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A Test of the Photoadaptability of the Zooxanthellae in *Madracis mirabilis*

Abstract

Effects of light intensity on zooxanthellae growing in Madracis mirabilis were studied at Discovery Bay Marine Laboratory, Discovery Bay, Jamaica. Field work was done on the forereef of this fringing reef. Three separate experiments were performed where Chlorophyll *a* content was analyzed in the differently treated zooxanthellae: 1) Pieces of coral from different colonies at 37 ft were transplanted to 90 ft. A control was also set up by transferring corals from 37 ft to another site at 37 ft. 2) A colony of coral was shaded for three days. A comparison of pre-shaded and shaded corals were done 3) Corals taken from colonies at two depths were studied. In the transplantation and shading experiments it was hypothesized that Chlorophyll *a* content would increase per cell. For both treatments, the results did not support these hypotheses. The amount of Chlorophyl/cell in transplantation experiment did not change significantly over a five day period. It was thought that this could have been due to the inability of shallow-water zooxanthellae to adapt to deep water light environments. The Chlorophyl/cell values for the shaded colony decreased after three days. This could have been caused by an overshading effect where light intensities were so low as to stimulate Chlorophyl breakdown rather than Chlorophyl synthesis. The results from the varied depth experiment did not support our original hypothesis that a higher Chlorophyl *a* content/cell would be found in zooxanthellae at lower depths. Chlorophyl content was lower in the 90 ft sample. However,

The lower depth sample was sponge encrusted which may have placed additional stress on the coral and its zooxanthellae. The observed trends may have been due to coral and/or zooxanthellae adaptation to stressed conditions

Introduction:

Scleractinian corals have been shown to utilize a variety of feeding strategies. The use of tentacles to capture zooplankton is the most obvious of these strategies. Others include: 1) the secretion of mucus strands from the polyp oral surface which net zooplankton and bacteria 2) the use of mesenterial filaments extruded from the mouth and through the body wall which have been observed capturing zooplankton and searching through sediments for food. (Porter: lecture notes 3-6-83) 3) direct assimilation of dissolved organic matter in sea water 4) the possible use of cilia on the polyp's oral disc which create currents which could push food into the polyps mouth (undocumented) (J. Gilbert lecture notes 2-19-83). The final "strategy" which is one of the most studied, is the relationship between zooxanthellae and corals. Zooxanthellae is a general term describing the endosymbiotic dinoflagellate algae which predominantly inhabit the cells of the oral endoderm in Cnidarian polyps. In corals these algae are considered to belong to one species Gymnodinium microadriaticum (Muscatine, 1977). Using radioactive tracers, (Muscatine, 1974) investigated the bilateral movements of metabolites (translocation) between these algal cells and their host cells. His data support the existence of an internal nutrient cycle where algae actively take up inorganic nitrogen and phosphorus from the host cells' waste. The zooxanthellae use these (animal waste products) to photosynthesize and secrete reduced organic carbon and nitrogen, primarily glucose, succinate, alanine and glycerol which are readily utilized by the coral cell. However these corals and algae do have alternate sources of these nutrients; most corals supplement their diet with

the strategies outlined above. While zooxanthellae may also obtain inorganic nitrogen and phosphorus by direct uptake from sea water. Nevertheless by minimizing excretory losses, both the algae and the corals reduce their dependence on these sources which are more energy consuming and less abundant in the nutrient deficient environment of the coral reef. This tight nutrient cycling is thought to be one of the major reasons for the high productivity associated with coral reefs (Muscatine, lecture notes 2-26-83)

Because symbiotic corals require light for their zooxanthellae to photosynthesize, none are found below the depth of 100m (Goreau 1979). Some coral species are found to grow over much of this depth range; their zooxanthellae are thus subjected to a large gradient in light intensity. (Muscatine source # 12) has found that similar to plants in terrestrial systems, the photosynthetic efficiency and P/R ratios for zooxanthellae decrease at the lower light intensities found at lower depths. Associated with this decrease in light intensity morphological, biochemical and behavioral adaptations have been observed in algae and different coral species. J Potter (lecture notes 3-6-83) has found a distinct change in feeding strategies in the different species of coral growing at different depths. He noted that some shallow water species are almost totally dependent on their zooxanthellae for their nutrition and are incapable of zooplankton capture. These species also possess morphologies which maximize the amount of light incident upon their surfaces. In deeper regions where light becomes limited, photosynthesis decreases causing corals to rely more on ingested food such as zooplankton

to fulfill their nutritional requirements. Similarly these corals possess morphologies better adapted to zooplankton capture.

