Variation in Coral Morphology in the Species Madracis mirabilis with Depth due to Relative Changes in the Importance of Zooplankton in the Energy Budget

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Abstract

Variations were found in several morphological characteristics of Madracis mirabilis with depth, supporting an adaptation to increased efficiency and importance of zooplankton capture. Specifically, significant changes were found in polyp density and concentration of nematocysts per polyp with depth. Several other factors measured were shown to stay constant over the 30'–90' depth variation used in this study.

Introduction

Individual coral species are found growing over a range of depths, some greater than others. This distribution suggests an ability of the coral to adapt to a wide set of environmental factors. The main factor considered in this experiment is the decrease of light intensity with depth, and certain corals have been shown to change morphologically with depth and the change in light levels. Examples include structural changes (Graus and Macintyre, '76), and changes in polyp density and number of zooxanthellae/cm^2 (Dustan, '79). Presently studies are being carried out on coral energy budgets relative to depth by Porter. It is felt that due to lower light levels, a larger percentage of energy requirements at greater depths must be met by zooplankton capture, although not enough information exists now to prove this point.

This study is designed to support the hypothesis that zooplankton capture becomes proportionally of greater importance at greater depths. Since a direct study of coral energy budgets was not feasible, it was decided to look for changes in morphology affecting feeding with depth, and to use their presence as an indicator of zooplankton capture importance.

The specific hypothesis tested was that the concentration of nematocysts/polyp should increase with depth to increase the efficiency of zooplankton capture. Other factors expected to change were polyp density, with a lower value at greater depths to lower respiration costs while maintaining feeding capabilities,

the Discovery Bay Marine Laboratory, and were taken out of water during transit. Since all the specimens showed full polyp extension 24 hours later, collections were not repeated in the more accepted fashion of transfer in a container with sea water. As little reef disturbance as possible was created.

In the lab each specimen was treated individually. First, all tissue was removed by water-pik blasting, using the standard technique, so details of the set up shall not be included in this paper. The total volume of fluid used, including as much mucus foam as possible, was determined. Two samples of the mixture were concentrated 10x by centrifuging for 5 minutes at a setting of 4 (exact r.p.m. value unattainable). The supernatant was kept in two cases for later analysis. The concentrate was mixed thoroughly and enough samples were examined in a hemocytometer to count 100 zooxanthellae and 100 nematocysts. The number of $1mm^2$ squares required to attain this amount of nematocysts, and the number of $\frac{1}{400}mm^2$ squares required for 100 zooxanthellae were counted. Each nematocyst measured was classified by shape and size.

The number of zooxanthellae and nematocysts per $1mm^2$ square was determined, and then multiplied by 1000 to account for the .0001 ml volume of the hemocytometer and the 10x concentration factor, to determine numbers/ml. These amounts were multiplied by the number of mls of solution gathered to get total numbers of zooxanthellae and nematocysts per sample. These in turn were divided by the surface area of the sample to obtain values /cm^2 and were divided by the number of polyps to get zooxanthellae
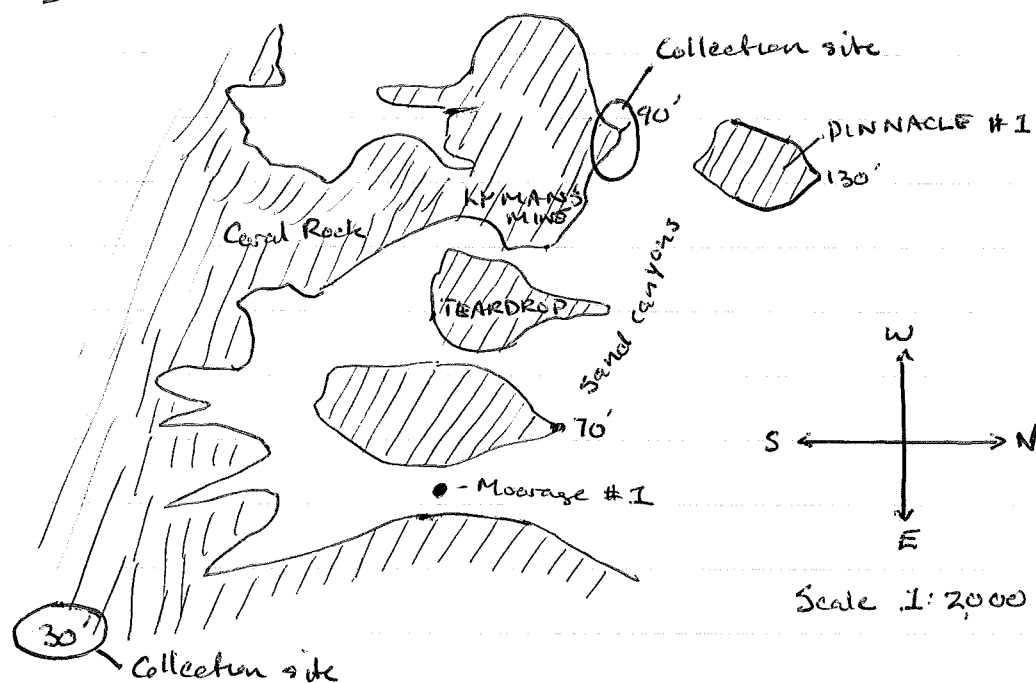
per polyp and nematocysts/polyp.

