

# CHANGES IN DISTRIBUTION OF GROWTH FORMS WITH DEPTH IN MILLEPORA (MILLEPORINA: HYDROZOA)

R. Scott Miller

Department of Biological Sciences

Dartmouth College, Hanover, NH.

March 6, 1984

ABSTRACT: Millepora spp. were sampled along a depth gradient on the West Fore Reef at Discovery Bay. Surveys were also conducted on the East Fore Reef and West Back Reef, where turbulence was different. A shift from branching varieties in deep water, thru plate-like varieties at 40', to sturdy box-like forms and encrusting forms at the surf zone was noticed. It is hypothesized that this shift is due to light availability, wave energy, food availability and substrate availability. The large variability and number of intermediate forms of Millepora indicate that the hydrozoan is one species with a large plasticity in growth form.

## INTRODUCTION

The calcareous hydrozoans of the genus Millepora are common organisms in Caribbean reefs. In fact, they may be the dominant reef builder in some shallow reef zones (Goreau, 1963). While very common in the shallow reef, Millepora has been observed to 115 feet below sea level on the north coast of Jamaica by the author.

Stearns and Riding (1973) describe three milleporid species found in the Caribbean. Millepora alcorni Linnaeus forms erect, delicate branches often spreading in one plane to form a fan. M. complanata Lamarck forms thin, gently folded erect blades or plates growing from a common base. The most sturdy form is M. squarrosa Lamarck which consists of erect plates with many lateral connecting plates fusing to form a boxwork structure. Other scientists argue that the three species are highly plastic growth forms of a single species (DeWaeert and DeKnijf, 1979). They base this on the number of intermediate and encrusting forms, which do not fit into any of the species categories. In fact, they found up to 80% of the Millepora colonies in a study were unidentifiable to species. This morphotypic plasticity indicates that environmental factors influence the growth form of the milleporid colonies (Stearns and Riding, 1973).

Furthermore, the distribution of these growth forms changes with depth. The sturdy box-like M. squarrosa occurs in the surf zone on the reef crest. Millepora complanata

is found over much of the reef slope below the surf zone, and is gradually replaced by the fragile M. alcicornis at greater depths. Thus, one or more environmental factors related to depth influence the relative distribution of these growth forms.

This investigation examines the range of morph variability in Millepora as well as the spatial distribution of the milleporid growth forms. Furthermore, the study attempts to elucidate the environmental parameters influencing the distribution of these morph changes. Finally, the issue of Millepora taxonomy will be discussed in terms of the distribution trends found on the reef.

### STUDY SITE

The study was conducted at Discovery Bay on the north shore of Jamaica. The fringing reef, which blocks the mouth of the bay, is divided by a ship channel cut through the reef (Figure 1). The geomorphology and community structure of the reef have been thoroughly described by Goreau (1959) and Liddell and Ohlhorst (1981).

Three study sites were chosen that varied in depth and/or turbulence. The primary site was at Mooring 1 on the west fore reef where Millepora was surveyed at 5', 20', 40', 60' and 80'. The surf zone on the reef crest (5') is strewn with piles of Acropora palmata rubble from Hurricane Allen (Woodley et al., 1981) with large clumps

of Millepora and A. palmata. At 20' the reef terrace extends seaward at a 15°-20° slope and is cut by sand channels, which carry sediment away from the reef crest (Lidell and Ohlhorst, 1981). Monastrea annularis, Porites astreoides, Diploria spp., Dendrogyna spp. and Millepora dominate the rough topography. At 40', Monastrea annularis, Agaricia spp., Meandrina meandrites, and Porites porites are common, as well as some small clumps of Acropora cervicornis. The 60' site is dominated by Monastrea annularis, M. cavernosa and Agaricia spp. Below this depth, the reef escarpment drops off steeply (45°) to a sand flat. The 80' survey was done on this slope, which was dominated by Monastrea spp. and Agaricia spp.

Two surveys were conducted on the east fore reef at 40' and 20'. Here the terrace is much broader and less steep (0°-5°) (Lidell and Ohlhorst, 1981). There are no coral mounds rising from the sand, but rather a flat field of small coral heads separated by patches of sediment. Monastrea annularis and Millepora are very common, but there are no visible dominants. There are also many more gorgonians at this site than on the west fore reef. Due to increased wind exposure and the geomorphology of this reef, it is exposed to greater turbulence than similar depths on the west fore reef (Brakel, 1976; Tunnicliffe, 1981).