Considered algal distribution with corals (Lasker 1977) a decrease and an increase in the percentage of zooxanthellae found in the polyps and coenosarcs respectively of colonies of M. cavernosa found at lower depths. He hypothesized that this was an adaptation to decreasing light intensities. The corals maximize the number of zooxanthellae exposed to daylight by reducing the number of zooxanthellae in polyps which are contracted during the day and increasing the number located in the coenosarc which is fully exposed during daylight hours.

When density of zooxanthellae per unit surface area has been investigated (Dustan 1979) noted a decrease whereas Porter (pers comm) Muscatine (pers comm) and (Drew 1972) found no significant difference between colonies at different depths. (Drew 1972) hypothesized that "the surface area available for the distribution of algal cells with a coral polyp had a limiting effect on the number of algal cells contained, whereas changes in light intensity with depth had little effect on algal cell density" Regardless of coral morphology or algal distribution zooxanthellae at any depth are adapted to maximize their photosynthetic rates. At lower depths zooxanthellae would require greater amounts of chlorophyl and other photosynthetic pigments to maximize light capturing capabilities.

In this study the effects of different light environments on the distribution, pigmentation and adaptibility of zooxanthellae growing within Madracis mirabilis (Poculloporidae) (Lewis, 1975) were investigated. Mg Chlorophyl a per cell zooxanthellae was

measured
at different depths and for different light intensity manipulations.
It was hypothesized that Chlorophyll a concentrations/cell would increase as a photoadaptive response to lower light levels.
Based on what has been observed in terrestrial and aquatic systems, that plants will adapt to varying light intensities by changing pigment concentrations, it was hypothesized that zooxanthellae would show similar adaptiveness. It was further hypothesized that when subjected to low light intensities by shading and transplantations to lower depths, that the zooxanthellae would increase their Chlorophyll a content. In an attempt to measure daily increases and thus calculate a rate of increase daily measurements were taken from the transplantation experiment.

Materials and Methods

materials: In all three treatments the following were used: diving knife, large black plastic trashbag liners, plastic bucket, tagging tape
With the addition of the following
1) Transplantation: plastic bottle floats, twine
2) Shading: Shading device constructed from the following: 4ft x 4ft square plastic pipe frame (pipe ~1" diameter), heavy twine large bottle floats, styrofoam pieces, cinderblocks (four of them)

Methods: All fieldwork was done at Mooring One using SCUBA. Feb 28

Transplantation: At a depth of 37ft (~10m from the mooring)

~ 40 multibranched pieces from different colonies of Madracis mirabilis were detached from its substrate with the aid of a diving knife. These were placed in a bucket and relocated to a site at 90ft. This site was located ~ 100m West of the mooring. There the coral pieces were separated and firmly planted into the sandy bottom in upright positions. At 37ft a control was set up by similarly relocating a colony to a site ~4m from its original substrate. Everyday from March 1 through March 5, 4 coral pieces were collected from the 2 sites. To prevent shock caused by direct exposure to the sun, ~~and~~ at each site all of the pieces were wrapped in black plastic trashcan liners, marked with tagging tape, placed in a bucket and towed to the surface. Once ashore the pieces were immediately frozen in ziploc bags.

Shading Experiment:

Construction of the shading apparatus: To the corners of a 4ft x 4ft 1 inch plastic pipe square frame were attached several styrofoam-filled plastic bottles with ~ 1m string-heavy twine slack. Four more 2m twine pieces were attached to the frame's corners to be later attached to 4 cinderblock anchors. Across the frame, 2 layers of lg plastic trashcan liners were stretched and fastened using twine.

