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PHOTOADAPTATION BY REEF CORALS TO INCREASING DEPTH

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Running head: Photoadaptation to depth by corals

## ABSTRACT

Reef corals exist over a strong depth-mediated light gradient spanning at least two orders of magnitude; many species are present at all depths along this gradient. Mechanisms of photoadaptation to these extremes were determined for the massive Caribbean reef-building coral Montastrea annularis from 1 m, 10 m, and 30 m on a Jamaican fore-reef using an in situ respirometer.

The weight of chlorophyll per alga cell is positively correlated with depth (1-35 m,  $r = 0.53$ ,  $p < 0.05$ ), ranging from 1.8 to 4.2  $\mu\text{g Chl } a \text{ cell}^{-1}$ , but the number of algal cells per unit area is significantly negatively correlated with depth (1-35 m,  $r = -0.61$ ,  $p < 0.01$ ), ranging from  $3.2$  to  $0.8 \times 10^6 \text{ cell cm}^{-2}$ . The result of these inverse relationships is that the amount of chlorophyll per unit area is constant over this depth range ( $3.2$ - $8.5 \mu\text{g Chl } a \text{ cm}^{-2}$ ). Further, the maximum productivity rate ( $p_c$  net max and  $p_c$  gross max) on a per chlorophyll basis also does not vary significantly with depth ( $4.6$  -  $7.0 \mu\text{g O}_2 \mu\text{g Chl } a^{-1} \text{ h}^{-1}$  for net productivity versus  $6.7$  -  $10.6$  for gross). Both net and gross productivity per unit area, however, are significantly higher in shallow water ( $81.6$  net and  $110.1$  gross  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$  in shallow specimen, and  $39.3$  net and  $55.3$  gross in deep specimen,  $p < 0.05$ ).

$\alpha$  (the initial slope of the P:I curve) is significantly higher for 30 m specimen than for 10 m specimen on a per unit area basis ( $0.48$  for deep specimen versus  $0.27$  for 10 m specimen), but not greater than the 1 m specimen.  $\alpha$  also increases monotonically with depth on a  $\mu\text{g Chl } a$  basis, from  $0.04$  at 1 m to  $0.06$  at 30 m, but this difference is significant only at the 0.15 confidence level due to scatter in data from

the 1 m station.  $I_k$  (the  $p_{max}$  onset point) is significantly lower for deep specimen ( $117 \mu E m^{-2} s^{-1}$  at 30 m versus 227 at 1 m), and likewise the compensation point (at which  $P_c \text{ net} = 0$ ) is also significantly less for deep specimen ( $34 \mu E m^{-2} s^{-1}$  at 30 m versus 58 at 1 m) demonstrating further that deep-water corals are more sensitive to low light intensities than shallow-water corals.

Polyp density increases significantly in shallow ( $p < 0.05$ ) as compared to deep-water specimen, as does the amount of tissue nitrogen per unit area ( $p < 0.05$ ). Respiration rate per unit area ( $-28 \mu g O_2 cm^{-2} h^{-1}$  for shallow versus 16 for deep) is significantly greater in shallow water ( $p < 0.05$ ), reflecting both increasing tissue biomass, polyp density, and greater carbon fixation in shallow water. Neither weight-specific respiration rate ( $28 - 36 \mu g O_2 mg \text{ TKN}^{-1} h^{-1}$ ) nor average nocturnal respiration rate on a per polyp basis ( $1.7$  to  $4.5 \mu g O_2 \text{ polyp}^{-1} h^{-1}$ ) is significantly different at any depth.

Increasing the number of algal cells per mg TKN as well as increasing weight of Chl a per cell with increasing depth results in a slight increase in  $p_{max} / mg \text{ TKN}$  with respect to  $R / mg \text{ N}$ . This serves to maintain a positive oxygen balance in the face of declining irradiance with depth. Tissue biomass therefore appears to control the number of endosymbionts present since cell number ( $10^6 \text{ cells cm}^{-2}$ ) and pigment content ( $\mu g \text{ Chl a cm}^{-2}$ ) are both tightly correlated with  $mg \text{ TKN cm}^{-2}$ ,  $p < 0.05$ . Consequently maximum photosynthetic production rate per unit area is also positively correlated with  $TKN cm^{-2}$  ( $p < 0.05$ ).

These results show that Montastrea annularis utilizes classical plant photosynthetic responses to decreased light intensity by raising

photosynthetic efficiency at sub-saturating light intensities ( $\alpha$ ) on a per unit area basis and, to a lesser extent, on a chlorophyll a basis as well. Whole-organism responses include an increase in the number of polyps per unit area, tissue biomass per unit area, and consequently the respiration rate in shallow water. P/R ratios are raised by doubling  $p_c$  gross above the level expected in the absence of photoadaptation, and by decreasing R by a factor of 2 at 30 m.

The overall result of these depth-related biological accommodations is to keep the integrated 24 hour gross ( $P_c$  gross /  $R_c$  24 hr total) ratios in excess of unity at all depths (1.8 P/R at 1 m, 1.2 at 10 m, and 1.3 at 30 m) under idealized irradiance conditions. Using interpretive models and defined biomass assumptions, we demonstrate that specimen at all depths meet all of their carbon and caloric requirements through photosynthesis under idealized light conditions. With ambient light levels at or above 56% of "cloudless day" conditions, corals from 1 m can meet their carbon and caloric requirements from photosynthesis. Corals from 10 and 30 m, however, require 80% or greater of the idealized irradiance to be self-sufficient. The results also show that if there were no photoadaptive response, deep-water specimen would acquire from photosynthesis less than half of their required carbon.

## INTRODUCTION

Reef building corals are symbiotic with the photosynthetic intra-cellular dinoflagellate alga Symbiodinium microadriaticum (Freudenthal) and exist over a strong light gradient associated with a natural depth range for coral of more than 70m. Several species, such as Montastrea annularis (Linnaeus) are present across this entire gradient (Goreau and Wells, 1976, pers. observ.). Exchange of material between host cnidarian tissue and endosymbiotic algae is well documented (Muscatine, 1980; Cook, 1983) and includes translocated carbon in the form of glycerol, alanine, and other low molecular weight carbon compounds (Muscatine, 1980; Trench, 1971a and b) as well as substantial amounts of lipid material (Crossland and Barnes, 1977; Crossland et al., 1980; Patton et al., 1977; Patton et al., in press).

Using defined biomass assumptions regarding the percent of photosynthetically fixed material translocated to the animal from the algae, and the percent of total colony metabolism attributable to the animal fraction, we have developed a theoretical framework in which to interpret integrated metabolic oxygen flux data (Porter, 1980; Muscatine, 1980; Muscatine et al., 1981). Actual demonstration of the caloric and carbon value of the symbiosis to corals reveals that for at least one branching species of Indo-Pacific coral, Stylophora pistillata (Esper), photosynthesis can meet all of its integrated daily requirements (Porter et al., in review; Muscatine et al., in review).

The relationship between light intensity and production has been modeled (Chalker, 1980) and quantified for several Pacific species (Wetthey and Porter, 1976; Falkowski and Dubinsky, 1981; and Kevin and

Hudson, 1979) and several Caribbean species (Chalker and Taylor, 1978; Porter, 1980) including Montastrea annularis (Barnes and Taylor, 1973). Likewise, the relationship between light intensity and calcification rate has been estimated for several corals (Goreau, 1959; Chalker and Taylor, 1978; Crossland and Barnes, 1977; Chalker, 1981). These production-irradiance curves, or calcification-irradiance curves have been determined using specimen from a single depth, generally from shallow water, and often under laboratory rather than submarine conditions.

Light intensity in reef waters has been shown to decrease logarithmically with depth increase (Wells, 1957; Brakel, 1979; Dustan, 1982). Since one can calculate productivity from knowledge of light intensity, based on determined P:I curves, it is tempting to extrapolate from productivity changes induced by diurnally ascending and descending light intensity to productivity changes induced by increasing depth. If P:I curves established for species from a single depth were representative for all depths, such a simple relationship would prove to be a powerful tool for ecosystem-level modeling of community productivity. Graus and Macintyre (1976) model coral growth and form in Montastrea annularis as a function of depth and make the assumption of a linear relationship between depth-related light intensity decrease and calcification rate.

We have established that several critical photosynthetic characteristics as well as overall metabolic parameters are not linearly related to light intensity but depend very much on the light history of the association (Porter et al., in review). In this respect, corals are similar to algae growing under differing light regimes (Falkowski, 1981). Further, for at least two species of coral, Acropora cervicornis from the

Atlantic (Porter, 1980), and Pavona praetorta from the Pacific (Wetthey and Porter, 1976), we also have evidence suggesting that depth differences effect photosynthetic characteristics as well as shading.

We are hampered in the creation of an ecologically useful model of coral growth and photosynthesis by three related lacunae in our knowledge: (1) the relationship between productivity and depth, (2) the relationship between daily production to respiration ratios, depth, and the contribution of algal photosynthesis to the coral animal's energetics, and (3) the relationship between photosynthesis and calcification. In this paper, we examine the first two of these points for the reef-building coral Montastrea annularis through analysis of oxygen flux data obtained with an in situ respirometer (Porter, 1980). These data are used to define the relationship between photosynthesis and light under natural irradiance conditions as well as respiration rates for specimen of M. annularis from depths of 1 to 30 m. Integrated 24 hour totals for gross photosynthesis and respiration are computed and used to assess the contribution of the endosymbiotic algae to the animal's energy requirements. Concurrent measurements of zooxanthellae photosynthetic pigment content, cell density, coral tissue biomass, and colony morphology are described in terms of their influence on the depth-dependence of photosynthesis and respiration in this species. Finally, we compare accomodations of the M. annularis symbiosis to depth-related changes in irradiance with patterns of photoadaptation associated with shading.

FIGURE 1 HERE

## MATERIALS AND METHODS

### Research locality

Caribbean reef environments frequently have eighty percent or greater cover by scleractinian corals from the surface to 50 meters (Porter et al., 1981). The most ubiquitous coral over the full extent of this depth range is the head-coral, Montastrea annularis (figure 1). In addition to this species' ubiquity, several intermediate and deep regions of the reef are dominated by this species on a planar projection basis (Porter et al., 1981).

### Collection

Sister colonies of Montastrea annularis were collected from depths of 10 m, 20 m, and 30 m on Long Term Sampling Reef (LTS) and from 1 m depth in the back-reef off the Discovery Bay Marine Laboratory, Jamaica, West Indies. Fragments of M. annularis are known to repair rapidly after being removed from a large colony (Bak et al., 1977). Specimen were left on the reef for 24 hours prior to being placed in experimental chambers. Replicate colonies from 1 m, 10 m, and 30 m were maintained under ambient conditions for 24 hours after removal from the substrate. The oxygen metabolism of these corals was then monitored for 24 hours using an in situ respirometer (Porter, 1980). Experimental chambers are stirred at 100 RPM by three-inch stir magnets and are flushed completely at four hour intervals. All coral specimen were returned to the laboratory in shaded buckets of seawater and maintained in running seawater until processed for biomass analysis.

### Biomass Analysis

All corals were processed within three hours of their return to the

laboratory. Coral tissue was cleared from the skeleton using the water-pick method (Johannes and Wiebe, 1970). The tissue slurry that resulted was further homogenized for one minute in a blender and the resulting solution subsampled for total nitrogen, zooxanthellae cell counts, and chlorophyll analyses. Total colony surface area was determined by fitting aluminum foil to the surface of the coral (Marsh, 1970). The area of the aluminum foil pieces was determined using a Hewlett Packard 9864A digitizer.

#### Photosynthetic Pigment Analysis and Cell Counts

Zooxanthellae cell densities were estimated from counts on a hemocytometer using either fresh tissue homogenate or Lugol's preserved homogenate.

Photosynthetic pigment content per zooxanthella cell was determined by centrifuging aliquots of the initial homogenate, washing and resuspending the algal pellet in fresh 0.45  $\mu\text{m}$  filtered seawater, and centrifuging at successively slower speeds. A minimum of three washes was required to obtain a pellet free of animal tissue. The total number of zooxanthellae cells in the pellet was estimated from replicate hemocytometric counts of this fresh material. Chlorophylls a and c<sub>2</sub> were extracted with cold 100% acetone in darkness until the algal pellet was devoid of color. Chlorophyll weights were then determined spectrophotometrically using the equation of Jeffrey and Humphrey (1975).

Total chlorophyll a content was assayed for a second series of respirometer corals using 90% acetone extracts of whole coral homogenate and analyzing these extracts on a Turner 110 fluorometer calibrated according to the methods of Holm-Hansen et al. (1965).

### Tissue Biomass

Aliquots of the water-picked homogenates were preserved with 4% unbuffered formalin in filtered seawater. These samples were subsequently analyzed for total nitrogen content using a micro-Kjeldahl digestion and ammonium content of the digests determined on a Technicon Autoanalyzer using standard methods (EPA, 1974).

### Polyp Number and Calyx Diameter

The tissue-free corallum of the experimental corals were assayed for polyp density by counting the number of polyps contained within 10 randomly positioned 1 cm<sup>2</sup> grids on each coral colony. Polyp diameter was estimated as the distance from edge to edge of the coral calix of 20 randomly selected polyps on each individual colony. The diameter was measured to the nearest 0.05 mm using a pair of steel vernier calipers.

### TABLE 1 HERE

### Analysis of Oxygen Flux Data

Oxygen concentration in three experimental chambers as well as ambient light intensity (Photosynthetically Active Radiation, determined by an in situ 4-pi LiCor irradiance sensor) was recorded on magnetic tape every minute for the 24 hour interval of the experimental incubations. Tapes from each experiment were subsequently read into a Tektronics 4054 microcomputer where four consecutive one-minute readings are averaged for each channel. Consecutive averages are then subtracted from one another, and the result multiplied by volume of the water in the incubation chambers to give net rates of oxygen production or consumption ( $\mu\text{g O}_2 \text{ h}^{-1}$ ). These oxygen flux values can then be normalized to any of the biomass units described above and can be converted to carbon equivalents by multiplying

by 0.375 and negative fluxes by the respiratory quotient and positive oxygen fluxes by the photosynthetic quotients (Muscatine et al., 1981).

Photosynthesis versus irradiance curves were then constructed for each experimental coral by computing average fluxes over small intervals of light intensity (maximum interval  $50 \mu E m^{-2} s^{-1}$ ). Average and standard error values for photosynthesis are reported only for light intensities in which three or more production values exist. These points are then fitted to a hyperbolic tangent function (Jassby and Platt, 1976):

$$p_c \text{ net max} = p_c \text{ gross max} [ \tan (\alpha I / p_c \text{ gross max}) ] - r_c$$

where  $p_c \text{ net max}$  = maximum net coral head photosynthetic oxygen flux per unit biomass,  $p_c \text{ gross max}$  = light saturated photosynthetic oxygen flux.  $\alpha$  = initial light-limited slope,  $I$  = ambient PAR irradiance, and  $r_c$  = average dark respiration rate of the experimental coral.