The final sites was on the west back reef at a depth of 5'. Most of the corals have been overgrown by algae. Madracis mirabilis and Millepora were the most

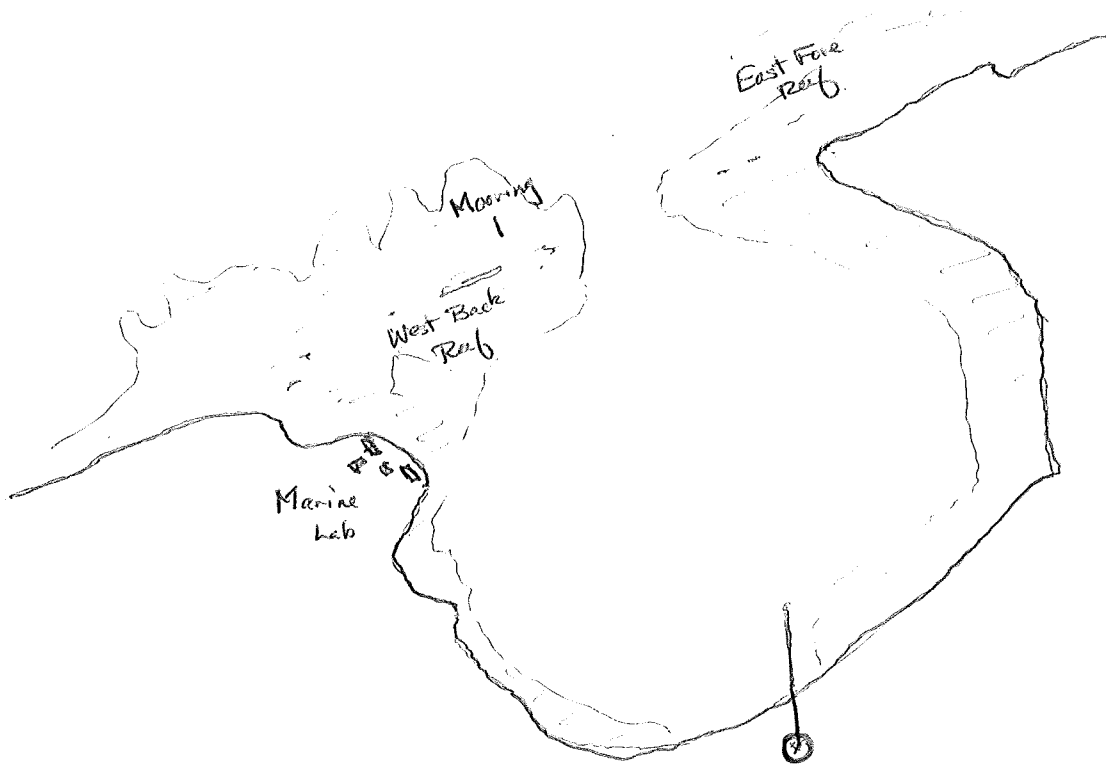


FIGURE 1 Diagram of Discovery Bay, Jamaica and the location of study sites.

commonly seen corals. The turbulence, while less than the surf zone on the fore reef, was still quite strong.

## METHODS

A survey of twenty-five Millepora colonies was conducted at each of the eight sites. The first twenty-five colonies that were seen while swimming perpendicular to the sand channels were counted, excluding those too small to have established a specific morph. Five growth forms along a gradient from most fragile to most sturdy were described:

- 1) branching colony (M. alcicornus)
- 2) an intermediate with fused branches and or flattened, plate-like branches.
- 3) blade-like colony (M. complanata)
- 4) an intermediate with plates in several planes which form incomplete boxes.
- 5) boxlike colony (M. squarrosa)

Other growth forms including encrusting individuals were also noted. The height, width, and number of branches/plates/boxes were also compiled, as well as individuals with an encrusting base of at least  $4\text{cm}^2$ . Finally, the orientation of the planar colonies (M. alcicornus and M. complanata and intermediates) were recorded in regards to the direction of water flow as determined by the sand channels. The study was conducted from February 27 to March 6, 1984.