A colony of M. mirabilis located on a coral knoll ~ 7m ~~from~~ from the transplantation control site at 37ft was chosen for this experiment. The shading apparatus was set up over this

Colony as shown in figure 1. This was done on March 2. Seven multibranched coral pieces were immediately collected using the wrapping-tagging techniques used in the transplantation experiments. Once ashore these too were frozen. On March 5, 7 more multibranched coral pieces were collected and frozen.

Varied Depth Experiment. Approximately 6 multibranched pieces were collected from M. mirabilis colonies at depths of 37ft, 60ft and 90ft. These samples were similarly collected and frozen as in the last 2 experiments.

Quantitative Analyses: Living tissue was removed from the coral skeleton by propelling filtered sea water at it with a Waterpik (TM). The resulting blastate was collected, measured for volume, homogenized in a blender for ~30 seconds and the following were measured: (Each sample consisted of 3 pieces of branch that were oriented vertically and were considered cylindrically shaped.)

1) Cell Count - Cells were counted on a standard hemocytometer. (depth .1mm). Four grids of 25 squares were counted for each sample.
total # cell removed = (mean count on hemocytometer)(10^4 cells/ml)

2) Chlorophyl a content. - 50 µl of homogenized blastate were added to 3 testube-cuvettes which contained 90% acetone solution. These were allowed to sit for 3 minutes away from light. Measurements were made on the fluorometer (TAYLOR) located in lab 5 at the Marine Lab (Isco Bay). Total amount of Chlorophyl a removed

from the sample = (mean fluorometer reading) $\frac{(3.048 \times 10^{-4})(.01)}{.05}$ (# ml of blastate sample)

↑ (machine calibration factor)

Surface Area - surface area for each coral piece was approximated by considering different sections of the coral branches as cylinders. M. mirabilis is a multipranching "finger" coral of max dia of branch ~ 1.0cm Pieces were chosen for their resemblance to cylindrical shape

Interpolyp Distances & Polyp size were measured for the 37/4 and 90/4 samples - 15 of distances and 15 polyps were measured on 5 pieces of coral from each sample.

