moon and its rising time. July 30 and July 31, 1972 were both nights of complete darkness with abundant plankton both on the reef and in the gut. August 1, 1972, an evening with a similar lunar regime, had, however, a rapidly dropping tide at sunset. This, may have caused a significant sweeping away of reefal plankton before complete feeding had taken place. Hence the low amount of gut plankton for that night. A number of factors are certainly important in determining how much plankton exists in the water column and its actual availability as food for corals.

Counts from plankton tows made in the same

locality as the gut extraction experiments for July 30 and 31 plus a vertical haul made on July 30 are listed in Table V. They represent very poorly, especially the vertical haul, the plankton ultimately found in the guts. Electivity indices performed on these counts in comparison to the gut content counts would show a significant over-representation in the guts for the bottom (mero and demersal) plankton and an under-representation of the holo plankton such as copepods. This supports the observation made above, but such a rigorous comparison between these counts is probably not valid for several reasons. The tows were taken in neither the same place nor at the same time as the coral feeding. As mentioned above, digestive states of most of the plankton indicate that most of the feeding had occurred near sunset, nearly two hours before these tows. Further, as dramatized by the ver-

tical haul, the open-water plankton is not likely to come in contact with reef coral populations unless when being swept over extremely shallow water coral formations such as *Porites* reef flats (Glynn, in press) and therefore would not be subject to the kind of coral predation as the plankton dwelling on or passing near the bottom at night. Finally, some zooplankton can swim out of nets after colliding with them, but most would never successfully evade contact with *M. cavernosa* tentacles.

It is impossible to assess at this time the significance of *M. cavernosa*'s diurnal activities in procuring food.

V. DISCUSSION

Much of the earliest work on coral feeding was done on Atlantic species (Agassiz, 1850; Duerden, 1902, 1904, 1906; Carpenter, 1910; Vaughan, 1912, 1919; Boschma, 1924, 1925, 1926) followed closely by corroborative observations on Indo-Pacific forms (Carlgren, 1905; Mayer, 1918, 1924; Matthai, 1918; Edmondson, 1929; Yonge, 1930a, b; Abe, 1938). The brine shrimp experiment described here is similar to the feeding observations made by Boschma (1925) and Nicholls (cited in Yonge, 1930a). They fed the corals plankters stained with neutral red, and by cutting open the polyps at intervals thereafter traced the digestion rate. They report for adult copepods (3mm.), that all of the body contents as well as all of the external soft parts disappeared after two hours; after three hours, only a disintegrated exoskeleton is left. Smaller forms took less time. These results agree precisely with the digestion rates observed for brine shrimp eaten by *M. cavernosa*.

In the wide ranging tank observations of Vaughan (1912), Abe (1938), Boschma (1925) and Yonge (1930b) a large variety of zooplankters were seen eaten readily. A partial list includes: copepods and other planktonic crustacea such as crab zoea, and pycnogonids, chaetognaths, medusae, salps, pteropods, annelids, young fish, and meat from fish, molluscs or beef, etc. From the gut content studies described above, it appears that this dietary diversity is prevalent in natural situations as well.

In feeding response, *M. cavernosa* belongs to a multi-generic group of extremely long, almost prehensile tentacled forms such as species in *Flabellum*, *Caryophyllia*, *Euphyllia*, *Symphyllia*, *Lobophyllia*, *Favia*, *Gonipora*, or *Fungia* (*Heliofungia*) etc. (Yonge, 1930b; Abe, 1938) which seize and transport living zooplankton prey firmly to the mouth. In addition, almost all the genera tested by Yonge (1930b) for the Pacific and by Vaughan (1912) for the Caribbean had some use of the tentacles during zooplankton capture. The *cavernosa*

feeding response differs from some of the other long tentacled forms in being able to employ one tentacle at a time during food capture and in being able to reach for zooplankton which are swimming by. Abe (1938) also observed this reaching movement during his work on *Fungia* and attributed it to following dilute chemical stimuli. This seems entirely reasonable for *M. cavernosa* as well since its chemical sensitivity for amino acids, which might be leaked from the plankter after puncture by an *M. cavernosa* nematocyst, has been demonstrated (Lehman and Porter, 1973).

Vaughan (1912, 1919) noted that meat was readily taken by *M. cavernosa* and that its mesenterial filaments not only could protrude freely through the column wall but also catch and digest food outside the gastric cavity. He noted that diatoms and chopped algae were invariably refused by *M. cavernosa*. During the course of my investigations, mesenterial filaments were rarely seen *in situ* except during the most intense feeding activity caused by light-attracted plankton. They were also seen in laboratory experiments when chunks of fish meat were placed on the coral. Despite the fact that plant filaments (fragments of *Zostera*?) appeared occasionally in the gut, the interpretation of Vaughan (1912) and others that plant material is not normally taken or digested seems valid. These tiny filaments (0.4 mm. at the longest) in the gut could possibly have been taken in during zooplankton feeding and showed no signs of digestion.