## RESULTS

The distribution of the different growth forms at the eight locations are shown in Table 1. There is a significant shift (chi-square,  $\chi^2 = 68.7$ ,  $df = 8$ ,  $p < .01$ ) from fragile forms at greater depths to more sturdy morphs near the reef crest. Variations between each 20' depth were also examined using G-tests for goodness of fit. From 80' to 60', there was a major shift ( $G = 8.44$ ,  $df = 1$ ,  $p < .01$ ) from all branching forms to a mixture of branching and plate forms. From 60' to 40', no difference in the morph distributions was noted ( $G = 0.12$ ,  $p > .05$ ). There was another significant shift ( $G = 15.69$ ,  $p < .01$ ) from branching to plate-like forms between 40' and 20'. Between 20' and 5', another significant change ( $G = 18.28$ ,  $p < .01$ ) occurred from plate-like forms to M. squarrosa and its intermediate forms. Three purely rock-encrusting colonies were also found in the surf zone.

The west back reef had more M. complanata and intermediates than the 5' zone on the west fore reef ( $G = 4.26$ ,  $p < .05$ ). This shift to more fragile forms corresponds to less turbulence in the back reef. The 40' and 20' comparisons between the east fore reef and west fore reef also showed significant shifts ( $G = 5.92$ ,  $p < .025$  at 40';  $G = 5.23$ ,  $p < .025$  at 20') toward less fragile forms on the more turbulent east fore reef. Interestingly, rock-encrusting colonies were found at 20' on the east fore reef and were not found until 5' on the west reef. Also there

TABLE 1 Distribution of Upright and Encrusting Growth Forms \*  
at the Different Study Locations \*

	WFR 80'	WFR 60'	WFR 40'	WFR 20'	WFR 5'	WBR 5'	EFR 40'	EFR 20'
<u>M. alaicornis</u>	22	13	16	6	-	-	1	2
Intermediate 1	1	5	7	7	3	2	5	2
<u>M. complanata</u>	-	3	1	8	2	6	8	8
Intermediate 2	-	-	-	4	6	12	6	7
<u>M. squamosa</u>	-	-	-	-	10	2	-	-
Total of Forms	23	21	24	25	21	22	20	19
Encrusting Gorgonians	2	3	1	-	1	1	5	4
Encrusting Rocks	-	-	-	-	3	2	-	2
Encrusting Corals	-	1 †	-	-	-	-	-	-
Total N	25	25	25	25	25	25	25	25

\* WFR = West Fore Reef (Mooring #1)

WBR = West Back Reef

EFR = East Fore Reef

† Encrusting live Acropora cervicornis



TABLE 2 % of colonies that fit species description, % with 4cm<sup>2</sup> encrusting base, number attacking coral, % perpendicular to current and Colony Height at Each Location

	WFR	WFR	WFR	WFR	WFR	WBR	EFR	EFR
	80'	60'	40'	20'	5'	5'	40'	20'
% Species forms	88%	64%	68%	56%	48%	32%	36%	40%
% Encrusting Base	24%	20%	28%	36%	76%	60%	44%	64%
# Attacking Coral	—	2*	1†	—	—	—	—	1†
% Perpendicular	60.9%	56.5%	72.0%	88%	100%	95%	71.4%	77.2%
Total Height (cm)	9.26 ± 7.69	11.70 ± 12.12	10.32 ± 7.53	11.02 ± 7.05	8.30 ± 6.02	19.32 ± 12.81	10.46 ± 12.67	9.20 ± 5.88

\* Encrusting one Agericia spp., and one Acropora

† Encrusting one Agericia spp.

were more colonies of encrusting gorgonians on the east fore reef, which probably reflects increased gorgonian density at this site (Table 1).

The number of colonies at each site which fit into one of the three discrete species descriptions are presented in table 2. There is a significant trend toward intermediate and encrusting forms as one moves toward shallow, more turbulent waters ( $G=10.96$ ,  $df=4$ ,  $p<.05$ ). There was no difference between the west fore and back reefs ( $G=1.35$ ,  $df=1$ ,  $p>.05$ ), since both contain a large number of intermediate and encrusting forms.

Between the east and west fore reefs, there was a difference ( $G=5.83$ ,  $p<.025$ ) in the number of intermediates, reflecting the increase in M. complanata / M. squarrosa intermediates and encrusting species on the

east reef.

The number of colonies with encrusting bases ( $>4\text{ cm}^2$ ) also decreased with depth (Table 2). The transition from 80' to 5' was very significant ( $G=21.8$ ,  $df=4$ ,  $p<.01$ ). Again, no difference was found between fore and back reefs ( $G=1.96$ ,  $p>.05$ ).