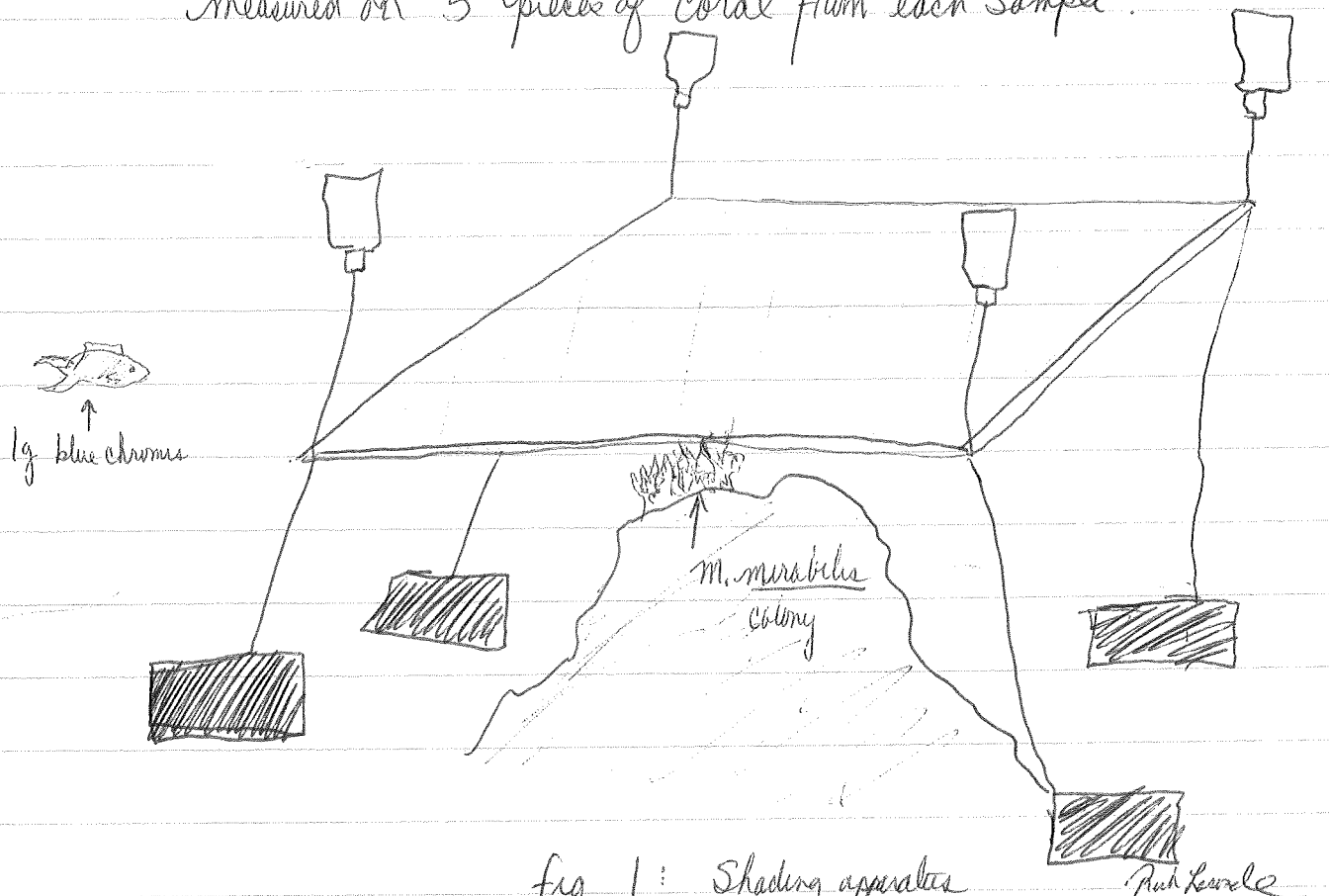

fig 1: Shading apparatus

Rick Lewis

Results

The results of the transplantation of Madracis Mirabilis from 37 to 90 feet are presented in Table I. Collections were made daily from both the experimental and control sites and we originally planed to analyze 3 samples (of 3 fingers each) from each collection. However, time constraints only allowed a lab workup of 3 of the collections from the experimental plot and 2 from the control site. In addition we had to cut our sample size to 2 for the control group.

Given the number of samples analyzed it would have been most instructive to work up collections from days 1, 3, and 5 for the experimental group and 1 and 5 for the control group. Unfortunately, we started the lab work with the expectation of finishing all our samples and initially no attention was paid to the order of samples analyzed.

In the transplantation experiment controls were performed to distinguish the effects due to the decreased light levels at greater depths from those due to the stress of the transplantation process itself. In particular we were concerned that corals brought down to 90 feet might expel their zooxanthellae. Zooxanthellae expulsion by stressed corals has been documented by Jaap (1979).

If corals brought to 90 feet preferentially expelled those zooxanthellae cells having a low chlorophyll a

Table I - Data From Transplant Experiments

	37 Feet → 90 Feet Transplants			37 Feet → 37 Feet Transplants	
	3/1 (Day 1)	3/2 (Day 2)	3/4 (Day 4)	3/2 (Day 2)	3/3 (Day 3)
mg Chlorophyll a / cell of Zooxanthellae	$\bar{X} = 2.23 \times 10^{-9}$ $SD = .75 \times 10^{-9}$ $CV = 33.6\%$ $n = 2$	$\bar{X} = 2.17 \times 10^{-9}$ $SD = 0.33 \times 10^{-9}$ $CV = 15.2\%$ $n = 3$	$\bar{X} = 2.24 \times 10^{-9}$ $SD = 0.57 \times 10^{-9}$ $CV = 25.4\%$ $n = 3$	$\bar{X} = 2.55 \times 10^{-9}$ $SD = 0.47 \times 10^{-9}$ $CV = 18.3\%$ $n = 2$	$\bar{X} = 1.53 \times 10^{-9}$ $SD = 0.01 \times 10^{-9}$ $CV = 0.92\%$ $n = 2$
# of cells Zooxanthellae / cm^2 Coral Surface	———	———	$\bar{X} = 1.22 \times 10^{6}$ $SD = .24 \times 10^{6}$ $CV = 18.6\%$ $n = 3$	———	$\bar{X} = 1.5 \times 10^{6}$ $SD = 0.12 \times 10^{6}$ $CV = 8.0\%$ $n = 2$
mg Chlorophyll a / cm^2 Coral surface	———	———	$\bar{X} = 2.95 \times 10^{-3}$ $SD = 8.89 \times 10^{-4}$ $CV = 30.1\%$ $n = 3$	———	$\bar{X} = 2.32 \times 10^{-3}$ $SD = 0.16 \times 10^{-3}$ $CV = 7.0\%$ $n = 2$