To determine polyp number, each polyp on a specimen was counted. To determine surface area, an approximation using cylinder, circle and triangle areas was made. This was probably the largest error source in the experiment.

Supernatant samples were examined in the hemocytometer, one at normal concentration, and one concentrated 10x, to see if the centrifuging technique removed all of the nematocysts from solution as expected.

Mann-whitney U tests were used to measure significance levels in each data treatment.
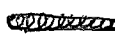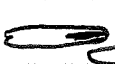
Fig #1 - Map of Collection site

Scale 1:2000

Results

Table #1 - Coral specimen measurements.

Specimen #	1	2	3	4		5	6	7	8
Depth	90'	90'	90'	90'		30'	30'	30'	30'
# of polyps	296	389	256	224		513	362	368	518
(cm²) surface area	12.5	15.4	10.3	9.6		13.95	12.85	12.0	19.3
polyps/cm²	23.7	25.2	24.1	23.3		36.7	28.2	30.6	26.8
# of nematocysts / cm²	$12.3 \cdot 10^4$	$7.0 \cdot 10^4$	$10.6 \cdot 10^4$	$7.9 \cdot 10^4$		$11.9 \cdot 10^4$	$10.2 \cdot 10^4$	$7.6 \cdot 10^4$	$7.2 \cdot 10^4$
# of nematocysts / polyp	$5.2 \cdot 10^3$	$2.8 \cdot 10^3$	$4.3 \cdot 10^3$	$3.4 \cdot 10^3$		$3.2 \cdot 10^3$	$3.6 \cdot 10^3$	$2.5 \cdot 10^3$	$2.7 \cdot 10^3$
# of zooxanthellae / cm²	$2.2 \cdot 10^6$	$1.7 \cdot 10^6$	$1.9 \cdot 10^6$	$1.6 \cdot 10^6$		$1.9 \cdot 10^6$	$1.6 \cdot 10^6$	$1.9 \cdot 10^6$	$1.9 \cdot 10^6$
# of zooxanthellae / polyp	$9.3 \cdot 10^4$ †	$6.7 \cdot 10^4$ †	$7.8 \cdot 10^4$ †	$7.0 \cdot 10^4$ †		$5.3 \cdot 10^4$ †	$5.8 \cdot 10^4$ †	$6.1 \cdot 10^4$ †	$7.3 \cdot 10^4$ †
% spirocyst type nematocysts	42	62	63	69		60	49	45	72
% type A+B nematocysts	5.5	5.0	3.6	5.8		2.2	2.8	7.8	2.8
% nematocysts >.35mm in length	4.6	17.4	8.1	5.8		6.0	6.5	12.6	1.9
% nematocysts type C	41	24	29	51		23	38	.45	15

† - This is not an accurate measurement due to the presence of zooxanthellae in the coenosarc tissue

Fig #2 - Nematocyst classifications and sizes

Type *	Size (length x width)	Depiction
Spirocyst-nematocysts	.14 - .35 mm x .03 - .06	- definite spiral coil
Oval - large (A)	.35 - .53 mm x .12 - .18	- fat oval shape
Oval - small (B)	.24 - .35 mm x .08 - .12	
Elongated ovals (C)	.14 - .35 mm x .04 - .07	with and without greenish rods
Small thins (D)	.14 mm x .03	very thin, often greenish in tinge