In the east and west reef comparisons, there was no increase in the encrusting bases at 40' ( $G=1.42$ ,  $p>.05$ ), but there was an increase at 20' where there is more turbulence ( $G=4.03$ ,  $p<.05$ ).

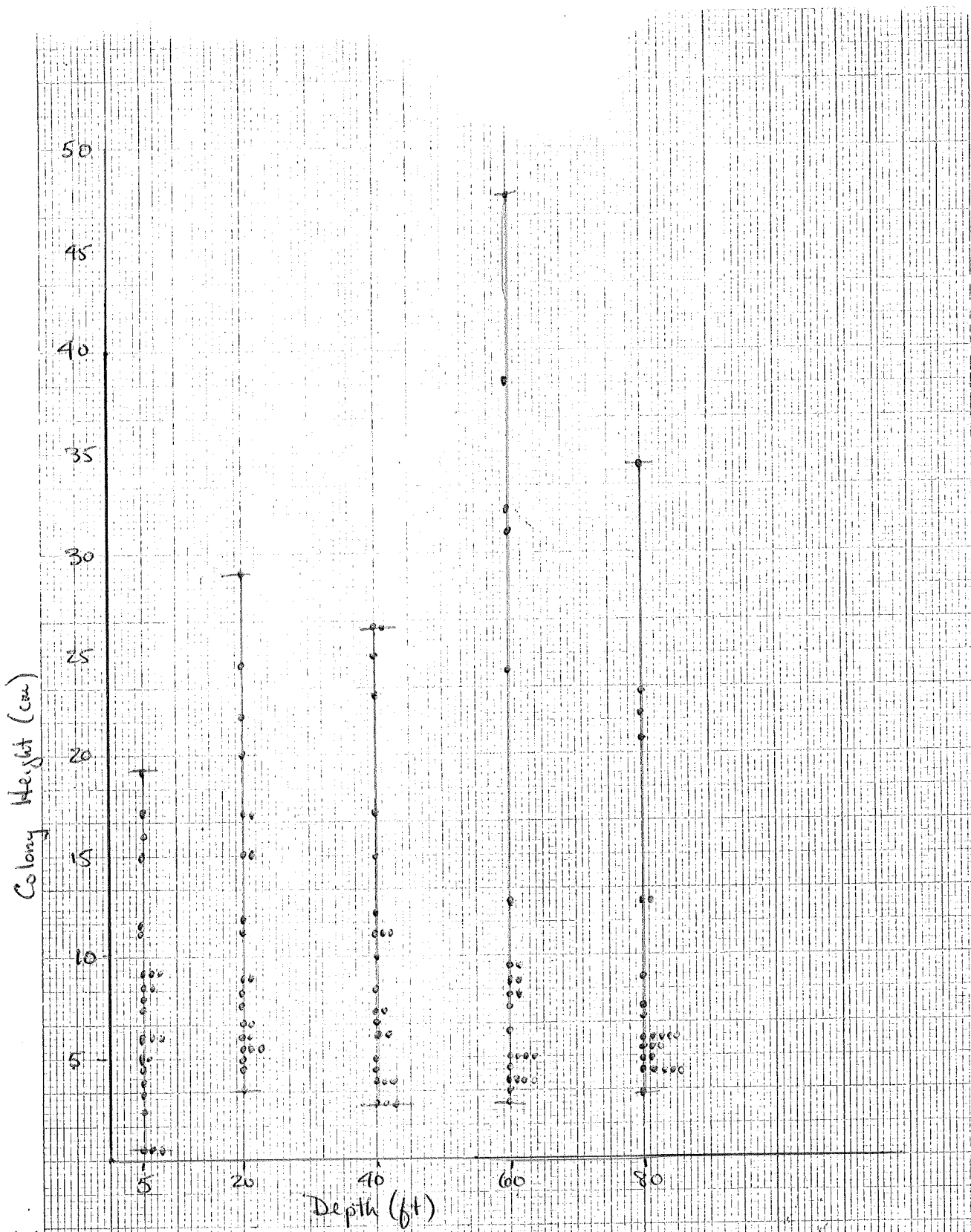
The number of planar colonies (*M. alcornus*, *M. complanata*, and intermediates) which oriented perpendicular to the wave surge was greater than 50% (Table 2).