The two parameters describing the hyperbolic tangent function are fitted to the data set using a nonlinear least squares regression program based on a Marquardt algorithm (Draper and Smith, 1966). Initial estimates of  $\alpha$  are obtained by linear regression of the light-limited oxygen fluxes. All night-time respiration values are averaged to calculate  $r_c$ .

The best-fit hyperbolic tangent function also computes coral colony compensation point ( $I_c$ ) and the break point ( $I_k$ ) where the P:I curve becomes non-linear and the onset of  $p_c \text{ max}$  begins.

Integrated 24 hour production values ( $P_c$  net total,  $P_c$  gross) are obtained by integrating under positive oxygen fluxes modeled by the hyperbolic tangent function responding to the continuous record of ambient irradiances obtained during each experimental incubation. Conversely, respiration ( $R_c$  net total) is obtained by integrating under the curve of negative oxygen fluxes. Total respiration ( $R_c$  24 hrs) is obtained by multiplying the average night-time respiration rate by 24.

Cloud conditions during the 1 m and 30 m incubations prevent direct comparison of integrated oxygen fluxes. Consequently, these values are obtained ( $P_c$  gross, idealized light) using idealized irradiances generated from a sine function:

$$I = I_{\max} [\sin (T/D)]$$

where  $I_{\max}$  = maximum intensity at solar noon ( $\mu E m^{-2} s^{-1}$ ),  $D$  = day length in hours,  $T$  = hours since sunrise. Values for  $I_{\max}$  were determined from in situ measurements using a LiCor 192S quantum sensor calibrated to a LiCor 185 meter. For 1 m,  $I_{\max} = 1,200$ , for 10 m,  $I_{\max} = 600$ , and for 30 m,  $I_{\max} = 250 \mu E m^{-2} s^{-1}$ .

The ratio of gross photosynthesis to total irradiance can also be calculated from either field or simulation irradiances.

#### Interpretative Model

In order to interpret the value of carbon fixed during photosynthesis to the host coral, we must estimate the amount available for transport to the coral ( $P_z$  net 24 hrs) as well as the percent of this material actually moved to host tissue (% translocation).

The expanded formula for  $P_z$  net 24 hrs is:

$$P_z \text{ net 24 hrs} = [(P_c \text{ gross})(\div PQ_z)] - [(\% \text{ of } R_c \text{ belonging to } R_z)(R_c)(RQ_z)].$$

$$R_a \text{ 24 hrs} = (\% \text{ of } R_c \text{ belonging to } R_a)(R_c)(RQ_a).$$

The methodology for estimating percent translocation is still in dispute (Muscatine et al., in review). We estimated minimum values of this term as 40 percent, measuremented by short-term  $^{14}\text{C}$  bicarbonate incubations on Montastrea annularis (Battey and Porter, in review), and maximum values of this term as 95 percent, extrapolated from cell division rates (Muscatine et al., in review) in order to ascertain the potential range in contribution of endosymbiont photosynthesis to animal respiration.

Applying PQ values of 1.1, and RQ values of 0.8 (Fitt and Pardy, 1981; Fitt et al., 1982; Muscatine et al., in review) allows us to calculate the percent of animal needs met by photosynthesis and translocation by the symbiotic algae. Based on literature values (Muscatine et al. in review), we model the effects of respiratory biomass positing that 95 percent of the total respiration ( $R_c$ ) belongs to the animal ( $R_a$ ) and 5 percent to the plant ( $R_z$ ); or alternatively 50 percent to each.

Our calculation of the ratio of  $P_z$  net 24 hrs /  $R_a$  24 hrs is similar to other developments of this model with the exception that our  $P_z$  net values take into account the 24 hr respiratory demands of the zooxanthellae rather than just zooxanthellae respiration occuring during daylight hours (Muscatine et al., 1981).

## RESULTS

Biomass Values

Table 1 lists variation in algal cell density, photosynthetic pigment content, nitrogen biomass, and gross morphological characteristics with respect to depth from 1 m to 35 m. These patterns, and their relationship to coral metabolism are plotted in figures 2 - 6. These values demonstrate several significant biomass modifications with increasing depth.

## FIGURE 2 HERE

The number of zooxanthellae cells per  $\text{cm}^2$  of coral surface is negatively correlated with depth from 1 to 35 m (figure 2 a; table 1). The best fit regression may be expressed as  $10^6 \text{ cells cm}^{-2} = 3.01 - 0.06 (\text{depth})$ ,  $r = -0.61$ ,  $p < 0.01$ ,  $N = 30$ . Corals from 1, 10, and 30 m have densities of 3.20, 2.92, and  $2.40 \times 10^6 \text{ cells cm}^{-2}$  respectively (a 25% decrease, table 1). In contrast to the cell density reduction, zooxanthellae chlorophyll a concentration increases with depth ( $r = 0.53$ ,  $p < 0.05$ ,  $N = 21$ ) from  $2.69 \text{ pg cell}^{-1}$  at 1 m to 4.21 at 35 m (table 1). There is a significant linear regression of chlorophyll a per cell and depth obtained for corals from 10-35 m (figure 2 b). The regression may be expressed as  $\text{pg Chl a cell}^{-1} = 1.03 + 0.09 (\text{depth})$ ,  $r = 0.88$ ,  $p < 0.001$ ,  $N = 14$ . No significant depth variation in the chlorophyll a /  $\text{c}_2$  ratio is observed from 1 to 35 m (table 1).

The overall effect of these inverse trends is to keep chlorophyll content per unit area relatively constant between 1 to 35 m (Figure 2 c, table 1). Corals from the 1, 10, and 30 m sites have mean values of 8.32, 5.34, and  $8.49 \text{ } \mu\text{g Chl a cm}^{-2}$  (table 1).

A 48 percent reduction in tissue biomass as measured by total Kjeldahl nitrogen per  $\text{cm}^2$  occurs between the shallow and deep water stations falling from  $0.96 \text{ mg TKN cm}^{-2}$  to  $0.50 \text{ mg TKN cm}^{-2}$  at 30 m ( $p < 0.001$ ) (table 1, figure 3 c). The variation in tissue nitrogen can be described as a hyperbolic function of depth [ $\text{mg TKN cm}^{-2} = 0.45 + 0.51 (\text{depth}^{-1})$ ,  $R^2 = 0.77$ ,  $p < 0.001$ ,  $N = 10$ ]. The majority of the reduction in tissue nitrogen content occurs between 1 and 10 m. Although the number of zooxanthellae cells per  $\text{cm}^2$  decreases with depth, zooxanthellae density per mg TKN increases by 35 percent from 1 to 10 m and by 23 percent between 1 and 30 m ( $3.8, 5.9$ , and  $5.0 \times 10^6$  cells  $\text{mg TKN}^{-1}$  at 1, 10, and 30 m, respectively,  $p < 0.025$ ,  $N = 10$ ) reflecting the reduction in tissue nitrogen content with depth.

#### FIGURE 3 HERE

Polyp density decreases with depth (figures 1 and 3 a), where  $\text{polyp cm}^{-2} = 12.38 - 0.25 (\text{depth})$ ,  $r = -0.92$ ,  $p < 0.001$ ,  $N = 20$ . In contrast, polyp diameter (cm) is positively correlated with depth (figures 1 and 3 b), where  $\text{polyp diameter} = 0.22 + 0.003 (\text{depth})$ ,  $r = 0.85$ ,  $p < 0.001$ ,  $N = 20$ . These patterns result in a decline in total polyp area, as represented by the percent of colony surface occupied by polyp calicies, with depth (figure 1, table 1).

The result of these trends in polyp morphology and tissue biomass distribution is that there is a reduction in nitrogen content from 1 to 10 m followed by an increase in polyp mass at 30 m, reflecting the depth-dependent increase in polyp size (table 1, figures 1b - d).

### Photosynthesis : Irradiance profiles

Analysis of the parameters of the hyperbolic tangent function describing the dependence of photosynthetic rate on ambient irradiance in colonies of Montastrea annularis reveals several responses by the algal symbionts and the association to reduction in incident light with increased depth. Parameters of the photosynthetic response curves are presented in table 2, and fitted curves with associated oxygen flux data (mean  $\pm$  one S.E. for each replicate) are normalized to living coral surface area in figures 4 a - d and to chlorophyll a content in figures 4 e - f. These patterns demonstrate that the ambient light available in the growth position of the coral has a significant effect on specific characteristics of the photosynthetic response curve. Determination of these parameters allows us to model photosynthetic responses under different solar inputs and estimate the percent of daily carbon and caloric requirements met by photosynthesis of the zooxanthellae.

#### TABLE 2 HERE

The light-limited region, or initial slope of the photosynthetic response curve,  $\alpha$ , for data normalized to surface area, is significantly higher for corals from 30 m than from 10 m (0.48 versus 0.27  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1} \mu\text{E m}^{-2} \text{ s}^{-1}$ ,  $0.10 > p > 0.05$ ,  $N = 10$ ; table 2, figures 4 a - d), but equivalent to that of corals from 1 m (0.49). In contrast, when the data are normalized to chlorophyll a content (table 2, figures 4 e - g), there is a tendency for  $\alpha$  to increase with habitat depth, although the differences are not statistically significant (0.04, 0.06, and 0.06  $\mu\text{g O}_2 \text{ Chl a}^{-1} \text{ h}^{-1} \mu\text{E m}^{-2} \text{ s}^{-1}$  at 1, 10, and 30 m respectively,  $r = 0.49$ ,  $0.20 > p > 0.10$ ,  $N = 10$ ) possibly due to scatter in the data

from the cloudy-day run in shallow water. Corals from 30 m also have a significantly higher  $\alpha$  than corals from either 1 m or 10 m when estimated from photosynthetic rates per zooxanthellae cell (0.22 versus 0.11 and 0.10  $\mu\text{g O}_2 \cdot 10^6 \text{ zoox}^{-1} \text{ h}^{-1} \mu\text{E m}^{-2} \text{ s}^{-1}$ ,  $p < 0.05$ ,  $N = 10$ , table 2). The enhanced capacity for photosynthesis under light-limited conditions exhibited by corals from the 30 m habitat indicates a photosynthetic response by the zooxanthellae to the reduced ambient irradiance associated with increasing depth.

#### FIGURE 4 HERE

When normalized to coral surface area, the light-saturated photosynthetic rate,  $p_c$  net max (figures 4 a - d, and 6a, and table 2), and  $p_c$  gross max (table 2) decreases by a factor of two between 1 and 10 m, with no change occurring between 10 and 30 m (110.1 versus 57.0 and 55.3  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$  at 1, 10 and 30 m respectively,  $p < 0.05$ ,  $N = 10$ ). Corals from 30 m exhibit a reduced chlorophyll a specific maximum gross photosynthetic rate compared to corals from 1 and 10 m (6.7 versus 9.3 and 10.6  $\mu\text{g O}_2 \mu\text{g Chl a}^{-1} \text{ h}^{-1}$ , respectively,  $0.20 > p > 0.10$ ,  $N = 10$ , figures 4 e - g and 6b, and table 2). The zooxanthellae specific maximum rate is equivalent at all depths, however (25.9, 19.1 and 22.6  $\mu\text{g O}_2 \cdot 10^{-6} \text{ zoox}^{-1} \text{ h}^{-1}$  at 1, 10, and 30 m respectively,  $p > 0.20$ ,  $N = 10$ , table 2.)

The chlorophyll and cell-specific maximum photosynthetic rates, as well as the  $\alpha$  values, indicate that the zooxanthellae of Montastrea annularis increases the size of their photosynthetic unit rather than the number of PSU's in response to reduced ambient light conditions. This is evidenced by increased efficiency of low-light utilization ( $\alpha$ ), reduction in maximum

photosynthetic rate per unit chlorophyll, and equivalence of cell-specific light saturation rates (Prezelin, 1981; Richardson *et al.*, 1983).

Several trends in biomass-specific respiration rate result from these biomass changes (table 1). The most important fact is that dark respiration rate,  $r_c$ , normalized to coral surface area, increases significantly in shallow water, resulting in a 43 percent difference in  $r_c$  between 30 and 1 m (28.2, 19.9, and 16.0  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$  at 1, 10, and 30 m respectively,  $p < 0.05$ ,  $N = 10$ ; figures 2 a - d and 6a, and table 2). This trend follows a pattern similar to that of maximum photosynthetic rate, which declines by 29 percent in the first ten meters (table 2) and is also significantly lower at 30 m than at 1 m (figure 6a). The similarity in the pattern of reduction in photosynthetic rate and respiration rate is consistent with a reduction in coral biomass per unit area associated with increasing depth (table 1, figure 3c).

Due to rapidly declining weight of tissue nitrogen with increasing depth (table 1), respiration rate per unit nitrogen increases consistently, but not significantly, with increasing depth (27.7, 36.5, and 36.4  $\mu\text{g O}_2 \text{ mg TKN}^{-1} \text{ h}^{-1}$  from 1, 10, and 30 m respectively,  $0.20 > p > 0.10$ ,  $N = 10$ , table 2).

The theoretical intersection of the initial slope with the light-saturated photosynthetic rate ( $I_k$ ) declines from 227  $\mu\text{E m}^{-2} \text{ s}^{-1}$  at 1 m to 117  $\mu\text{E m}^{-2} \text{ s}^{-1}$  at 30 m ( $p < 0.05$ ).  $I_k$  is not significantly different between 1 and 10 m.

The compensation light intensity,  $I_c$  (where net coral photosynthesis rate = 0) is lowest for corals at 30 m (34  $\mu\text{E m}^{-2} \text{ s}^{-1}$  at 30 m versus

$58 \mu E m^{-2} s^{-1}$  at 1 m,  $0.10 > p < 0.05$ , table 2). The magnitude of  $I_c$  is dependent on  $\alpha$  as well as on the dark respiration rate of the coral colony (multiple correlation,  $r = 0.99$ ,  $p < 0.01$ ). As with  $I_k$  values, compensation points between 1 and 10 m are not significantly different.

#### Diel photosynthesis and respiration

Analysis of photosynthesis : irradiance profiles gives an indication of photoadaptation by the Montastrea annularis symbiosis in terms of their short-term response to light intensity variation. Of greater importance, with respect to growth and survival of the association, are influences these rate adaptations exert on daily integrated values of photosynthesis and respiration (table 3). A comprehensive understanding of these metabolic totals also allows an insight into the percent of daily requirements met by algal photosynthesis.