It is well known that corals have the greatest proportion of prey capture surface to tissue bulk of any other group of animals (Yonge, 1930b; Goreau *et al.*, 1971) and that corals can eat and digest with ease a variety of animal prey (Yonge, 1931; Lenhoff, 1968). Many of the early investigators, however, were impressed by the absence of food from the coelenteron of freshly collected or preserved specimen, (Duerden, 1902; Gardiner, 1903; Pratt, 1906; Walther, 1919). Since all of the fresh specimen (and presumably all of the preserved ones too) were collected in the daytime and since most zooplankton are digested rapidly, this is not surprising. Nevertheless, Boschma (1925) noted in the gastric cavity of freshly collected specimen of *As-trangia danae* the remains of small plankters, especially the appendages of small crustaceans, and Gardiner (1900) found a small crustacean in the polyp of *Dendrophyllia*. Similar observations were made for *Mussa* (Carpenter, 1910), *Favia* (Boschma, 1924), and East Indian corals (Boschma, 1925).

Coles (1969) has shown that under force-feeding situations, *Montastrea cavernosa* can ingest enough brine shrimp to meet its daily energy requirements (based on respiration measurements) under laboratory conditions. The caloric intake

due to zooplankton feeding *in situ*, however, is still unquantified.

In terms of its caloric contribution to *M. cavernosa*, the zooplankton found in the gut two hours after sunset appears to make up only a small amount of the daily energy requirement based on published respiration rates. It has, on the other hand, been clearly demonstrated that this species is capable of voracious feeding whenever the opportunity presents itself, and it seems reasonable that this opportunistic ability remains adaptive, as demonstrated by the successful feeding on the nights of July 30 and 31. Such an opportunistic approach to planktivory is predictable considering the highly fluctuating supply of the plankton over the reef. As Clarke and Bishop (1948), Odum and Odum (1955), and Johannes *et al.* (1970) have pointed out, the value of the zooplankton may also be in the trace elements, such as phosphorus, or nitrogen which they supply. This would obviously be important to reef organisms which are growing in habitually phosphorus-poor water (Odum and Odum, 1955). The demonstrated sensitivity of *cavernosa* to amino acids (Lehman and Porter, 1973) suggests also the importance of micro-organics which the zooplankton might contribute as well, from the amino acids to proteins, vitamins, enzymes, *etc.* The controversy over the net accumulation or loss of these organics under natural conditions, however, must still be resolved (Johannes *et al.*, 1969; Reiswig, 1972). These results lend strong support for the tight recycling of reef plankton and organics envisioned by Goreau *et al.* (1971). Perhaps it might be useful to view coral tentacles and mesenterial filaments as roots on a plant-animal symbiont living in a tightly recycling ecosystem such as a rain-forest.

Fig. 8 shows a somewhat natural experiment of a coral being raised in a zooplanktonless environment. Growing in the base of a *Sphaciospongia vesparia* (?) in two metres of water is *Porites furcata*. As Reiswig (1971) has shown, the exhalant oscula of sponges can be producing water free of most particles larger than $1-5\ \mu$. While the pumping periodicity of this sponge species is not known (Reiswig, personal communication) both day and night observations showed that this sponge was keeping up a strong constant exhalant current around the coral. Even heavy coarse calcareous sand particles dropped over the sponge were deflected away. The amount of zooplankton reaching this particular *P. furcata* during the several months of our observations (June, 1971 to July, 1972) was therefore miniscule, indicating at least some degree of independence from zooplankton feeding in this species.

As mentioned earlier, the Caribbean corals vary considerably in their skeletal and soft-part mor-



Figure 8: *Sphaciospongia vesparia* 1.5 metres in diameter growing at two metres depth (Ulacsucun Reef, San Blas, Panama) with a colony of *Porites furcata* growing on its base. The sponge is keeping up a strong, constant exhalant current of water around the coral which is therefore growing in a relatively zooplankton-free environment.

phology. In general, there is a correlation between the two in that the ramose, branching forms, those engaged in an "over-topping" strategy in space competition on a reef (Porter, 1973), have smaller polyps than those coral species in the "understory" layer of corals beneath the branchers. It is tempting to speculate that the canopy species, such as the acroporids, poritids, pocilloporids, *etc.* are relatively more autotrophic in their existence, and corals in the understory closer to the plankton supply, such as *Montrastrea cavernosa*, favids, or mussids are more heterotrophic. This is consistent with both the size of the feeding tentacles and the light competitive abilities.

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