* More divisions can be made, but resolution was not fine enough to allow an in depth survey of all nematocyst types

Significant differences were found between the two depths in polyps/cm². The mean for the 90' depth was 24.1 ± .8 S.D., and for the 30' depth was 30.6 ± 4.4 S.D. By a Mann-Whitney U test, (used in all of the significance calculations,) the difference between the two groups was significant to the .014 level. The high significance value and relatively low standard deviations indicate that there are more or less constant distinct polyp densities associated with each depth (Table #1).

The number of nematocysts/cm² did not vary significantly with depth. Means were $9.5 ± 2.4 \cdot 10^4$ S.D for 90' and $9.2 ± 2.2 \cdot 10^4$ S.D for 30'.

The number of nematocysts/polyp did vary with depth, with a mean of $3.9 ± 1.1 \cdot 10^3$ S.D at 90', and of $3.0 ± .5 \cdot 10^3$ S.D. at 30'. The significance level of .1 is questionable, but consideration must be given to the low sample size and the roughness of the experimental design. In addition, sample #2 (see Table #1), gave a very low value here, unlike the more evenly grouped values at 30', and could be the result of experimental error. A quick evaluation will show that this sample gives the lowest values in all of the measurements except one. For the purposes of this paper, this difference will be considered significant.

The means for number of zooxanthellae/cm² were $1.9 ± .3 \cdot 10^6$ S.D at 90' and $1.8 ± .2 \cdot 10^6$ S.D. These values appear to be very similar and indeed, when tested did not show a significant level of difference. The small standard deviations show little variance in this value both within and between groups.

Contrary to expectations, the number of zooxanthellae per polyp increased with depth, from a mean of $6.1\pm.9\cdot10^4$ S.D at 30' to $7.7\pm1.2\cdot10^4$ S.D. at 90'. This difference was significant to the .057 level. However, as noted below Table #1, this value is not entirely accurate due to the presence of zooxanthellae in the coenosarc tissue. The percentage values are unknown, so the value of this data figure are in question, and impossible to determine given this experimental technique.

No differences were found in the percentage of nematocysts in each descriptive class (see Fig. #2) with depth, at least not to a significant degree. A trend is visible in the percentages of nematocyst types A and B, lower at 30', but an unusually high value in sample #7 (see Table #1) lowers the significant difference to a .171 level. A fairly high variance between specimens within each depth group is visible, and could be due to sampling error.

A comment should be made on the accuracy of all of the values in Table #1. Due to loss of fluid by a small amount of splashing out of the plastic blasting sack, and in the form of mucus-foam, the number of mls of solution collected in each case was most likely smaller than the actual amount. In addition, although blasting with a water pick is one of the best methods for removing coral tissue, some tissue could have been left on the coral skeleton. A value of 80% was verbally communicated to me by Neil Josephson, but this value was questioned. Regardless, the sum effect is to lower all of the reported values by an unknown amount. Relative

comparisons, however, should be unaffected.

One other tested source of nematocyst loss was the examination of the centrifuge supernatant. In the unconcentrated sample, no nematocysts were found in 6 1mm² hemocytometer squares. The 10X supernatant concentrate revealed that approximately 1 nematocyst per every ten 1mm² hemocytometer squares was left in the supernatant. This amount was considered negligable and left out of the calculations. It remains, however, a slight source of error.

Discussion

Several major differences in morphology were found between the two sample sets of <u>Madracis mirabilis</u>. These indicate that adaption to depth has occured.

The 90' specimen showed a lower level of polyp density than the 30' sample. This follows, as noted in the introduction, established trends. Lesser polyp density reduces respiration rates for the colony as a whole (Porter, 76), and according to this same author, maintains zooplankton capture ability. Apparently the polyp plane is still able to catch all of the zooplankton impinging on it at polyp densities much lower than those optimum for photosynthetic production. I am unaware of any studies actually measuring the efficiency of different polyp densities in feeding. However, I assume that the density at each depth reflects the optimal balance between respiration and zooplankton capture, so indirectly this

supports the idea that a reduction of polyp density does not have a major effect on feeding capabilities.