Table II - Data from Shading Experiments

	Pre-shaded at 37 feet	Shaded for 4 days at 37 feet
mg Chlorophyll a / cell of Zooxanthellae	$\bar{X} = 1.86 * 10^{-9}$ $SD = 0.86 * 10^{-10}$ $CV = 4.6\ \%$ $n = 3$	$\bar{X} = 1.49 * 10^{-9}$ $SD = 0.06 * 10^{-9}$ $CV = 3.8\ \%$ $n = 3$
# of cells / cm^2 of Coral Surface	$\bar{X} = 1.83 * 10^{6}$ $SD = 0.27 * 10^{6}$ $CV = 14.86\ \%$ $n = 3$	$\bar{X} = 1.72 * 10^{6}$ $SD = 0.58 * 10^{6}$ $CV = 33.45\ \%$ $n = 3$
mg Chlorophyll a / cm^2 of Coral Surface	$\bar{X} = 3.39 * 10^{-3}$ $SD = 0.36 * 10^{-3}$ $CV = 10.6\ \%$ $n = 3$	$X = 2.59 * 10^{-3}$ $SD = 0.93 * 10^{-3}$ $CV = 35.73\ \%$ $n = 3$

Table III - Comparison of Corals Found at 2 Depths

	Collection From 37 Feet	Collection From 90 Feet
mg Chlorophyll a / cell of 300 xanthellae	$\bar{X} = 1.95 * 10^{-9}$ $SD = 0.42 * 10^{-10}$ $CV = 21.55\%$ $n = 3$	$\bar{X} = 1.48 * 10^{-9}$ $SD = 0.131 * 10^{-9}$ $CV = 8.8\%$ $n = 3$
# of cells / cm^2 of coral surface	$\bar{X} = 1.56 * 10^{6}$ $SD = 0.06 * 10^{6}$ $CV = 4.07\%$ $n = 3$	$\bar{X} = 2.48 * 10^{6}$ $SD = 5.87 * 10^{5}$ $CV = 23.69\%$ $n = 3$
mg Chlorophyll a / cm^2 of Coral Surface	$\bar{X} = 3.30 * 10^{-3}$ $SD = 0.30 * 10^{-3}$ $CV = 9.00\%$ $n = 3$	$\bar{X} = 3.62 * 10^{-3}$ $SD = 0.59 * 10^{-3}$ $CV = 16.4\%$ $n = 3$

content, one would observe an increase in chlorophyll a content per cell which would be distinctly different from a photoadaptive increase in chlorophyll content by the zooxanthellae cells. A daily comparison of the number of cells per cm^2 in the control vs. the experimental group allows one to determine if expulsion is taking place and due to which stress.

Crucial to our determination of the degree of expulsion was our ability to accurately calculate the number of cells per cm^2. Initial difficulties with the water picking technique - both human and mechanical - does not allow us to have much confidence in the accuracy of the data found in rows 2 and 3 of Table I. Note, for mg chlorophyll a per cell it is only important to obtain some of the cells found in the coral but for both parameters involving coral surface area the total amount of zooxanthellae found on a coral piece must be isolated. Thus, we can not be sure if expulsion occured in either the experimental or the control group — the cell concentration data is somewhat varied, and slightly lower than our later and more reliable calculations. Nevertheless, there was virtually no change in the mean calculation of mg chlorophyll a/cell in the experimental samples analyzed.

The data from the shading experiment is presented in Table II. To control for any inter-colony

variations in zooxanthellae characteristics we obtained the pre-shaded samples by collecting coral pieces from our experimental colony before setting up the shading apparatus.