Interestingly, a significant difference along the gradient from 80' to 5' was observed ( $\chi^2=10$ ,  $df=4$ ,  $p<.05$ ).

Only 60% of the colonies oriented at 80', while all did near the surf zone. No differences in orientation were found between the fore back reefs or east and west reef sites.

Figure 2 is a histogram of the height of the individual colonies along a gradient from 80' to 5'.

While the means don't differ due to the huge variances (Table 2), the sizes of the largest individuals seem to increase with greater depth when there is less turbulence. I observed even larger colonies of *M. alcornus* (over 90 cm long) below 100' further supporting this trend (Miller, unpub data).



**FIGURE 2** Histogram of Colony Height Frequencies at Various Depths (total range in red)

## DISCUSSION

A wide range of growth forms were observed at the various locations. Branching forms (Millepora alcicornis) dominate at greater depths and are in fact the only morph found below 60'. Within the M. alcicornis, there appears to be some variation as I noticed taller, spindly, less compact branching individuals at greater depths (80'-115'). The transition to M. complanata, the plate form, begins around 40' and continues to 20'. It is important to note that M. alcicornis is still abundant at 20' as well. The transition to box-like M. squarrosa and rock encrusting forms occurs between 20' and the surf zone (Table 1).

Along this depth gradient, many intermediates between the major <sup>forms</sup> species are observed (Table 2). 52% of the milleporids in the surf zone are intermediates or other forms, and this increases to 68% on the west back reef. In fact, De Weerd and De Kruif (1979) found up to 80% intermediates and unidentifiable forms in some areas. These observations are in direct contrast to Stearn and Riding (1973), who noted an absence of continuous variation between the three species.

While this distribution of growth forms changes with depth, several environmental parameters associated with depth could be ~~determinants~~ involved in the determination of growth form. These include light, wave energy or turbulence, sediment and food availability. Sediment load will not be discussed here, although it is likely

to be involved in the absence of Millepora in the back lagoon..

Light has been shown to be a very important influence in growth form in a number of coral species including Acropora cervicornis, Agaricia spp., and Monastrea spp. (Tunncliffe, 1983; Jaubert, 1977; Ceraus and McIntyre, 1976; Barnes, 1973).

Millepora, like the scleractinians, contains zooxanthellae in their outer tissues. Therefore, theories of growth form to maximize light reaching the coral apply to hydrocorals as well.

The intensity of light reaching the sea floor declines rapidly then tapers out in greater depths. In 20' of water, only 50% of the surface light reaches the bottom, while at 80' approximately 15% reaches the sea floor (Brakel, 1976). Two growth strategies are employed to increase the amount of light reaching the coral: branching which increases the surface area-to-volume ratio, and plating which maximizes the surface area receiving light (Hughes, 1983). Millepora appears to be branching to increase light reception. The other possibility is that branching increases zooplankton capture rate, which will be discussed later. Interestingly, in most branching corals the branches become longer and less dense as one approaches the surface (Jaubert, 1977; Barnes, 1973). However, Millepora alcicornis appears to form smaller, more dense branches in shallow waters. This trend is also seen in the branching coral A. cervicornis and appears to be due to turbulence. Rather than growing up where wave action would break the fragile branches in shallow water, the Acropora branches more densely, thus maintaining a uniform height (Tunncliffe, 1983).

The formation of plates at greater depth to increase the surface area that is illuminated is probably not an option for Millepora. Such a strategy would require extensive calcium carbonate deposition. Millepora spp. require substantial light (i.e. shallow water) in order to have high growth and  $\text{CaCO}_3$  deposition rates (Strömberg, 1976). Therefore, there is not enough light for Millepora to grow rapidly at great depths. This explains the observations that Millepora colonies in deep water are small with little carbonate buildup, while M. squarrosa and M. complanata can form six foot high colonial mounds and are considered major reef builders in shallow water. In summary, the branching growth forms may be a response to capture more light for the zooxanthellae.

Wave energy is also a major environmental factor that can affect growth form. Bottom turbulence decreases from the reef crest to 80' (Brake, 1976). Therefore, short, compact and sturdy growth forms such as the box-like M. squarrosa and rock encrusting morphs would be predicted to grow in high turbulence areas such as the reef crest. This is, in fact, the case (Table 1). This also explains why a greater number of the colonies had encrusting bases in the more turbulent waters (Table 2). If the plate or branch broke off, the basal encrusting part of the colony would survive and grow back. This is what happened to such colonies after Hurricane Allen (Woodley, pers. comm.).