#### TABLE 3 HERE

Diel patterns of oxygen flux and ambient irradiance are presented along with the estimated oxygen flux curve based on the P to I analysis for representative corals from 1, 10 and 30 m (figures 5 a, b, and c). Mean values of total coral net photosynthesis and net respiration,  $P_c$  net and  $R_c$  net normalized to coral surface area, are presented in table 3. Both net photosynthetic production and net respiration decline with increasing depth mimicking the depth-dependent declines in light-saturated photosynthesis and dark respiration rate (table 2).

#### FIGURE 5 HERE

Estimates of integrated respiratory demands ( $R_c$  24 hrs) are

significantly higher for colonies of Montastrea annularis from 1 m as compared to those from 10 or 30 m (677 versus 477 or 383  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ d}^{-1}$ , respectively,  $p < 0.05$ , table 3).

Cloud cover during the 1 and 30 m incubations (figures 5 a and c) precludes direct comparison of integrated gross production values under in situ light regimes. Consequently, gross production estimates were computed by integration of the oxygen flux curves derived from the application of sinusoidal light regimes to the P versus I response curves of the experimental corals. These values are listed in table 3 as "idealized light" values. Data obtained from these simulations are in good agreement with with gross production values for corals under natural field conditions (table 3). Under cloudy field conditions, gross production decreases by 69 percent between 1 and 30 m (840 to  $262 \mu\text{g O}_2 \text{ cm}^{-2} \text{ d}^{-1}$ ) whereas a 60 percent decline in gross production is observed using the idealized light regimes (table 3). It must be kept in mind that these idealized values are used as a basis for comparison between experiments conducted under variable weather patterns; these "idealized light" values would be unrealistically optimistic predictors of sustained field production levels.

By setting respiration rate to zero, idealized gross productivity totals for shallow water corals can be estimated at  $1187 \mu\text{g O}_2 \text{ cm}^{-2} \text{ d}^{-1}$ , slightly more than double that for deep water corals, which produce  $470 \mu\text{g O}_2 \text{ cm}^{-2} \text{ d}^{-1}$  during the same 24 hour period. Gross totals at 10 m and 30 m are not significantly different. Depth-related reductions in gross production by Montastrea annularis colonies reflect reductions in daily irradiance with depth (table 3). They exemplify the significance of zooxanthellae photoadaptation to coral production values: integrated

irradiance declines 80 percent from 1 to 30 m compared to only a 60 percent reduction in gross production over the same depth range.

#### FIGURE 6 HERE

The integrated gross production to respiration rate,  $P_c \text{ gross} / R_c \text{ 24 hrs}$  (table 3), is a maximum estimate of the contribution of zooxanthellae photosynthesis to the energy and carbon requirements of the symbiotic corals. This value declines with depth (table 3), as a result of the differential reduction in gross photosynthesis (60 percent) and respiration (43 percent) from 1 to 30 m. These ratios indicate that, in general, colonies of Montastrea annularis from 1 m habitats will receive a greater proportion of their energy requirement (potentially > 100 percent) than corals from deeper habitats. Corals from 10 and 30 m may exhibit ratios in excess of 1 only under full sunlight conditions. Reductions in irradiance due to cloud cover cause this ratio to fall below 1 with the effects most pronounced at the 30 m depth contour (1.34 in full sunlight to 0.75 under cloudy conditions). Since cloud cover is expected under natural conditions, deepwater M. annularis are probably existing under gross P/R ratios less than unity.

A sense of the differing photosynthetic performance between shallow and deep specimen can be obtained by comparing the amount of photosynthetic fixation per unit light (figure 7, table 3). This ratio demonstrates that deep water specimen are significantly more adept at utilizing ambient irradiance than shallow water specimen are at using their own ambient irradiance ( $0.84 \text{ versus } 0.43 \text{ g O}_2 \text{ E}^{-1}$ ,  $p < 0.05$ ). Subjecting corals from 1 and 10 m to the idealized light regime found at 30 m, however, reveals that the ratios of shallow-water corals under

## DISCUSSION

Biomass Values

The response of algal-coelenterate symbiotic associations to habitat variation in light intensity may occur by metabolic changes at the level of the individual cosymbiont or by an integrated response of the association. Our analysis of oxygen metabolism of Montastrea annularis over a depth-dependent light gradient reveals that responses occur at both levels.

Dustan (1982) reported chlorophyll concentration per zooxanthellae cell between 2.94 and 4.43 pg cell<sup>-1</sup> in Montastrea annularis and initially claimed to have identified a significant decrease in pigment content per cell with increasing depth (Dustan, 1979). This range is similar to values reported in the present study (table 1), but our data demonstrate a significant increase in chlorophyll content with depth (table 1). Dustan (1982), after recalculating his data, suggests a "bimodal pattern" in photosynthetic pigment content with depth, but the data presented demonstrate no significant increase in chlorophyll content with increasing depth to 50 m. Dustan (1982) comments, however, that if his data set is "disregarded [sic] there appears to be a consistent general increase in photosynthetic pigment content per cell with depth."

Our results demonstrate that the chlorophyll a content per zooxanthellae cell is higher in specimen from deeper, lower irradiance environments. These results are consistent with data for corals growing in shade (Porter et al., in review). The increase in chlorophyll a per cell is similar in direction, but different in magnitude between these two studies. Zooxanthellae from Stylophora pistillata colonies growing

response to light reduction caused by shading shows no cell density change. This can be restated that cell density correlates with depth and not with light intensity per se. On a  $\text{cm}^2$  basis, these trends will be related to differences in coral tissue biomass per unit area.

The weight of chlorophyll a per unit area of coral surface is highly variable and exhibits no systematic or significant trend with depth between 1 and 30 m. This is consistent with other published studies (Dustan, 1979 and 1982; Falkowski and Dubinsky, 1981; Titlyanov et al., 1980). The apparent independence of areal chlorophyll content and ambient light regimes in Montastrea annularis is in striking contrast to the differences in chlorophyll a content per unit area in light and shade-adapted colonies of Stylophora pistillata where shade forms have 400 percent higher chlorophyll content (Falkowski and Dubinsky, 1981; Porter et al., in review). The differences in variation in the areal chlorophyll content with respect to ambient irradiance are due in part to previously described differences in total irradiance experienced by the corals as well as responses of zooxanthellae cell density and chlorophyll a content per cell between colonies of M. annularis and S. pistillata.

Chlorophyll a /  $c_2$  ratios are constant over depth (table 1) similar in response to shaded corals (Porter et al., in review), but dissimilar to this ratio over greater depth extremes in M. annularis (Battey and Porter, in review).

Our counts for polyp number per unit area at the three depths

demonstrate a significant reduction in polyp number with increasing depth as well as a significant increase in the size of polyp with increasing depth (table 1, figures 3 a and b). While Dustan (1979) likewise finds a reduction in polyp density with increasing depth, he also claims that polyp diameter does not increase. This is incorrect as indicated by the data in figure 3 b and visually in figure 1. Our results demonstrating a reduction in polyp density under conditions of reduced light due to depth are consistent with data from corals growing in shade (Porter et al., in review). These data suggest that a general response to decreased light, either due to shading or depth, is a reduction in polyp density, possibly resulting from a reduction in growth rates or changes in the major axis of skeletal growth (Dustan, 1975 and 1979).

Total Kjeldahl nitrogen content per unit area of coral tissue is significantly lower in corals from the 10 and 30 m habitats compared with those from 1 m (table 1, figure 3 c). We also observed a decline in tissue biomass of Montastrea annularis measured as protein content per unit area (Bsttey and Porter, in review). A similar trend has been observed for light and shade colonies of Stylophora pistillata, with shade colonies having lower nitrogen content (Porter, et al., in review). S. pistillata colonies growing in the light have  $0.29 \text{ mg TKN cm}^{-2}$ ; those growing in shade have  $0.18 \text{ mg TKN cm}^{-2}$ . Therefore the large-polyped, mound-building coral M. annularis is roughly three times as fleshy as the branching coral S. pistillata.

A general response to light reduction due either to shade or depth appears to be a reduction in tissue nitrogen weight per unit area. This response is a reflection of the reduction of light energy available for photosynthesis under these conditions.

The number of zooxanthellae, and consequently the areal productivity of Montastrea annularis appears to be controlled by tissue biomass. Zooxanthellae cell number and weight of chlorophyll a per unit area are both positively correlated with the nitrogen content per unit area ( $r = 0.66$ ,  $p < 0.001$ ;  $r = 0.74$ ,  $p < 0.001$ ,  $N = 19$ , respectively). When normalized to total nitrogen content, zooxanthellae cell density and chlorophyll a concentrations increase with habitat depth. This is true also for Stylophora pistillata (Porter et al., in review). These trends suggest that while there is a general reduction in coral and algal biomass per unit area with increasing habitat depth or shade. The number of photosynthetic components per weight of tissue increases with increasing depth, leading to an enhancement of photosynthetic production under light-limited conditions (figure 6).

#### Photosynthesis : Irradiance Curves

Specimen of Montastrea annularis from 30 m have higher initial slopes ( $\alpha$ ) of the photosynthesis-irradiance response curve than corals from 10 and 1 m when the photosynthetic rates are normalized to chlorophyll a and zooxanthellae number (table 2). This relationship indicates that one function of the higher chlorophyll a content per zooxanthellae cell in deep water is to increase the efficiency of the utilization of low light levels. An increase in  $\alpha$  with increasing habitat depth has been observed in other coral species (Wetthey and Porter, 1976) and phytoplankton raised

under low light conditions (Prezelin and Sweeney, 1978; Richardson et al., 1983).

When the photosynthetic rates are normalized to coral surface area, the resultant  $\alpha$  values are similar at 1 and 30 m and higher than the value for 10 m corals (table 2; figure 4). A significant positive correlation exists between  $\alpha$  per  $\text{cm}^2$  and chlorophyll a per  $\text{cm}^2$  ( $r = 0.74$ ,  $p < 0.05$ ,  $N = 10$ ) suggesting that the utilization of low light intensities by the coral symbiosis is influenced not only by pigment concentration of the zooxanthellae cell, but also by algal cell density in the coral tissue.

In striking contrast, shade-adapted colonies of Stylophora pistillata have significantly lower  $\alpha$  on a per unit chlorophyll a basis, but significantly higher  $\alpha$  on a per  $\text{cm}^2$  basis compared to light-adapted colonies (Falkowski and Dubinsky, 1981; Porter et al., in review). This pattern is consistent with a model for control of  $\alpha$  on a per  $\text{cm}^2$  by colony chlorophyll a content since shade colonies of S. pistillata maintain higher chlorophyll a concentration per  $\text{cm}^2$ . The smaller  $\alpha$  values on a per chlorophyll a basis in shade colonies suggests that although increasing chlorophyll a content per  $\text{cm}^2$  enhances utilization of low light intensities, such large increases in chlorophyll a content per cell (Porter et al., in review) has the concomitant cost of self-shading (Platt and Jassby, 1976; Dubinsky et al., in review).

$\alpha$  correlates more strongly to  $p_c$  gross than to  $I_{\text{max}}$  suggesting that the the slope of this line is as much controlled by the difference between nocturnal respiration rate and diurnal production rate as by the ambient irradiance regime. Particularly if it is true that respiration rate is stimulated under high light intensity (next section), then  $\alpha$  will prove to be high under high light conditions due to the increased distance

between  $p_c$  net max and respiration, as well as at low light intensity where its value is controlled by changes in chlorophyll pigment content relative to accessory pigments. This might explain high  $\alpha$  per  $\text{cm}^2$  values at 1 and 30 m (table 2).

Accessory pigments are more sensitive to blue light and are known to increase with increasing depth in Montastrea annularis (Dustan, 1982; Battey and Porter, in review). Such an increase in accessory pigments has not yet been documented in colonies from shallow shaded regions. A working hypothesis therefore might be that adaptation to increased depth involves an increase in accessory pigment concentration to accommodate depth-mediated shifts in spectral quality, and to a lesser extent, relative to shade-adaptation, an increase in chlorophyll a concentration to increase low light interception. Adaptation to shade in shallow water, however, might involve mostly a proportionally greater increase in chlorophyll a concentration. This hypothesis could explain contrasting patterns of chlorophyll measures of  $\alpha$  between adaptation to depth versus shade. Differences between spectral quality shifts accompanying shade and increased depth are needed before this idea can be evaluated.

Both compensation point ( $I_c$ ) and saturation - initial slope intersection point ( $I_{k'}$ ) occur at lower light intensities as depth increases (table 2), regardless of which normalizing biomass units are employed. Davies (1977) also measured declining compensation points on laboratory-maintained specimen of Montastrea annularis ranging between 280 and 122 foot candles ( $\cong 56$  and  $24 \mu \text{E m}^{-2} \text{s}^{-1}$ ) for specimen from 2 and 40 m respectively. These values are identical to values reported here.  $I_c$  also decreases during adaptation to shade (Porter et al., in review)

and suggests that the response by all coral symbiotic associations to lowered irradiance levels involves not only an increase in photosynthetic efficiency but also reductions in metabolic rate per unit area, thereby lowering the compensation light intensity (table 2). Davies (1977) does not calculate  $I_k$  directly but lists roughly comparable saturation points between 650 and 346 foot candles ( $\cong 130$  and  $69 \mu E m^{-2} s^{-1}$ ) for colonies from 2 and 40 m respectively. These saturation points are slightly lower than  $I_k$  points listed in table 2.

$p_c$  net max and  $p_c$  gross Values, Shallow and Deep

Light saturated photosynthetic rates ( $p_c$  net max and  $p_c$  gross max, table 2) are significantly higher for 1 m colonies than 10 or 30 m colonies when computed per unit area. This pattern (figure 6 a) echoes that of the decline in tissue biomass with depth (figure 3 a) as well as a reduction in zooxanthellae cell density with depth (figure 2 a, table 1). Colonies from 30 m have the lowest  $p_c$  max values when normalized to chlorophyll a. Although 1 and 30 m corals have similar chlorophyll a content (table 1) this is achieved in the former by a high zooxanthellae density, and in the later by increasing the chlorophyll a content per cell.