The amount of zooxanthellae /cm² was nearly equal for the two treatments indicating that no expulsion took place. However, we found that the amount of chlorophyll a/cell zooxanthellae was lower in the shaded treatment. This trend was significant to $p = .05$ using the Mann-Whitney U test. In accordance with the lower chlorophyll a values per cell we calculated a lower value of chlorophyll /cm² in the shaded sample. This trend was not found to be statistically significant.

The last comparison of corals was between samples from a colony found at 37 feet and one found at 90 feet. The coral specimen collected at 90 feet was not characteristic of Madracis Mirabilis found on the reef. The 90 foot sample was being overgrown (actually undergrown) by a sponge, and only the upper parts of the colony's fingers were protruding above the sponge growth. In addition the corals structure was somewhat deformed — it was mainly gnarled and skinny fingers. Data from these two groups is presented in Table III.

The amount of chlorophyll a/cell was lower in

the coral samples taken from 90 feet. However, because of the small sample size this difference was not found to be statistically significant with the Mann-Whitney U test ($p = .1$). In addition cell density was higher in the deeper sample. The difference in these distributions was found to be significant with $p = .05$. And because of the higher cell densities the amount of Chlorophyll a / cm^2 was actually higher in the sample from 90 feet, despite the lower Chlorophyll a amount per cell. This difference was not significant ($p = .1$)

In the corals collected from 37 and 90 feet we also compared polyp size and inter polyp distance. This data is presented in Table 4.

Table 4 Polyp size and inter polyp Distance in 37' and 90' Samples

37 Feet	90 Feet
Inter Polyp Distance:	Interpolyp Distance:
$\bar{X} = 1.95$ mm	$\bar{X} = 1.88$ mm.
$SD = .28$	$SD = .28$
$CV = 13.96\%$	$CV = 15.2\%$
$n = 15$	$n = 15$
Size:	Size:
$\bar{X} = 1.38$ mm	$\bar{X} = 1.24$
$SD = .19$	$SD = .18$
$CV = 13.98\%$	$CV = 14.7\%$
$n = 15$	$n = 15$

Inter-polyp distance was found to be smaller in the deeper water samples but the difference in data distribution was not statistically significant. The polyp size was found to be smaller in the deeper samples and this difference in data distribution was found to be significant to $p \leq .05$ with the Mann Whitney U test.

Discussion

We had expected the transplant experiment to provide the most illuminating data. Moving a coral to a deeper sit not only exposes it to lower light intensity but it also limits the wavelength of light available to the zooxanthellae. Thus a transplantation experiment should allow one to determine the adaptive qualities of zooxanthellae to conditions found over different depths. And by taking daily collections we hoped to determine photo adaptation rate. Unfortunately, this aspect of our study provided the least interpretable data.

From the Data in Table I there appears to be no light adaptation over time in the experimentally transplanted samples. It is possible that full adaptation occured sometime before day 2. In fact the amount of chlorophyll a per cell in each of the experimental trials exceeds that of other samples collected at 37 feet (See Tables II & III). Alternatively, and more likely, the time span of the experiment may be too short to observe any noticeable photoadaptation over the depth range this transplantation spanned. Falkowski waited weeks before seeing a large adaptation in moved corals (1982). This still does not explain the high chlorophyll a content per cell seen in these samples or the great variability in the control group. Expulsion could possibly explain both. If zooxanthellae with low chlorophyll a contents were initially expelled than one would expect a higher cellular

concentration of chlorophyll a to be observed. Moreover, with only 2 samples examined it is possible that the controls of 3/2 (Day 2) contained coral pieces in which expulsion had taken place while samples collected on 3/3 for some reason had not lost any zooxanthellae. Unfortunately, not enough cell density data was ~~collected~~ calculated to answer this question, and the data which is presented is not reliable.