Therefore, there seems to be a tradeoff between light and wave energy at any given depth in exposed reefs. Where light is maximal on the shallow fore reef, so is wave energy.

Where light is reduced ( $> 60'$ ), turbulence is not a factor. Thus the hydrocoral would be predicted to adopt a growth form which maximizes light reception, while being sturdy enough to withstand the forces of turbulence. From this prediction, the increase in height range with depth (Figure 2) can be explained. Branching form, although more delicate, can grow much taller at great depths since they aren't affected by turbulence. In shallower waters, these branches would be broken off by wave action. In these areas, short, compact corals which can survive the turbulence are able to capture enough light since more light reaches the sea floor. Since milleporids receive energy and nutrients from zooplankton capture (in addition to photosynthetic products from the zooxanthellae), wave energy may be a greater determinant in growth form than available light.

DeWaeleert and DeKroijf (1979) attempted to address this issue using transplant experiments. Several individuals of each "species" were transplanted to other depths. At the time of publication, the only noticeable difference in growth form was in M. complanata in the surf zone, which appeared to be growing transverse plates. This may be a shift towards the box-like growth of M. squarrosa.

There is one other factor to consider when discussing the effects of wave energy on hydrocorals. This is asexual reproduction by fragmentation, which does occur in Millepora. To what extent, the milleporids reproduce asexually is unknown. Turnncliffe (1981) has shown that A. cervicornus

reproduces largely by fragmentation of branches. If the branch is reduced to rubble, the pieces will not survive and grow into new colonies. Therefore, a branching structure that will fragment, but not fracture into small pieces, increases the fitness of the colony (Hughes, 1983). This model likely applies to Millepora as well.

Thirdly, food availability could affect growth form and orientation. The case for light and the availability of photosynthetic products produced by the zooxanthellae has already been made. To what extent the hydrocoral depend on zooxanthellae is unknown, although growth rates decrease in reduced light (Strömberg, 1976). Millepora also feeds on small zooplankton which are captured by the gastrozooids and dactylozooids (deKruif, 1975). This helps explain why the planar colonies tend to orient perpendicularly to the current. This orientation maximizes capture area, although this orientation puts greater stress on the hydrocoral skeleton to withstand turbulence. The observation that fewer colonies orient perpendicularly in greater depths (Table 2) may be related to weaker water currents at these depths. An effective water current to carry zooplankton may not exist at 60'.

The milleporid colonies were also observed to encrust gorgonians and Acropora cervicornis. In fact, Wahle (1980) has shown that Millepora senses and actively grows towards gorgonians in order to encrust them. This encrusting growth form appears to be an adaptive strategy to increase surface area and thus light captured at minimal energy.



cost. The gorgonian also provides a large substrate area which is easily colonizable (Wahle, 1980). There is one disadvantage to this growth form, namely the encrusting layer eliminates the flexibility of the gorgonian, and the fire coral is highly susceptible to breakage. This was observed on a large scale after Hurricane Allen (Woodley et. al., 1981).

These theories which explain the distribution of growth forms of Millepora as seen on a depth gradient still leave the issue of taxonomy open to question. Stearn and Riding (1973) argue that this shift in growth form with depth is a species shift, not a continuous variation between growth forms. Furthermore, they noted a large overlap of the species at different depths. Their methodologies are very limited, however, since they only sampled to 33'. This study and one by De Weerd and De Kruijt (1979) refute their arguments. Many intermediate forms were found, sometimes in excess of 50%, and specific depths where each form dominates were noted (Table 1).

Since the only valid criterion for separating the species is the form of the corallum (Stearn and Riding, 1973) I feel the Millepora colonies are all variable forms of a single species. The different form distributions with depth are a function of light, wave energy, food availability, and substrate availability (i.e. a gorgonian). Two arguments support this 'one species hypothesis'. The first is the number of intermediate and encrusting growth forms. If 50% of the colonies are not categorizable, and there is already great variability within the species categories (Stearn and Riding, 1973)

Then no distinct growth forms occur. Rather, one species that is extremely plastic and able to assume many growth forms depending on microhabitat conditions is more likely to exist.