Maximum photosynthetic rates for Montastrea annularis are much higher than those from Stylophora pistillata, both on an area and a chlorophyll a basis. Net photosynthetic rates average between  $18.84$  and  $20.16 \mu g O_2 cm^{-2} h^{-1}$  and between  $5$  and  $1.5 \mu g O_2 \mu g Chl a^{-1} h^{-1}$  for light and shade colonies, respectively; M. annularis colonies average between  $81.6$  and  $39.3 \mu g O_2 cm^{-2} h^{-1}$  and between  $7.0$  and  $4.6 \mu g O_2 \mu g Chl a^{-1} h^{-1}$  for 1 and 30 m colonies. These differences result from the higher tissue

biomass per unit area in M. annularis as well as higher zooxanthellae cell densities compared with colonies of S. pistillata. These results compare well with results from other studies of coral photosynthetic response (Porter et al., in review) with the exception of an extremely low  $p_c$  gross value of  $0.16 \mu\text{g O}_2 \mu\text{g Chl a}^{-1} \text{h}^{-1}$  reported for M. annularis by Barnes and Taylor (1973).

The overall higher photosynthetic rates per unit area in Montastrea annularis relative to Stylophora pistillata may be due to morphological differences between the two corals. M. annularis is a mound-building coral and all of its tissue will be uniformly exposed to sunlight; S. pistillata is a finger coral and includes tissue unevenly exposed to light. Planar projections of the highly convoluted surface of Stylophora show it to be more productive per unit area of reef occupied, but on an individual specimen basis, a fairer comparison of the photosynthetic performance of these two species might be between the rates per unit area of an evenly illuminated branch of Stylophora and an upwardly facing surface of Montastrea.

$P_c$  net and gross max values based on chlorophyll a are similar between 1 and 30 m (table 2). Dustan (1982) presents maximum net photosynthesis rates for isolated zooxanthellae obtained from Montastrea annularis colonies at 1 and 50 m. His values ( $5.03 \mu\text{g O}_2 \mu\text{g Chl a}^{-1} \text{h}^{-1}$  versus 1.23 for 1 and 50 m, respectively) are somewhat lower than our in situ determinations of light-saturated rates which also include animal respiration (table 2).

The enhancement of  $\alpha$  and depression of  $p_c$  max on a chlorophyll a basis in deep-water corals accompanying higher chlorophyll a concentrations in deep-water zooxanthellae is interpretable as resulting

from an increase in size rather than number of photosynthetic units (Prezelin and Sweeney, 1978; Prezelin, 1981; Richardson et al., 1983). Even without data on  $\alpha$ , Dustin (1982) also interprets his data as supporting a similar conclusion. Adaptation to shade in shallow water also seems to be by this mechanism (Porter et al., in review).

#### Photoadaptation : Animal Accomodations

On a per unit area basis, one of the strongest "photoadaptive" responses to existence in shallow water is not photosynthetic pigment adaptation, but rather respiratory rate increase (table 2). Shallow water Montastrea annularis colonies are characterized by high respiration rates per unit area (table 2). This shallow-water response has also been observed for the Red Sea coral Stylophora pistillata growing under high light intensities (Porter et al., in review), several Caribbean corals (Davies, 1980; Porter, 1980), and two Indo-Pacific species (Wethey and Porter, 1976; Falkowski and Dubinsky, 1981). This pattern, at least in the case of M. annularis, is due in part to higher levels of tissue biomass in shallow-water colonies.

Davies (1977 and 1980) lists respiration rates for laboratory-maintained Montastrea annularis colonies from 25.8 to 14.8  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$  from 2 and 40 m, respectively in Jamaica. These values are in good agreement with our in situ determinations of dark respiration rates in this species (table 2) and also exhibit a depth-dependent reduction in rate. Johannes et al. (1970), however, report respiration rates of 45.83  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$  for M. annularis colonies from Bermuda. We measured sporadic, but never sustained rates of this magnitude (figure 5).

Davies (1980) demonstrates that dark respiration rates of Montastrea annularis, based on tissue dry weights decline with depth. Our data reveals a small but non-significant increase in nitrogen-specific respiration rate with increasing depth (table 2, figure 6 b). The discrepancy in the depth relationship of weight-specific respiration is probably due primarily to differences in the measures of tissue biomass. Davies (1980) data, although not presented in the paper, indicates an increase in tissue dry weight per unit area with increasing depth, while we find a significant decline in tissue nitrogen content (table 1, figure 3 c) as well as protein content per cm<sup>2</sup> (Battey and Porter, in review). On a surface area basis, the reduction in dark respiration rate, maximum photosynthetic rate (table 2), and zooxanthellae cell density (table 1) argue for a reduction in total tissue biomass per unit area with depth. If the inverse trends for tissue carbon dry weight and total nitrogen content with depth are accurate, then it suggests an increase in the carbon to nitrogen ratios of coral tissue with depth. Further work on the biochemical and elemental composition of coral tissues with depth is warranted.

#### Diel Photosynthesis and Respiration

As to be expected from the dark respiration rates, shallow-water colonies of Montastrea annularis corals respire 1.5 times the amount of oxygen as 30 m corals. These values are roughly double the respiration totals measured on branched Stylophora pistillata colonies (Porter et al., in review).

These calculations reveal that shallow water colonies of Montastrea annularis are capable of fixing slightly more than double the amount of carbon of deep water specimen (3.2 times under field irradiance, table 3). Davies (1977) lists  $P_c$  gross values for 1 and 40 m colonies between 2.94 and  $0.59 \text{ g C m}^{-2} \text{ d}^{-1}$ . Using PQ values of 1.1 and an oxygen:carbon conversion value of 0.375, our values are approximately 1.5 times higher, between 4.05 and  $1.60 \text{ g C m}^{-2} \text{ d}^{-1}$  for 1 and 30 m, respectively.

The ratio of gross photosynthesis to total respiration establishes the photo-autotrophic potential of the coral head. Field ratios are all lower than idealized ratios based on the variable cloud cover that reduced production rates. At both 10 and 30 m, weather conditions lowered the observed P/R ratio below unity under field conditions (figure 5), but idealized values at all depths exceed one (table 3). These values suggest that at all depths down to 30 m, the symbiotic association can produce excesses of between 22 and 79 percent of carbon required for standard metabolism. This value, however, occurs only under idealized conditions. These values compare well with integrated totals for Stylophora colonies in the sun, but Stylophora colonies under intense shade have  $P_{\text{gross}} / R_{\text{total}}$  ratios less than one. As mentioned before, cave irradiance is less than 7 percent of exposed reef irradiance at the same depth, but 30 m irradiance is 20 percent of 1 m levels.

If we use the 95 percent translocation efficiency and a 95 percent animal biomass proportion,  $P_z \text{ net} / R_a$  ratios are similar to  $P_c \text{ gross} / R_c \text{ total}$  ratios (tables 3 and 4). They further substantiate that the Montastrea annularis symbiotic association has the potential to meet the respiratory carbon requirements of both the algal and animal

components through zooxanthellae photosynthesis at least to 30 m. Based on lower measured rates of production, Davies (1977) suggests that M. annularis at and below 10 m depth can not meet metabolic demands through photosynthesis. Our data does not support this contention and suggests that even to depths of 30 m, this species has the capability to do so. Wave action and cloud cover, however, will reduce the energy supply below the idealized level and potentially also below colony compensation point. This effect is most pronounced at 30 m (table 5).

The effectiveness with which light is utilized can be approximated by calculating the ratio of gross production to total ambient irradiance (table 3, figure 7). Corals from 30 m have a significantly higher ratio demonstrating their enhanced capacity at utilizing ambient light (table 3). When corals from 1 and 10 m are subjected to light from 30 m, however, their ratios improve significantly to the point where there is no difference between ratios generated by 1 and 10 m colonies under these artificial lighting conditions and the ratios generated by 30 m corals under 30 m irradiance (figure 7). Shallow water corals spend a substantial proportion of the day at or above saturating light intensities (figures 4 a and e). Therefore it is the inefficient use of high light intensities that is responsible for low production / irradiance ratios of 1 and 10 m corals. The low values at 1 m also suggests that these colonies are not light limited. Lowered  $I_c$ ,  $I_k$ , and higher  $\alpha$  values also contribute to the superior performance of 30 m colonies under ambient irradiance by maximizing the proportion of daylight hours spent in net production.

Table 5 lists the irradiance level as a percent of idealized irradiance required to balance the  $P_z \text{ net } 24 \text{ hr} \times \% \text{ Tr} / R_a \text{ } 24 \text{ hr}$  equation. While only 56 percent of the "cloudless day" irradiance is needed at 1 m, 80 percent of this idealized condition is needed at 30 m. Table 5 demonstrates that any reduction in light intensity due to absorption by clouds or scatter by waves will lower the P/R ratios to a greater extent for deep water corals faster than for shallow water corals. At 30 m, Montastrea annularis was never light-saturated (figures 4 c and g), and existence throughout the day in the light-limited portion of the P:I curve stresses the importance of higher  $\alpha$  in deep-water corals. Higher  $\alpha$  is an adaptive response to both lowered light intensity and lowered P/R ratio. Clearly deep-water corals are much closer to their photoautotrophic compensation point than shallow water corals.

#### Heterotrophic Potential

Lewis (1977) measured clearing rates in the laboratory for Montastrea annularis of  $41.2 \text{ ml of seawater cm}^{-2} \text{ h}^{-1}$ . Assuming M. annularis respire at a rate of  $1.10 \text{ mg O}_2 \text{ cm}^{-2} \text{ d}^{-1}$ , Lewis calculated that M. annularis requires  $0.77 \text{ mg dry organic matter cm}^{-2} \text{ d}^{-1}$  to offset basal metabolic demand. Further, assuming the above cited clearing rate applies all day, Lewis calculated that M. annularis filters  $0.99 \text{ l cm}^{-2} \text{ d}^{-1}$ . In Barbados, Lewis cites the concentration of suspended particulates as  $0.33 \text{ dry organic matter per liter}$ , implying that half of this species' daily metabolic requirements are met by suspension feeding. Our total

respiratory demand ( $R_c$  24 hrs) are considerably less than the  $1.10 \text{ mg O}_2 \text{ cm}^{-2} \text{ d}^{-1}$  used in Lewis's calculation. Our values for 1 m colonies are 0.68 and for 30 m colonies are  $0.38 \text{ mg O}_2 \text{ cm}^{-2} \text{ d}^{-1}$ , suggesting that if Lewis's filtration calculations were accepted for field conditions, M. annularis would not need any photosynthetically fixed carbon at any depth to survive.

Coles (1969) examined zooplankton feeding in Montastrea cavernosa. Ingestion rate, in calories of Artemia consumed, was compared to caloric demand determined by respirometry during the first hour of night. When colonies of this species were fed Artemia ad libidum, they ingested three times their daily caloric requirement. Based on tentacle morphology, M. cavernosa might be expected to be a better planktivore than the shorter-tentacled M. annularis, but two other coral species with even stubbier tentacles ( Porites porites and Manicina areolata ) were also able to ingest up to six times their daily caloric requirement (Coles, 1969).

While the studies by Lewis (1977) and Coles (1969) both examine potential rather than realized caloric or carbon intake by Montastrea, it is clear that from suspension feeding, zooplankton capture, or photosynthesis, this coral is capable of meeting its daily metabolic requirements through several alternative means. Our data indicate that M. annularis may function photoautotrophically with respect to carbon when daily irradiance levels exceed 56 percent of cloudless day irradiance in shallow water and over 80 percent of the idealized irradiance at 10 and 30 m. Colonies of M. annularis on Jamaican coral reefs probably exist over a cline from complete photoautotrophy in shallow water to partial

photoautotrophy at depth.

The necessity for deep water colonies to meet carbon demands from non-photosynthetic sources correlates with and may partially explain the demonstrated increase in polyp diameter with increasing depth (figures 1 and 3). Increases in polyp diameter may enhance particulate feeding in deep water specimen (Porter, 1976; Lasker, 1976; Sebens, 1981). A reduction in polyp density at depth may also contribute to reduced respiration rates in deep-water colonies.

The demonstrable ability of Montastrea annularis in acquiring food and energy from so many alternative means may in part explain the extraordinary success of this species on all reefs and over great depths throughout the Caribbean.

#### CONCLUSIONS

We can make several general statements regarding similarities and differences between photoadaptation by corals to shade or depth. Both shade and depth result in biomass accommodations such as an increase in the chlorophyll a content of the symbiotic zooxanthellae, a reduction in polyp number per unit area by the animal, and a reduction in tissue nitrogen weight per unit area by the whole organism. Biomass patterns in adaptation to shade and depth contrast in that zooxanthellae density per unit area shows no change in shade-adapted corals but lowered density in depth-adapted corals. Further, chlorophyll a concentration per unit area is strikingly higher in shade-adapted specimen, but shows no significant trend over depths to 30 m.

Photosynthetic characteristics and respiratory patterns likewise show similarities and differences in adaptation to light reductions due

to shade or depth.  $\alpha$  is higher on a per unit area basis in both. On a per unit chlorophyll basis, however,  $\alpha$  is significantly higher in depth adaptation but significantly lower in shade adaptation. This may be due to self-shading in highly pigmented, shade-adapted zooxanthellae versus reduced self-shading in less highly pigmented depth-adapted algae. In all cases, compensation point ( $I_c$ ) and break point ( $I_k$ ) are lower in shade or depth-adapted specimen. Maximum rates of production (net or gross) are significantly higher in shallow-water specimen per unit area but not different per unit chlorophyll a. These rates show a converse relationship in adaptation to shade: net and gross production is not significantly different per unit area but is higher per unit chlorophyll a in light-adapted specimen.

In every instance, respiration rates and totals are highest for individuals growing at high light intensities. P/R ratios fall with decreasing irradiance, but fall at a lower rate than would be predicted on the basis of either maximum instantaneous ambient irradiance or integrated irradiance. Low-light corals spend most of their time under light-limited conditions; high-light corals spend most of their time under conditions limited by other resources.

Research is needed to contrast responses to shade versus depth in C/N ratios, and chlorophyll a / c<sub>2</sub> ratios. Further, data on accessory pigment concentration in shade-adapted individuals, and the spectral quality of light in shade is needed. Although both shade-adapted and depth-adapted corals appear to increase the size rather than the number of photosynthetic units during adaptation to reduced-light conditions, inconsistencies between the actual photoadaptive patterns observed and the theoretical development of the PSU hypothesis warrant further field research and a critical examination of the PSU concept.