The specific hypothesis of variance in nematocyst concentration with depth was supported, with the conditions listed in the results section. The increase in number of nematocysts/polyp is a much more valuable measurement than nematocysts/cm^2, since all the nematocysts are in the polyps and not coenosarc tissue. Another factor, that of variations in polyp size with depth, has a bearing on this finding. If variances in polyp size did exist, and polyps were larger at greater depths, then the concentration of nematocysts/polyp might only be a result of variations in polyp size. However, a brief examination of two specimens of coral from 30' and 90' did not reveal a significant polyp size difference. The sample size here was too small to include as data, and the two pieces might not be representative of their depth levels. Dustan, 79, found no variation in polyp size with depth in _Montastrea annularis_, only a decrease in polyp density. This supports my findings of lack of size variations, but one should not assume that all corals follow the same morphological trends.

Assuming that polyp sizes do stay constant, then the concentration of nematocysts per polyp volume has increased, and thus zooplankton capture ability and the data indicates a greater reliance on zooplankton feeding.

Of the two statistics on zooxanthellae density, zooxanthellae per surface area is of greater value due to the undetermined concentration of zooxanthellae in the coenosarc tissue. The lack of a significant differences with depth was unexpected, and contrary to Dustan's findings with _Montastrea annularis_. This only reinforces the principle

that generalizations can not always be made between coral species.

Of course, the depth range used in this experiment might not be large enough to exhibit strong differences, and the results found might not be applicable to greater ranges in depth. In this particular case, the lack of variation may indicate that the zooxanthellae are present in similar configurations, most likely in a single layer as described by Dustan. This is, however, only conjecture.

A comment should be made here on the accuracy of zooxanthellae measurements. Losses have been recorded when deep water coral specimens have been brought up to bright sunlight and kept in an altered sub-optimal condition. Since the original hypothesis of this experiment concerned nematocyst densities, necessary precautions were not taken in specimen care. If shock did result, then one would expect greater loss from the deeper specimens, which would actually increase zooxanthellae concentrations found in the deeper samples.

If the majority of algal cells are present in the polyp tissue, then more questions arise, such as what the value of an increased concentration of zooxanthellae with depth is. A study of polyps independent of coenosarc tissue should be made to determine relative concentrations.

The lack of variation in nematocyst type-proportions could have several explanations. First, this factor might be genetically constrained in M. mirabilis. Secondly, the proportions found may be optimal for prey capture at all depths. Finally, the depth range again might not vary enough to show significant differences. The value of differing proportions of nematocyst types in prey capture would be difficult to measure, and I am presently

unaware of any literature on the subject. The large variety of nematocyst types leads one to believe that they all have specific functions.

An unrelated qualitative observation concerning morphological changes with depth is increased branching of coral colonies at shallower depths. The internodal distances seem to be smaller at 30' than 90'. This could be due to increased light levels making more heavily branched forms more favorable (Porter). This could also be an adaptation to higher turbulence levels in shallow waters.

There are other possible depth modification beyond the scope of this experiment that could increase energy efficiency of M. mirabilis. Specifically, it would be interesting to measure expansion times to see if they decrease with depth, occuring at only peak plankton activity periods. The specimens collected at 90' exhibited day-time expansion, so either light levels are still high enough for production to balance respiration, or the coral can't vary its expansion times. Other factors are also likely to be involved.

Conclusion

Statistically significant differences are found with depth in polyp density and number of nematocysts per polyp. A qualitative difference in branching morphology was also indicated. No differences were found in number of zooxanthellae per cm^2 and nematocyst type-proportions. The differences indicate that M. mirabilis has the ability to adapt to different conditions over a depth range, and specifically to increase zooplankton feeding capabilities, as reflected in the increase of nematocyst concentrations per polyp. This indirectly supports an increased reliance on zooplankton capture to supply energy requirements at greater depths. More studies are definitely needed, and a repetition of this study with greater sample numbers and at a greater range and number of depth classifications would help clarify many of the questions raised in this study.

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Study is very well conceived, described, and evaluated. Excellent presentation of data, analysis of results, and discussion.

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