This is further supported by my second point, which is the amount of plasticity within one colony. Many colonies had large ( $>4\text{cm}^2$ ) encrusting bases, in addition to plates or branches. One colony at 40' showed a plate-like form, a rock encrusting form, a gorgonian-like encrusting form and finger-like projections off the gorgonian stalk. Such plasticity within a colony could surely account for the plasticity seen in the <sup>entire</sup> population over depth.

However, the only method to conclusively show whether the growth forms are one or three species is by histocompatibility graft experiments (Nildemann et al., 1977).

Recent studies by Müller et al. (1983) have indicated the histocompatibility experiments are feasible for Millepora.

However, it still would be difficult to find two clones with different growth forms to graft, especially if asexual reproduction is not the common reproductive mode. However, such a study, albeit a long shot, would conclusively settle the taxonomic argument of the Millepora species.

LITERATURE CITED

- Barnes, D. J. 1973. Growth in colonial scleractinians. *Bulletin of Marine Sciences* 23: 280-298.
- Brakel, W. N. 1976. The ecology of coral shape: microhabitat variation in the colony form and corallite structure of *Porites* on a Jamaican reef. Ph.D Thesis, Yale University. 246 pp.
- De Kruijt, H. A. M. 1975. General morphology and behavior of gastrozooids in two species of *Millepora* (Milleporina, Coelenterata). *Marine Behavioral Physiology* 3: 181-192.
- De Kleedt, W. and H. A. M. de Kruijt. 1979. On the growth forms of *Millepora*. *Caribbean Marine Biology Institute*, p. 58-59.
- Goreau, T. F. 1959. The ecology of coral reefs. I. Species composition and zonation. *Ecology* 40: 67-90.
- Goreau, T. F. 1963. Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Annals of New York Academy of Sciences* 109: 127-167.
- Graus, R. R. and I. G. MacIntyre. 1976. Light control of growth form in colonial reef corals: computer simulation. *Science* 193: 895-897.

Hildemann, W.H., R.L. Raison, C. Cheung, C.J. Hall, L. Akaka, and J. Okamoto. 1977. Immunological specificity and memory in a scleractinian coral. *Nature*, 270: 219-223.

Hughes, R.N. 1983. Evolutionary ecology of colonial reef organisms, with particular reference to corals. *Biological Journal of the Linnean Society* 20: 39-58.

Jaubert, J. 1977. Light, metabolism and growth forms of the hermatypic scleractinian coral Synaraea concinna Verrill in the lagoon of Moorea. *Proceedings of the Third International Reef Symposium*, pp 488-488.

Liddell, W.D. and S.L. Ohlhorst. 1981. Geomorphology and community structure of two adjacent reef areas, Discovery Bay, Jamaica. *Journal of Marine Research*, 39: 721-804.

Müller, W.E.G., A. Maichhofer, R.K. Zahn and I. Müller. 1983. Histoincompatibility reactions in the hydrocoral Millepora dichotoma. *Coral Reefs* 1: 237-241.

Stearns, C.W. and R. Riding. 1973. Forms of the hydrozoan Millepora on a recent coral reef. *Lethaia* 6: 187-200.

Strömberg, T. 1976. Skeleton growth of the hydrocoral Millepora complanata Lamour in relation to light. *Limnology and Oceanography* 21: 156-160.

Tunncliffe, V. 1981. Breakage and propagation of the stony coral Acropora cervicornis. Proceedings of the National Academy of Sciences, 78: 2427-2431.

———, 1983. Caribbean staghorn coral populations: pre-Hurricane Allen conditions in Discovery Bay, Jamaica. Bulletin of Marine Science. 33: 132-151.

Wahle, C.M. 1980. Detection, pursuit and overgrowth of tropical gorgonians by milleporid hydrocorals: *Perseus* and *Medusa* revisited. Science 209: 689-691.

Woodley, J.D., E.A. Chornesky, P.A. Clifford, J.B.C. Jackson, L.S. Kaufman, N. Knowlton, J.C. Lang, M.P. Pearson, J.W. Porter, M.C. Rooney, K.W. Rylaarsdam, V.J. Tunncliffe, C.M. Wahle, J.W. Walff, A.G.S. Curtis, M.D. Dallmeyer, B.P. Japp, M.A.R. Koehl, J. Neigel and E.M. Sides.  
1981. Hurricane Allen's Impact on Jamaican Coral Reefs.  
Science 214: 749-755

Excellent study and discussion.  
Superb coverage of literature.