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#### REFERENCES

- Bak, R.P.M., Brouns, J.J.W.M., & Heys, F.M.L. 1977 Regeneration and aspects of spatial competition in the scleractinian corals. Proc. Third Internat. Coral Reef Symp. 1, 143-148.
- Barnes, D.J. & Taylor, D.L. 1973 In situ studies of calcification and photosynthetic carbon fixation in the coral Montastrea annularis. Helgolander wiss. Meeresunters. 24, 284-291.
- Batley, J.F., & Porter, J.W. in review Photoadaptation as a whole organism response by Montastrea annularis. Proc. Roy. Soc. Lond. B
- Brakel, W.H. 1979 Small-scale spatial variation in light available to coral reef benthos: Quantum irradiance measurements from a Jamaican reef. Bull. mar. Sci. 29, 406-413.
- Chalker, B.E. 1980 Modelling light saturation curves for photosynthesis: An exponential function. J. theoret. Biol. 84, 205-215.
- Chalker, B.E. 1981 Simulating light-saturation curves for photosynthesis and calcification by reef-building corals. Mar. Biol. 63, 135-141.
- Chalker, B.E. & Taylor, D.L. 1978 Rhythmic variations in calcification and photosynthesis associated with the coral Aeropora cervicornis (Lamark). Proc. Roy. Soc. Lond. B 201, 179-178.
- Coles, S.L. 1969 Quantitative estimates of feeding and respiration for three scleractinian corals. Limnol. Oceanogr. 14, 949-953.

- Cook, C.B. 1983 Metabolic interchange in algae-invertebrate symbiosis. Internat. rev. Cytol. 14, 177-210.
- Crossland, C.J. & Barnes, D.J. 1977 Gas exchange studies with staghorn coral, Acropora acuminata, and its zooxanthellae. Mar. Biol. 40, 185-194.
- Crossland, C.J., Barnes, D.J. & Borowitzka, M.A. 1980 Diurnal lipid and mucus production in the staghorn coral, Acropora acuminata. Mar. Biol. 60, 81-90.
- Davies, P.S. 1977 Carbon budgets and vertical distribution of Atlantic reef corals. Proc. Third Internat. Coral Reef Symp. 1, 392-396.
- Davies, P.S. 1980 Respiration in some Atlantic reef corals in relation to vertical distribution and growth form. Biol. Bull. 158, 187-194.
- Draper, N. & Smith, N. 1966 Applied regression analysis. New York: John Wiley & Sons, Inc.
- Drew, E.A. 1972 The biology and physiology of algal-invertebrate symbioses. II. The density of symbiotic algal cells in a number of hermatypic hard corals and alcyonarians from various depths. J. exp. mar. Biol. Ecol. 9, 21-25.
- Dubinsky, Z., Falkowski, P.G., Muscatine, L. & Porter, J.W. in review The absorption and utilization of radiant energy by light and shade-adapted colonies of the symbiotic coral Stylophora pistillata Proc. Roy. Soc. Lond. B.
- Dustan, P. 1975 Growth and form in the reef-building coral Montastrea annularis. Mar. Biol. 33, 101-107.

- Dustan, P. 1979 Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef building coral Montastrea annularis Ellis and Solander in relation to depth on a West Indian coral reef. Bull. mar. Sci. 29, 79-95.
- Dustan, P. 1982 Depth-dependent photoadaptation by zooxanthellae of the reef coral Montastrea annularis. Mar. Biol. 68, 253-264.
- Environmental Protection Agency. 1974 Methods for chemical analysis of water and wastes. EPA-625-6-74-003. Office of Technology Transfer; Washington, D.C.
- Falkowski, P.G. 1981 Light-shade adaptation and assimilation numbers. J. Plankton Res. 3, 203-216.
- Falkowski, P.G. & Dubinsky, Z. 1981 Light-shade adaptation of Stylophora pistillata, a hermatypic coral from the Gulf of Eilat. Nature 289, 172-174.
- Falkowski, P.G. & Owens, T.G. 1978 Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. Mar. Biol. 45, 289-295.
- Falkowski, P.G. & Owens, T.G. 1980 Light-shade adaptation. Two strategies in marine phytoplankton. Plant Physiol. 66, 592-595.
- Falkowski, P.G., Owens, T.G., Ley, A.C., & Mauzerall, D.C. 1981 Effects of growth irradiance levels on the ratio of reaction centers in two species of marine phytoplankton. Plant Physiol. 68, 969-973.
- Fitt, W.K. & Pardy, R.L. 1981 Effects of starvation, and light and dark on the energy metabolism of symbiotic and aposymbiotic sea anemones, Anthopleura elegantissima. Mar. Biol. 61, 199-205.

- Fitt, W.K., Pardy, R.L. & Littler, M.M. 1982 Photosynthesis, respiration, and contribution to community productivity of the symbiotic sea anemone, Anthopleura elegantissima (Brandt, 1835). J. exp. mar. biol. Ecol. 61, 213-232.
- Goreau, T.F. 1959. The physiology of skeleton formation in corals. I. A method for measuring the rate of calcium deposition by corals under different conditions. Biol. Bull. 115, 59-75.
- Goreau, T.F. & Wells, J.W. 1967 The shallow-water scleractinia of Jamaica: Revised list of species and their vertical distribution range. Bull. mar. Sci. 17, 442-453.
- Graus, R.R. & Macintyre, I.G. 1976 Light and control of growth form in colonial reef corals: computer simulation. Science 193, 895-897.
- Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W. & Strickland, J.D. 1965 Fluorometric determination of chlorophyll. J. Cons. permint. int. Explor. Mer. 30, 3-15.
- Jassby, A.D. & Platt, T. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. 21, 540-547.
- Jeffrey, S.W. & Humphrey, G.F. 1975 New spectrophotometric equations for determining chlorophylls a, b, c<sub>1</sub>, and c<sub>2</sub> in higher plants, algae, and natural phytoplankton. Biochem. Physiol. Pflanz. 167, 191-194.
- Johannes, R.E. & Wiebe, W.J. 1970 A method for determination of coral tissue biomass and composition. Limnol. Oceanogr. 15, 822-824.
- Johannes, R.E., Coles, S.L. & Kuenzel, N.T. 1970 The role of zooplankton in the nutrition of some scleractinian corals. Limnol. Oceanogr. 15, 579-586.

- Kevin, K.M. & Hudson, R.C.L. 1979 The role of zooxanthellae in the hermatypic coral Plesiastrea urvillei (Milne Edwards and Haime) from cold waters. J. exp. mar. Biol. Ecol. 36, 157-170.
- Lasker, H.R. 1976 Intraspecific variability of zooplankton feeding in the hermatypic coral Montastrea cavernosa. In Coelenterate ecology and behavior (ed. G.O. Mackie), pp. 101-110 New York: Plenum Press.
- Lewis, J.B. 1977 Suspension feeding in Atlantic reef corals and the importance of suspended particulate matter as a food source. Proc. Third Internat. Coral Reef Symp. 1, 405-408.
- Marsh, J.A. 1970 Primary productivity of reef-building calcareous red algae. Ecology 51, 255-263.
- Muscatine, L. 1980 Productivity of zooxanthellae. In Primary productivity in the sea (ed. P.G. Falkowski), pp. 381-402. New York: Plenum Press.
- Muscatine, L., Falkowski, P.G., Porter, J.W. & Dubinsky, Z. in review Fate of photosynthetically fixed carbon in light and shade-adapted colonies of the symbiotic coral, Stylophora pistillata. Proc. Roy. Soc. Lond. B
- Muscatine, L., McCloskey, L.R. & Marian, R.E. 1981 Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. Limnol. Oceanogr. 26, 601-611.
- Patton, J.S., Abraham, S. & Benson, A.A. 1977 Lipogenesis in the intact coral Pocillopora capitata and its isolated zooxanthellae: Evidence for a light-driven carbon cycle between symbiont and host. Mar. Biol. 44, 235-247.

- Patton, J.S., Battey, J.F., Rigler, M.W., Porter, J.W., Black, C.C., & Burris, J.E. 1983 A comparison of the metabolism of bicarbonate  $^{14}\text{C}$  and acetate  $1\text{-}^{14}\text{C}$  and the variability of species lipid compositions in reef corals. Mar. Biol. (in press).
- Platt, T. & Jassby, A.D. 1976 The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12, 421-430.
- Porter, J.W. 1976 Autotrophy, heterotrophy, and resource partitioning in Caribbean reef-building corals. Amer. Natur. 110, 731-742.
- Porter, J.W. 1980 Primary productivity in the sea: Reef corals in situ. In Primary productivity in the sea (ed. P.G. Falkowski), pp. 403-410. New York, Plenum Press.
- Porter, J.W., Muscatine, L., Dubinsky, Z. & Falkowski, P.G. in review Primary production and photoadaptation in light and shade-adapted colonies of the symbiotic coral, Stylophora pistillata. Proc. Roy. Soc. Lond. B.
- Porter, J.W., Woodley, J.D., Smith, G.J., Neigel, J.E., Battey, J.F., & Dallmeyer, D.G. 1981 Population trends among Jamaican reef corals. Nature 294, 249-250.
- Prezelin, B.B. 1981 Light reactions in photosynthesis. Canad. Bull. Fish. Aquat. Sci. 210, 1-46.
- Prezelin, B.B. & Sweeney, B.M. 1978 Photoadaptation of photosynthesis in Gonyaulax polyedra. Mar. Biol. 48, 27-35.
- Richardson, K., Beardall, J. & Raven, J.A. 1983 Adaptation of unicellular algae to irradiance: an analysis of strategies. New Phytol. 93, 157-191.

- Sebens, K.P. 1981 The allometry of feeding, energetics, and body size in three sea anemone species. Biol. Bull. 161, 152-171.
- Titlyanov, E.A., Shaposhnikova, M.A. & Zvalinskii, V.I. 1980 Photosynthesis and adaptation of corals to irradiance. Contents and native state of photosynthetic pigments in symbiotic microalgae. Photosynthetica 14, 413-421.
- Trench, R.K. 1971 a The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. I. The assimilation of photosynthetic products of zooxanthellae by two marine coelenterates. Proc. Roy. Soc. Lond. B 177, 225-235.
- Trench, R.K. 1971 b The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. III. The effects of homogenates of host tissues on the excretion of photosynthetic products in vitro by zooxanthellae from two marine coelenterates. Proc. Roy. Soc. Lond. B 177, 251-264.
- Wells, J.W. 1957. Coral reefs. Mem. Geol. Soc. Amer. 67, 609-631.
- Wetley, D.S. & Porter, J.W. 1976 Sun and shade differences in productivity of reef corals. Nature 262, 281-282.
- Zvalinskii, V.I., Titlyanov, E.A., Leletkin, V.A. & Novozhilov, A.V. 1978. Adaptation of corals to light. Trans. Far East Sci. Center, Inst. Mar. Biol., Acad. Sci. U.S.S.R. 12, 29-52.
- Zvalinskii, V.I., Leletkin, V.A., Titlyanov, E.A. & Shaposhnikova, M.A. 1980 Photosynthesis and adaptation of corals to irradiance 2. Oxygen exchange. Photosynthetica 14, 422-430.

Figure 1. Monstastrea annularis colonies from different depths in Discovery Bay, Jamaica. Figure 1 a, M. annularis colony from 10 m on the windward fore-reef slope. Note the continuous change in form of this single colony from knobby on top, through lobate, to plating on the sides, suggesting that every individual in the population has the genetic potential to achieve several well developed, but intergrading forms. Polyp density (see figure 3 a), and polyp diameter (see figure 3 b), as well as other parameters (table 1) change systematically with depth. Figure 1 b is from 1 m (Specimen Number UGA 357; table 1), figure 1 c is from 10 m (Specimen Number UGA 349), and figure 1 d is from 30 m (Specimen Number UGA 353). Bar in the photograph represents 1 cm.

#### FIGURE 2 COORDINATE DESCRIPTION

Figure 2 a ord zooxanthellae,  $10^6$  cells  $\text{cm}^{-2}$

abs depth, m

Figure 2 b ord zooxanthellae chlorophyll, pg Chl a  $\text{cell}^{-1}$

abs depth, m

Figure 2 c ord chlorophyll,  $\mu\text{g}$  Chl a  $\text{cm}^{-2}$

abs depth, m

Figure 2. Variation in algal biomass parameters with increasing depth in Montastrea annularis. Zooxanthellae density ( $10^6$  cells  $\text{cm}^{-2}$ ) (figure 2 a), weight of chlorophyll a per zooxanthellae cell (pg Chl a  $\text{cell}^{-1}$ ) (figure 2 b), and weight of chlorophyll a per unit area ( $\mu\text{g}$  Chl a  $\text{cm}^{-2}$ ) (figure 2 c) are plotted as a function of depth (table 1). Significant regressions are indicated by a solid line.

## FIGURE 3 COORDINATE DESCRIPTION

Figure 3 a ord polyp density, polyps  $\text{cm}^{-2}$

abs depth, m

Figure 3 b ord polyp diameter, cm

abs depth, m

Figure 3 c ord nitrogen, mg N  $\text{cm}^{-2}$

abs depth, m

Figure 3. Variation in polyp density (polyps  $\text{cm}^{-2}$ ) (figure 3 a), polyp diameter (cm) (figure 3 b), and weight of nitrogen per unit area (mg N  $\text{cm}^{-2}$ ) (figure 3 c) are plotted as a function of depth (m) for Montastrea annularis (table 1). Significant regressions are indicated by a solid line.

## FIGURE 4 COORDINATE DESCRIPTION

Figures 4 a-d ord net oxygen flux,  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$

abs ambient irradiance,  $\mu \text{E m}^{-2} \text{ s}^{-1}$

Figures 4 e-h ord net oxygen flux,  $\mu\text{g O}_2 \mu\text{g Chl a}^{-1} \text{ h}^{-1}$

abs ambient irradiance,  $\mu \text{E m}^{-2} \text{ s}^{-1}$

Figure 4. In situ net photosynthesis - irradiance curves for replicate specimen of Montastrea annularis from 1 m (figures 4 a and e), 10 m (figures 4 b and f), 30 m (figures 4 c and g), and summary P:I curves (figures 4 d and h). Photosynthetic characteristics listed in table 2 were calculated on the basis of these curves. Biomass units are either as area ( $\text{cm}^2$ ) (figures 4 a - d) or weight of chlorophyll a (figures 4 e - h). All specimen were incubated in the respirometer at their depth of collection. Maximum irradiance approached  $425 \mu \text{E m}^{-2} \text{ s}^{-1}$  at 1 m,  $450 \mu \text{E m}^{-2} \text{ s}^{-1}$  at 10 m, and  $200 \mu \text{E m}^{-2} \text{ s}^{-1}$  at 30 m. Mean points and standard error bars for oxygen flux at  $50 \mu \text{E m}^{-2} \text{ s}^{-1}$  intervals are included for each specimen.

## FIGURE 5 COORDINATE DESCRIPTION

Figures 5 a-c abs time, h

left ord net oxygen flux,  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$

right ord ambient irradiance,  $\mu \text{E m}^{-2} \text{ s}^{-1}$

Figure 5. In situ respiration and net production are plotted versus time of day for replicate specimen of Montastrea annularis incubated under ambient irradiances at their depth of collection. Production-irradiance curves in figure 4 are derived from the same specimen. Total radiant input between treatments was quite dissimilar due to differences in depth and cloudiness during the incubations (table 3).