In our shading experiment we hypothesized that lower light intensities would cause a photoadaptive response in the zooxanthellae of the shaded corals. In addition we expected this result to be more pronounced than the transplant experiments because of the dramatic change in light intensity. The results obtained directly oppose our hypothesis - the zooxanthellae of the shaded corals exhibited a significant decrease in chlorophyll a content. The in sample variance was low and since both coral specimens came from the same colony, it appears that this trend is a result of the shading. In this case the shading was complete and represented a light level never received by Madracis Macabilis in nature. The coral shaded in this manner was probably receiving the same amount of light it would have if placed at a depth of 1000 feet (Jim Porter, Pers. Comm.) Under such a high stress situation it seems likely that the chlorophyll a in the zooxanthellae

will begin to degenerate. Curiously this stress situation did not result in zooxanthellae expulsion. Perhaps expulsion due to shading stress only occurs after a certain degree of pigment degeneration.

In comparing corals living at 37 feet with those found at 90 feet we also expected to see an increase in chlorophyll content with depth. Even if the photoadaptive capabilities of the zooxanthellae, as tested by earlier experiments, was not great we expected to find that those corals living in greater depths would harbor zooxanthellae with a high chlorophyll a content. This is exactly what Dustin found in his study on Montastrea Annularis (1979). However, the density of zooxanthellae with depth should not change considerably according to several researchers (Muscatine & Porter Pers. comm., Hoeksema '75). In contrast Dustin reports a marked decrease in density with depth in his study.

Our results contradicted both possibilities. The chlorophyll a /cell was smaller in the 90 foot sample and the density of zooxanthellae was much greater than in any other treatment. However, despite the low chlorophyll a content of each cell the 90 foot sample also exhibited the highest level of chlorophyll per cm^2.

There are two possible explanations for this observed trend. The 90 foot sample of Madracis Mirabilis was under severe interspecific competition from an encrusting sponge

Perhaps, the stress placed on the coral also prevented the zooxanthellae from maintaining a high level of chlorophyll a. If this were the case then more cells would be needed to supply the coral with the same amount of photosynthate. Thus, the coral may be regulating the amount of zooxanthellae present and compensating for the decreased chlorophyll a/cell concentrations.

Alternatively, the size of the zooxanthellae themselves may be smaller. This might be a zooxanthellae response to the reduce nutrient levels available in a dying coral. A smaller cell would increase the surface area : volume ratio and thereby allow more efficient absorbance of nutrients. Finally, a remote possibility is that the corals control the zooxanthellae cell size and in high stress situations reduce that size to allow for more efficient removal of photosynthate.

To determine what is happening in this 90 foot Sample one must know the cost to the coral of maintaining zooxanthellae and/or the cost to the zooxanthellae of increasing their concentration. Little is known about which member of the zooxanthellae - coral symbiosis is the controlling organism. It has been suggested by Drew (1972) that space is the limiting resource for the zooxanthellae, while Venholt (1968) showed that the numbers of symbiotic algae present in zooanthids is related to the zooanthoid production of glycine. Perhaps the expulsion

observed is really a fleeing tactic of the zooxanthellae. The controlling factors behind zooxanthellae densities in corals needs to be further examined.

Photoadaptation of pigments in zooxanthellae is only one means by which a coral can increase the efficiency of its light gathering capabilities. Other strategies include morphological changes such as increased surface area - for example the structure of Acropora Palmata increases its light gathering ability. Morphological changes can also reduce respiration which is a possible strategy a coral could employ if found in low light conditions. Reduced respiration can be accomplished by decreasing polyp size and/or density (Porter - Pers. Comm). Thus we examined these two parameters in the 37 and 90 foot samples and found that the deeper coral samples had a significantly smaller polyp size while there was no difference in density. This trend was not observed by Jeff Burgess (Pers. Comm.) in his work on the same species at found at 30 and 90 feet and may, in fact, be an artifact of our sponge encrusted sample.

The design of this study could be improved by using a greater transplantation depth range such as 10 to 90 feet. In addition it is best to use the same colony for both control and experimental transplants. This method controls for possible inter-colony variance. In contrast one should take many different samples from different colonies when comparing corals found at different depths. In this

way colony based differences would average out and differences due to depth would be more apparent. One might also want to use partially shaded samples if considering shading experiments. Finally, a larger sample size is always desirable and at least 3 replicates of the control group should be performed.

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A well-designed and carefully-conducted study. The results are well-presented and critically analyzed. The project and its write-up show a lot of work and thought.

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