## FIGURE 6 COORDINATE DESCRIPTION

Figure 6 a ord respiration and photosynthesis,  $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$

abs depth, m

Figure 6 b ord respiration and photosynthesis,  $\mu\text{g O}_2 \text{ mg N}^{-1} \text{ h}^{-1}$

abs depth, m

Figure 6. Variation in oxygen flux characteristics with increasing depth in Montastrea annularis. Respiration rate ( $r_c$ , closed squares) and net photosynthetic rate ( $p_c$  net max, open circles) per unit area ( $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ ) are plotted (mean point  $\pm$  95% confidence limits) as a function of depth (m) in figure 6 a. Respiration rate (closed squares) and photosynthetic rate (open circles) per weight of nitrogen ( $\mu\text{g O}_2 \text{ mg N}^{-1} \text{ h}^{-1}$ ) are plotted (mean  $\pm$  one S.E) a function of depth (m) in figure 6 b.

## FIGURE 7 COORDINATE DESCRIPTION

left ord gross production / irradiance,  $\text{g O}_2 \text{ E}^{-1}$

right ord irradiance,  $\text{E m}^{-2} \text{ d}^{-1}$

abs depth, m

Figure 7. Variation in the ratio of idealized gross primary production to idealized irradiance ( $\text{g O}_2 \text{ E}^{-1}$ , open squares) and the idealized irradiance ( $\text{E m}^{-2} \text{ d}^{-1}$ , open circles) are plotted (mean  $\pm$  95% confidence interval) versus depth (m) for Montastrea annularis. Solid squares represent the idealized gross production / irradiance ratio expected of corals from 1 and 10 m if they were to receive 30 m irradiances.

Table 1. Biomass variation for colonies of Montastrea annularis  
from different depths. Values shown are mean  $\pm$  one S.D.  
with number of samples in parenthesis.

| Characteristic              | Units                                       | Ambient Depth                    |                         |                     |                         |                     |
|-----------------------------|---------------------------------------------|----------------------------------|-------------------------|---------------------|-------------------------|---------------------|
|                             |                                             | 1 meter                          | 10 meters               | 20 meters           | 30 meters               | 35 meters           |
| Zooxanthellae               | $10^6$ cells $\text{cm}^{-2}$               | $3.20 \pm 1.31$ (10)             | $2.92 \pm 1.22$ (9)     | $1.43 \pm 0.32$ (3) | $2.40 \pm 0.23$ (5)     | $0.76 \pm 0.06$ (3) |
| Pigments                    | pg Chl <u>a</u> cell $^{-1}$                | $2.69 \pm 1.09$ (7)              | $1.83 \pm 0.29$ (6)     | $3.15 \pm 0.74$ (3) | $3.16 \pm 0.11$ (2)     | $4.21 \pm 0.63$ (3) |
| "                           | $\mu\text{g}$ Chl <u>a</u> $\text{cm}^{-2}$ | $8.32 \pm 4.40$ (10)             | $5.34 \pm 2.28$ (9)     | $4.39 \pm 0.68$ (3) | $8.49 \pm 1.62$ (5)     | $3.16 \pm 0.47$ (3) |
| "                           | Chl <u>a</u> / <u>c</u> <sub>2</sub> ratio  | $1.12 \pm 0.37$ (7)              | $1.02 \pm 0.12$ (6)     | $1.34 \pm 0.12$ (3) | $0.81 \pm 0.16$ (2)     | $1.40 \pm 0.10$ (3) |
| Nitrogen                    | mg TKN $\text{cm}^{-2}$                     | $0.96 \pm 0.09$ (5)              | $0.48 \pm 0.12$ (9)     | ---                 | $0.50 \pm 0.15$ (5)     | ---                 |
| Polyp density               | number $\text{cm}^{-2}$                     | $11.4 \pm 1.0$ (7)               | $11.2 \pm 1.1$ (6)      | $5.7 \pm 0.7$ (3)   | $3.9 \pm 0.8$ (5)       | $4.1 \pm 0.4$ (3)   |
| Calyx diameter              | cm                                          | $0.24 \pm 0.02$ (7)              | $0.22 \pm 0.01$ (6)     | $0.30 \pm 0.01$ (3) | $0.32 \pm 0.01$ (5)     | $0.33 \pm 0.02$ (3) |
| Polyp nitrogen              | $\mu\text{g}$ TKN polyp $^{-1}$             | $81.7 \pm 10.8$ (5)              | $42.9 \pm 8.5$ (9)      | ---                 | $129.0 \pm 34.2$ (5)    | ---                 |
| Specimen Field<br>Numbers ‡ |                                             | UGA 356-358,<br>362-364; 374-377 | UGA 347-352,<br>368-370 | UGA 359-361         | UGA 353-355,<br>371-372 | UGA 365-367         |

‡, Cnidaria Collection, Museum of Natural History, University of Georgia, Athens, GA 30602 U.S.A.

TABLE 2. Variation (mean  $\pm$  one S.E.) in photosynthesis-light utilization characteristics for colonies of *Montastrea annularis* from different depths.

| Characteristic      |                        | Units                                                                                     | Ambient Depth      |                      |                      | Statistical Comparisons      |   |
|---------------------|------------------------|-------------------------------------------------------------------------------------------|--------------------|----------------------|----------------------|------------------------------|---|
|                     |                        |                                                                                           | 1 meter<br>(N = 2) | 10 meters<br>(N = 4) | 30 meters<br>(N = 4) |                              |   |
| $\alpha$            | (cm <sup>2</sup> )     | $\mu\text{gO}_2\text{cm}^{-2}\text{h}^{-1}\mu\text{Em}^{-2}\text{s}^{-1}$                 | 0.49 $\pm$ 0.21    | 0.27 $\pm$ 0.14      | 0.48 $\pm$ 0.07      | <u>10</u> <u>1</u> 30        | † |
|                     | (Chl <u>a</u> )        | $\mu\text{gO}_2\text{Chl } \underline{a}^{-1}\text{h}^{-1}\mu\text{Em}^{-2}\text{s}^{-1}$ | 0.04 $\pm$ 0.03    | 0.06 $\pm$ 0.03      | 0.06 $\pm$ 0.02      | <u>1</u> <u>10</u> <u>30</u> |   |
|                     | (10 <sup>6</sup> zoox) | $\mu\text{gO}_2 10^6\text{zoox}^{-1}\text{h}^{-1}\mu\text{Em}^{-2}\text{s}^{-1}$          | 0.11 $\pm$ 0.06    | 0.10 $\pm$ 0.06      | 0.22 $\pm$ 0.04      | <u>1</u> <u>10</u> < 30      | * |
| $I_k$               | (cm <sup>2</sup> )     | $\mu\text{Em}^{-2}\text{s}^{-1}$                                                          | 227 $\pm$ 38       | 210 $\pm$ 49         | 117 $\pm$ 44         | <u>1</u> <u>10</u> > 30      | * |
| $I_c$               | (cm <sup>2</sup> )     | $\mu\text{Em}^{-2}\text{s}^{-1}$                                                          | 58 $\pm$ 9         | 73 $\pm$ 19          | 34 $\pm$ 25          | <u>10</u> <u>1</u> 30        | † |
| $p_c$ net max       |                        | $\mu\text{gO}_2\text{cm}^{-2}\text{h}^{-1}$                                               | 81.6 $\pm$ 16.1    | 37.1 $\pm$ 24.2      | 39.3 $\pm$ 14.5      | 1 > <u>10</u> <u>30</u>      | * |
|                     |                        | $\mu\text{gO}_2\mu\text{gChl } \underline{a}^{-1}\text{h}^{-1}$                           | 7.0 $\pm$ 2.4      | 6.9 $\pm$ 6.0        | 4.6 $\pm$ 2.7        | <u>1</u> <u>10</u> <u>30</u> |   |
| $p_c$ gross max     |                        | $\mu\text{gO}_2\text{cm}^{-2}\text{h}^{-1}$                                               | 110.1 $\pm$ 16.1   | 57.0 $\pm$ 24.2      | 55.3 $\pm$ 14.5      | 1 > <u>10</u> <u>30</u>      | * |
|                     |                        | $\mu\text{gO}_2\mu\text{gChl } \underline{a}^{-1}\text{h}^{-1}$                           | 9.3 $\pm$ 2.5      | 10.6 $\pm$ 5.9       | 6.7 $\pm$ 2.7        | <u>1</u> <u>10</u> <u>30</u> |   |
|                     |                        | $\mu\text{gO}_2 10^6\text{zoox}^{-1}\text{h}^{-1}$                                        | 25.9 $\pm$ 5.1     | 19.1 $\pm$ 12.5      | 22.6 $\pm$ 6.3       | <u>1</u> <u>10</u> <u>30</u> |   |
| Average $r_c$ night |                        | $\mu\text{gO}_2\text{cm}^{-2}\text{h}^{-1}$                                               | 28.2 $\pm$ 2.7     | 19.9 $\pm$ 5.1       | 16.0 $\pm$ 3.4       | 1 > <u>10</u> <u>30</u>      | * |
|                     |                        | $\mu\text{gO}_2\mu\text{gChl } \underline{a}^{-1}\text{h}^{-1}$                           | 2.3 $\pm$ 2.0      | 3.6 $\pm$ 1.4        | 2.1 $\pm$ 1.6        | <u>1</u> <u>10</u> <u>30</u> |   |
|                     |                        | $\mu\text{gO}_2\text{mgTKN}^{-1}\text{h}^{-1}$                                            | 27.7 $\pm$ 8.0     | 36.5 $\pm$ 5.4       | 36.4 $\pm$ 24.1      | <u>1</u> <u>10</u> <u>30</u> |   |
|                     |                        | $\mu\text{gO}_2\text{polyp}^{-1}\text{h}^{-1}$                                            | 2.5 $\pm$ 0.7      | 1.7 $\pm$ 0.7        | 4.5 $\pm$ 3.7        | <u>1</u> <u>10</u> <u>30</u> |   |

0.10 > p > 0.05  
p < 0.05

TABLE 3. Variation (mean  $\pm$  one S.D.) in photosynthesis and respiration totals for colonies of Montastrea annularis from different depths.

| Characteristic                    | Units                     | Ambient Depth      |                      |                      | Statistical Comparisons |
|-----------------------------------|---------------------------|--------------------|----------------------|----------------------|-------------------------|
|                                   |                           | 1 meter<br>(N = 2) | 10 meters<br>(N = 4) | 30 meters<br>(N = 4) |                         |
| Daylength (field)                 | hrs                       | 12.6               | 11.9                 | 10.1                 |                         |
| (idealized light)                 | hrs                       | 12.0               | 12.0                 | 12.0                 |                         |
| Irradiance (field)                | $E\ m^{-2}d^{-1}$         | 9.2                | 9.7                  | 2.6                  |                         |
| (idealized light)                 | $E\ m^{-2}d^{-1}$         | 27.5               | 16.5                 | 5.6                  |                         |
| $R_c$ net total                   | $\mu gO_2\ cm^{-2}$       | $358.5 \pm 75.3$   | $273.5 \pm 59.0$     | $254.2 \pm 80.2$     |                         |
| $P_c$ net total                   | $\mu gO_2\ cm^{-2}$       | $513.7 \pm 10.6$   | $234.2 \pm 53.1$     | $133.2 \pm 22.6$     |                         |
| $P_c$ gross (field)               | $\mu gO_2\ cm^{-2}d^{-1}$ | $840.0 \pm 74.9$   | $438.0 \pm 85.7$     | $262.1 \pm 13.4$     |                         |
| (idealized light)                 | $\mu gO_2\ cm^{-2}d^{-1}$ | $1186.6 \pm 45.6$  | $571.5 \pm 108.8$    | $469.5 \pm 28.9$     | 1 > <u>10</u> 30 *      |
| $R_c$ 24 hrs                      | $\mu gO_2\ cm^{-2}d^{-1}$ | $676.8 \pm 33.6$   | $477.4 \pm 62.6$     | $383.0 \pm 41.4$     | 1 > <u>10</u> 30 *      |
| $P_z$ net 24 hrs ‡                | $\mu gO_2\ cm^{-2}d^{-1}$ | $1152.8 \pm 44.3$  | $547.6 \pm 104.2$    | $450.4 \pm 27.7$     | 1 > <u>10</u> 30 *      |
| $P_c$ gross/ $R_c$ 24 hrs (field) | ratio                     | $1.26 \pm 0.15$    | $0.93 \pm 0.11$      | $0.75 \pm 0.17$      |                         |
| (idealized light)                 | ratio                     | $1.79 \pm 0.30$    | $1.22 \pm 0.18$      | $1.34 \pm 0.28$      | 1 > <u>10</u> 30 *      |
| $P_z$ net 24/ $R_a$ hrs ‡         | ratio                     | $1.79 \pm 0.30$    | $1.21 \pm 0.17$      | $1.24 \pm 0.24$      | 1 > <u>10</u> 30 †      |
| $P_c$ gross/irradiance (field)    | $gO_2\ E^{-1}$            | $0.60 \pm 0.04$    | $0.21 \pm 0.04$      | $0.69 \pm 0.04$      |                         |
| (idealized light)                 | $gO_2\ E^{-1}$            | $0.43 \pm 0.01$    | $0.35 \pm 0.06$      | $0.84 \pm 0.05$      | <u>1</u> 10 < 30 *      |

†  $0.10 > p > 0.05$

\*  $p < 0.05$

‡  $P_z$  net 24 hrs =  $P_c$  gross -  $R_z$  24 hrs; assumes  $R_z = 5\% R_c$

Table 4. Percent of coral animal metabolic requirements met by algal photosynthesis ( $P_z$  net 24 hrs x % Tr /  $R_a$  24)† for Montastrea annularis from different depths based on idealized light regimes and different biomass assumptions.

| Percent Translocation | Percent of $R_c$ belonging to $R_a$ | Ambient Depth |           |           |
|-----------------------|-------------------------------------|---------------|-----------|-----------|
|                       |                                     | 1 meter       | 10 meters | 30 meters |
| 95%                   | 95%                                 | 1.8           | 1.2       | 1.2       |
| 95%                   | 50%                                 | 2.4           | 1.3       | 1.4       |
| 40%                   | 95%                                 | 0.7           | 0.5       | 0.5       |
| 40%                   | 50%                                 | 1.0           | 0.6       | 0.6       |

†  $P_z$  net 24 hrs =  $[(P_c \text{ gross}) (\div PQ_z)] - [(\% \text{ of } R_c \text{ belonging to } R_z)(R_c)(RQ_z)]$ .  
 $R_a$  24 hrs =  $(\% \text{ of } R_c \text{ belonging to } R_a)(R_c)(RQ_a)$ . See table 3 for empirical values of  $R_c$  24 hrs and  $P_c$  gross, and text for a discussion of photosynthetic and respiratory quotients.

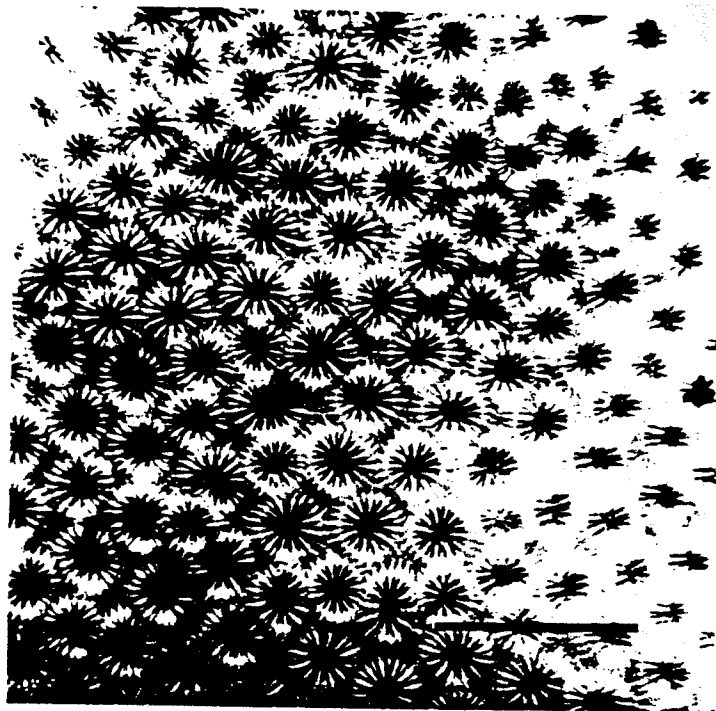
Table 5. Irradiance levels necessary to sustain corals photoautotrophically\* as a percent of idealized irradiance.

|                                        | Ambient Depth |            |           |
|----------------------------------------|---------------|------------|-----------|
|                                        | 1 meter       | 10 meters  | 30 meters |
| Irradiance level ( $E\ m^{-2}d^{-1}$ ) | 15.3 (56%)    | 13.7 (83%) | 4.5 (80%) |

\* Where  $P_z$  net 24 hrs x % Tr /  $R_a$  24 hrs = 1. Calculations in this table assume (1) percent translocation = 95%, (2)  $R_a = 0.95 R_c$ , (3)  $PQ = 1.1$ , (4)  $RQ = 0.8$ , and (5)  $P_c$  gross (idealized light),  $R_c$  24 hrs, and  $P_c$  gross/irradiance (idealized light) are as in table 3.



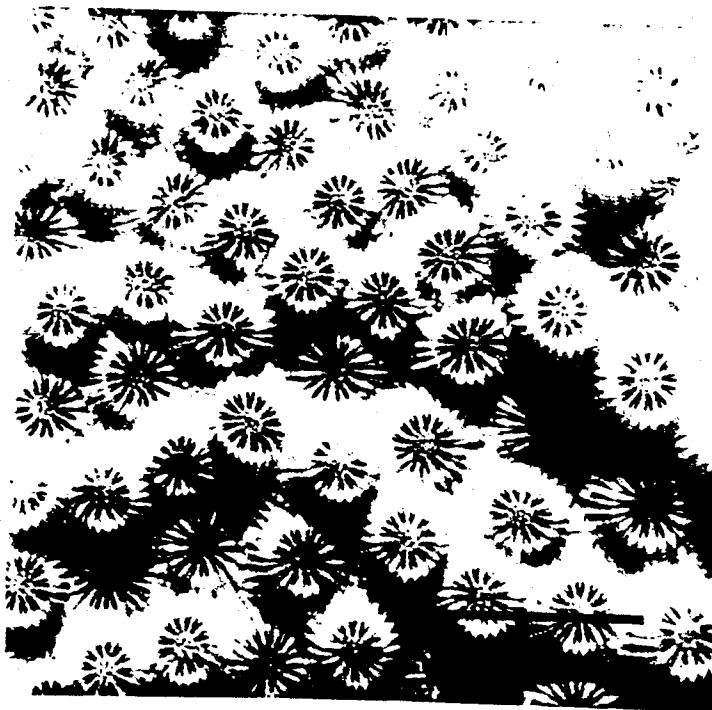
M. ann. 1m



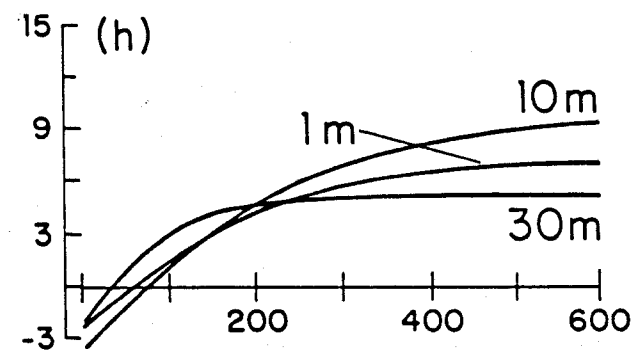
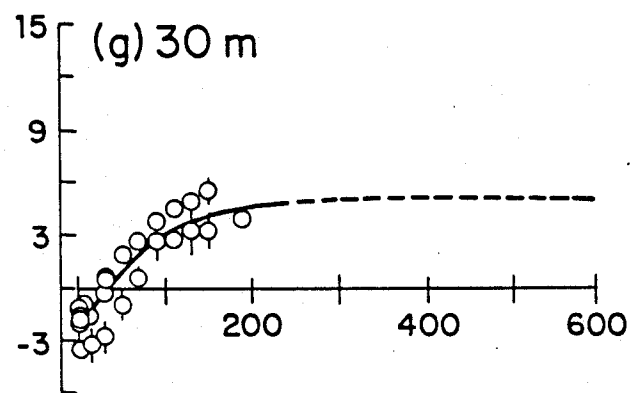
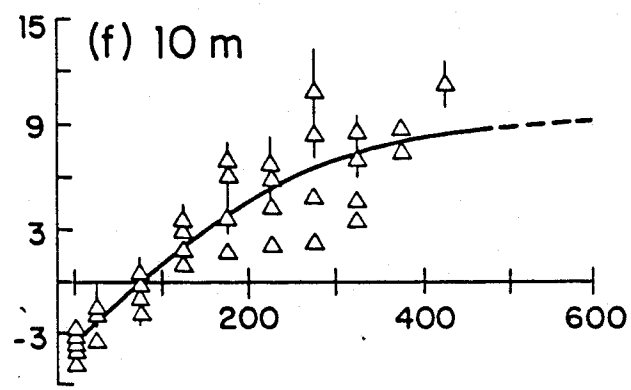
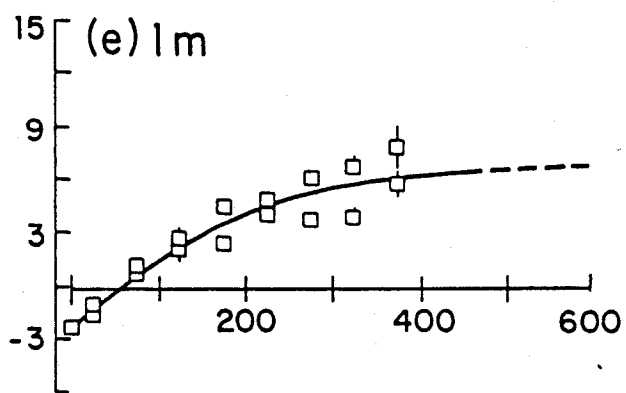
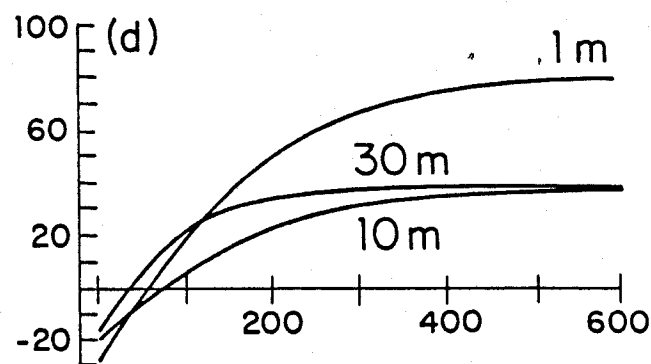
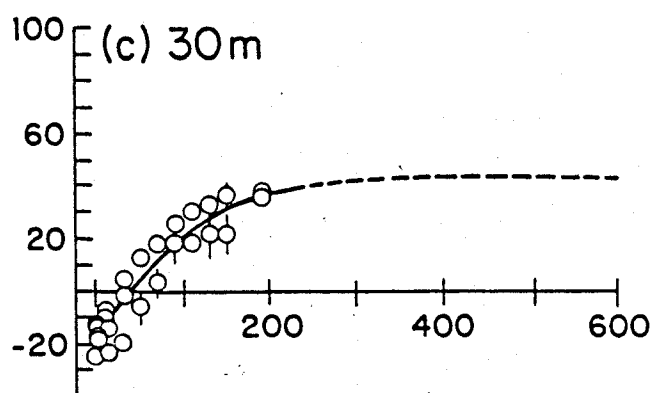
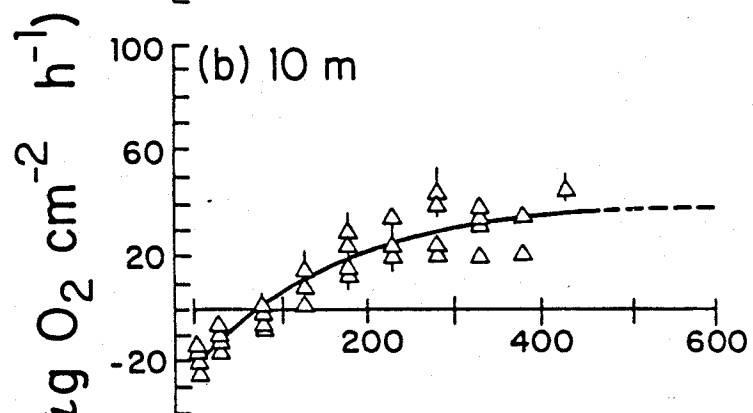
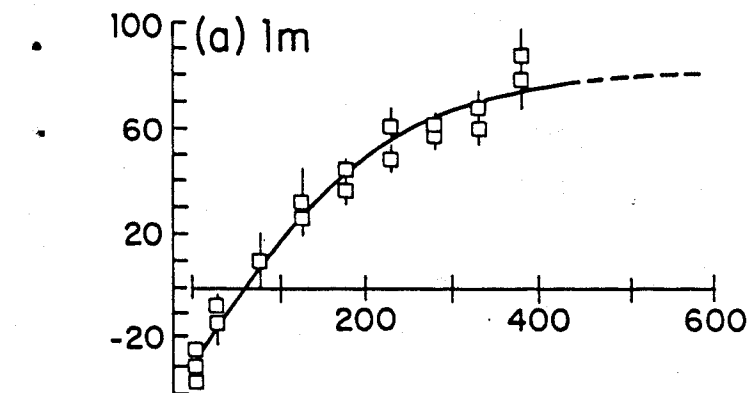
1 m



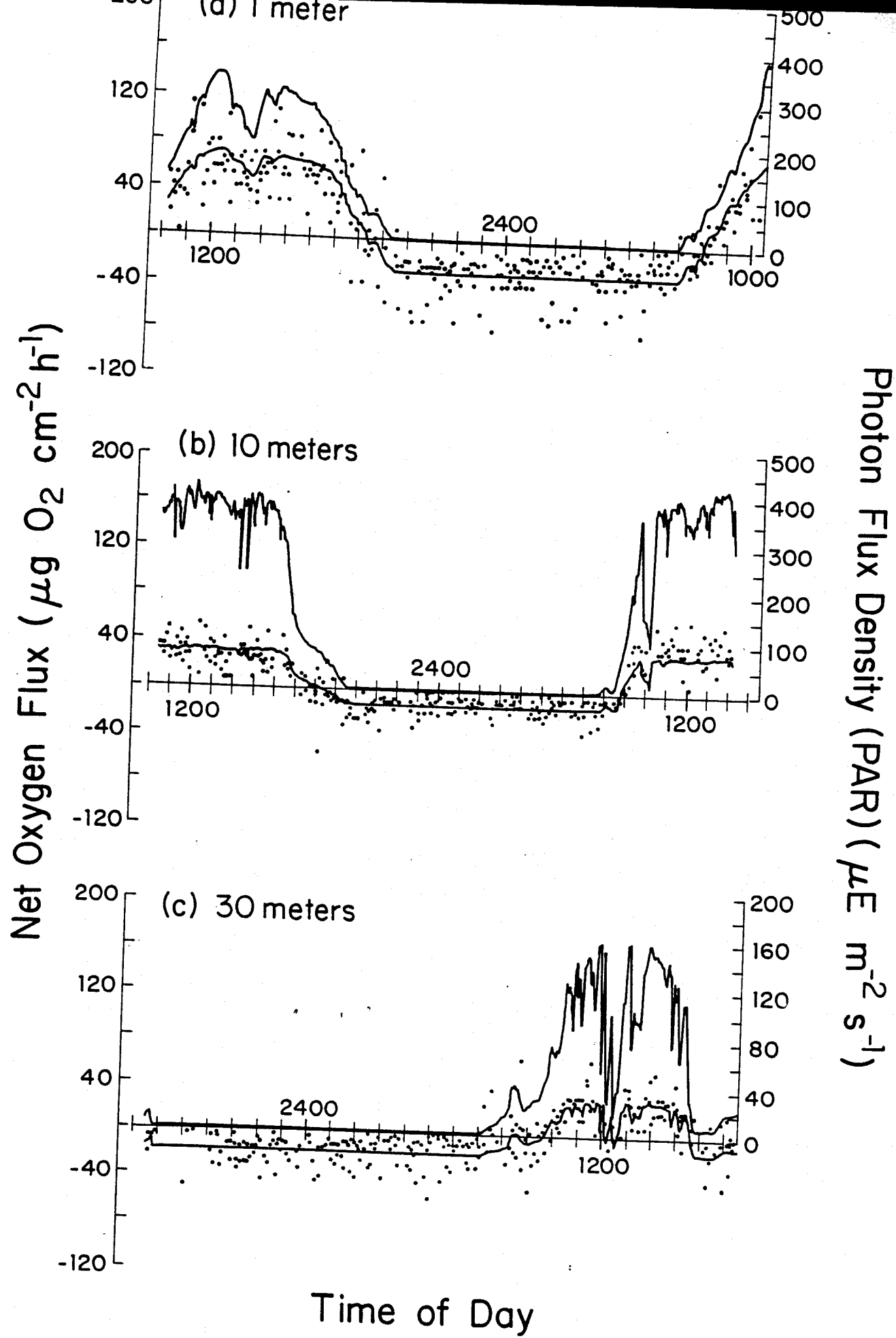
10 m



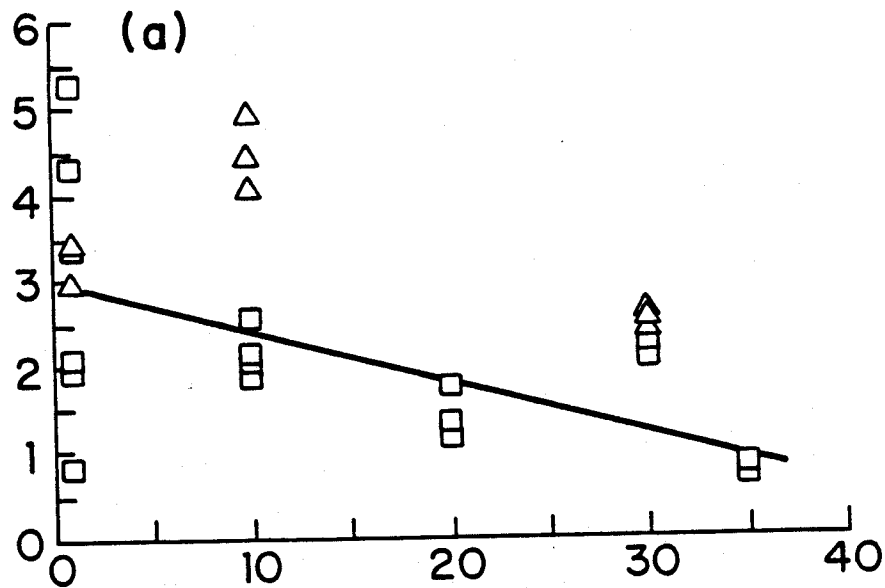
30 m



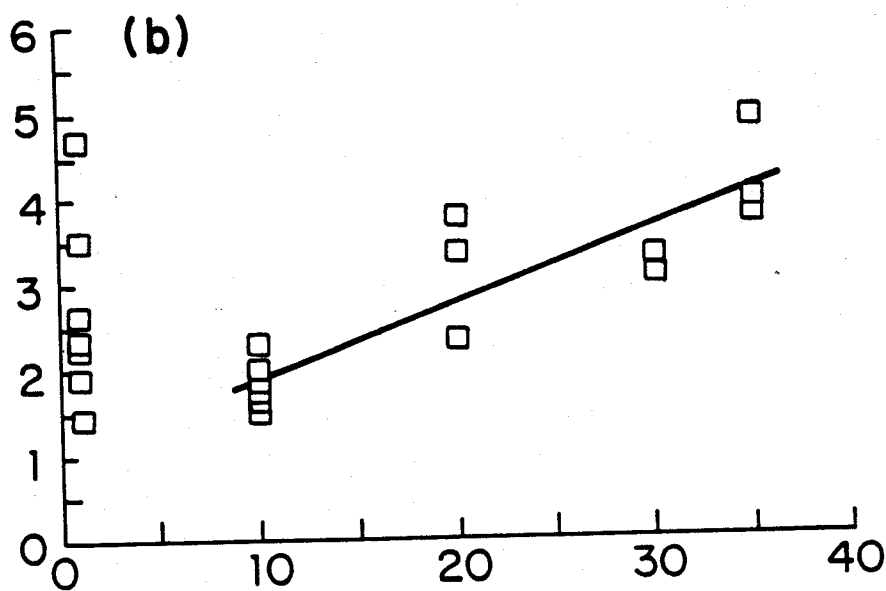
Photon Flux Density ( $\mu\text{E m}^{-2} \text{ s}^{-1}$ )



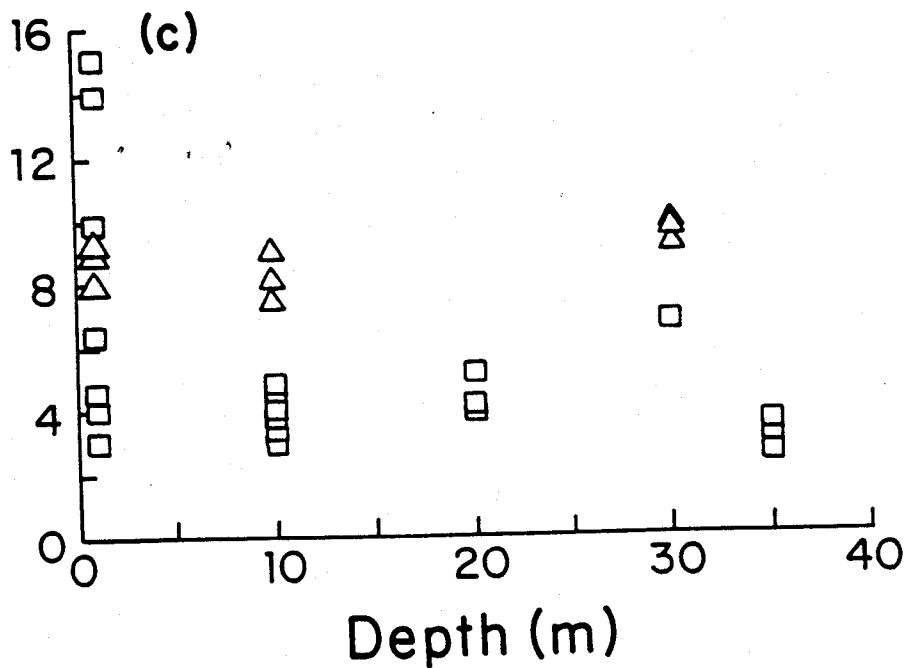
Zooxanthellae  
( $10^6$  cells  $\text{cm}^{-2}$ )

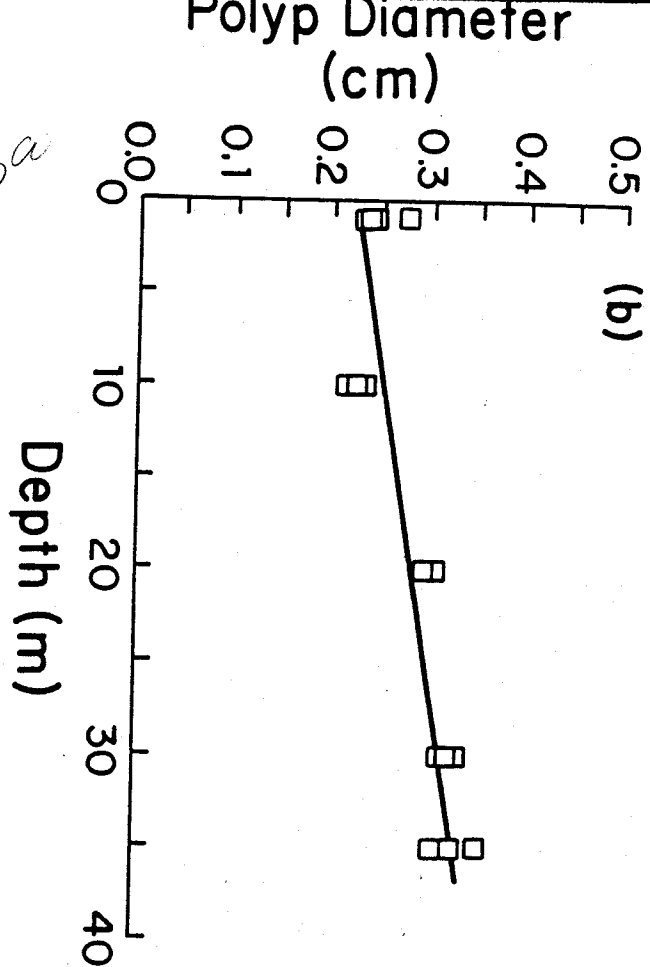
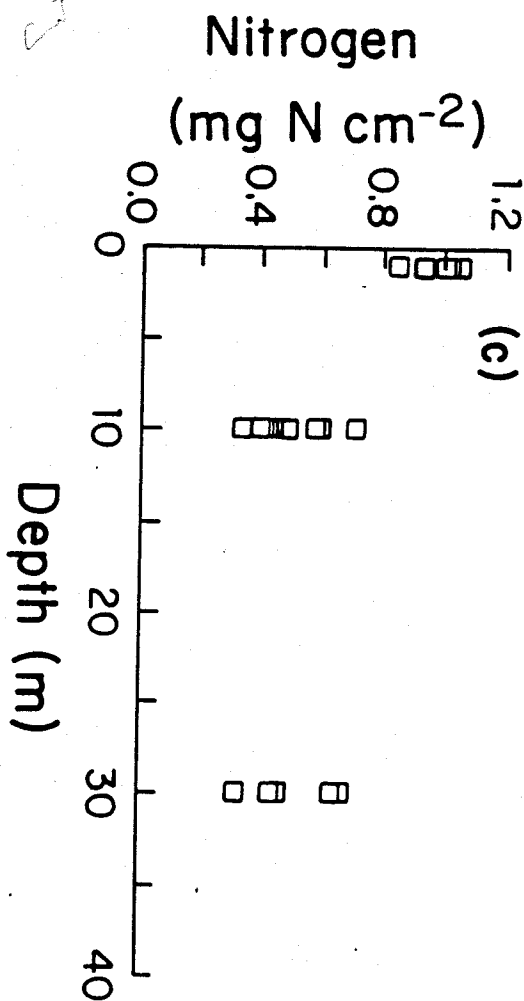
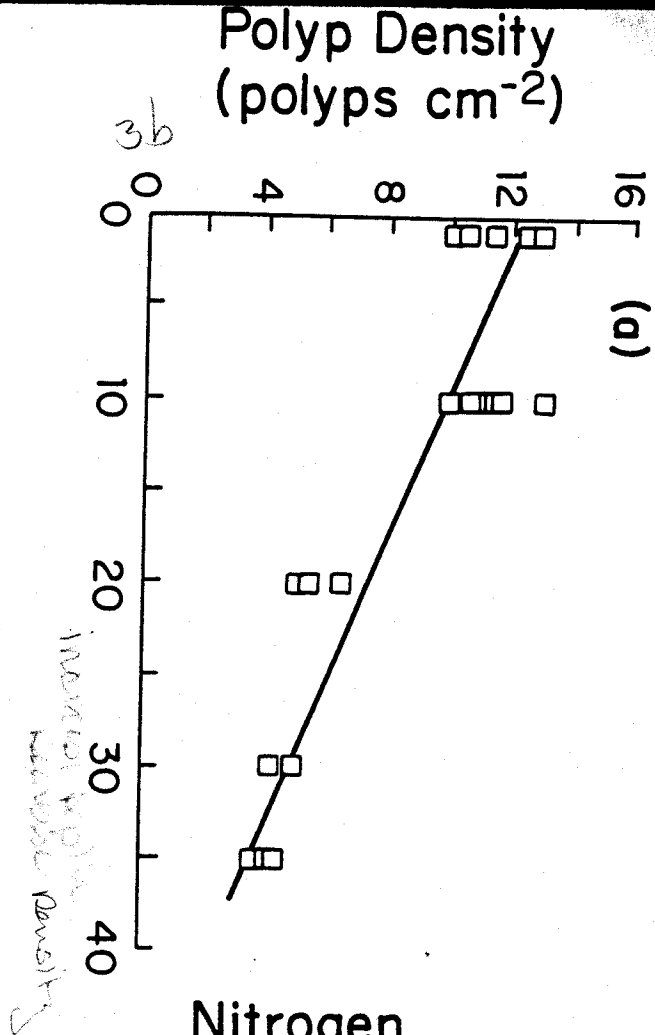


Zooxanthellae Chlorophyll  
(pg Chl *a* cell $^{-1}$ )

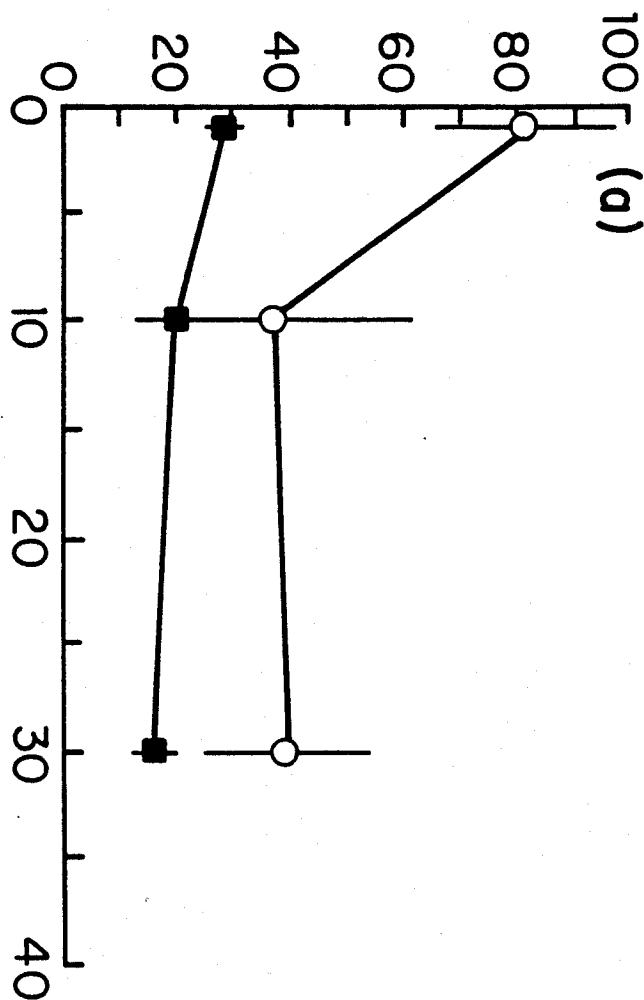


Chlorophyll  
( $\mu\text{g}$  Chl *a*  $\text{cm}^{-2}$ )





Respiration and  
Photosynthesis  
( $\mu\text{g O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ )



Respiration and  
Photosynthesis  
( $\mu\text{g O}_2 \text{ mg N}^{-1} \text{ h}^{-1}$ )

