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PHOTOADAPTATION AS A WHOLE ORGANISM RESPONSE IN MONTASTRAEA ANNULARIS

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ABSTRACT

Both algal and animal components of the symbiotic complex respond to decreasing irradiance across the 80 meter depth distribution of Montastraea annularis. Utilizing two-hour 14CO2 incubations, photosynthetic carbon fixation by the zooxanthellae of M. annularis decreases by more than 93% between 0.5 and 50 m, from 4.05 to 0.27 mg C mg Chl $a^{-1}h^{-1}$. Chlorophyll a and c2 concentrations per unit area and per algal cell increase with increasing depth. The efficiency of light utilization by the zooxanthellae for photosynthetic carbon fixation also increases with increasing depth. Total protein per surface area of coral skeleton steadily decreases from 0.97 ± 0.07 mg cm^{-2} at the surface to 0.37 ± 0.05 at 50 m, a 62% decrease in the amount of biomass to be supported by the decreasing photosynthetic carbon fixation of the zooxanthellae. This response is probably instrumental in allowing M. annularis to occupy one of the largest depth distribution of any known symbiotic scleractinian coral.

INTRODUCTION

Montastraea annularis (Ellis and Solander) is a hermatypic scleractinian coral common throughout the Caribbean. It is of major ecological importance as the primary frame-work building coral on most western Atlantic coral reefs (Goreau 1959), covering 10-50% of the reef surface area (Dustan 1975a; Porter et al. 1981). M. annularis has an extremely broad depth distribution, ranging from 1-80 meters below the sea surface (Goreau and Wells 1967; pers. observ.). The unicellular algal symbionts Symbiodinium microadriaticum (zooxanthellae), contained in the gastroderm cells of M. annularis are therefore exposed to a wide range of light intensities of varying spectral quality. With light intensity decreasing exponentially with depth in tropical water (Brakel 1979; Dustan 1982), zooxanthellae of increasingly deep-water colonies receive rapidly declining amounts of light energy for photosynthesis, decreasing the potential carbon and energy input to the symbiosis. As the red wavelengths of the light spectrum are the most rapidly attenuated by transmission through seawater, deep-water corals must also adapt to a spectrum containing an increasing proportion of energy in blue wavelengths.

Montastraea annularis adapt to this decreasing energy input by modification of the whole organism. It has been suggested that each of the three basic components of the symbiosis, the zooxanthellae (Dustin 1975a, 1979, and 1982), the coelenterate host tissue (Porter et al. 1984; Porter et al. in review), and the CaCO3 skeleton (Dustan 1975b; Graus and Macintyre 1976) are modified to maximize light capture and efficient utilization of photosynthetically fixed carbon. This study represents the first examination of the metabolic fate of photosynthetically fixed 14CO2 in a scleractinian coral incubated in situ across a broad depth range.

MATERIALS AND METHODS

Specimens of the hermatypic coral, Montrastraea annularis were selected from six depths near Discovery Bay on the north coast of Jamaica. Sites at 10, 20, 30, 40 and 50 m were located on the fore reef slope of Long-Term Sampling (LTS) Reef. The 0.5 m site was in Dairy Bull Cove. All colonies chosen for the experiments described in this paper were of a yellow-brown color, with yellow-brown stomadeal discs. Yellow-brown colonies represent over 80% of the five color morphs found from 1 to 50 m on Discovery Bay reefs (pers. observ.).

The rate of carbon fixation by M. annularis was determined at each of the six sites by 2 hour in situ incubations with NaH14CO3 (New England Nuclear, specific activity 40 to 60 mCi/m mole) spiked seawater. Incubations were done in 1200 ml acrylic chambers fitted with 0.3 cm thick quartz glass tops to allow UV penetration (Worrest et al. 1980). Aliquots of 53 μCi each of NaH14CO3 were added to each of 3 chambers through a serum stopper with a 2 ml syringe. The chamber contents were mixed by simultaneous withdrawal and replacement of incubation media with two 10 ml glass syringes. Previous fluoroscein dye studies indicated this method achieved complete mixing. No stirring or flushing occurred during the incubation period. Ten milliliters of the incubation media was brought back to the laboratory for determination of initial specific activity.

Incubations were terminated by removing the coral from the chamber, covering it with aluminum foil and bringing it to the surface. On reaching the surface, the corals were sealed in Zip-Loc plastic bags containing 0-2°C seawater. The bags were placed in an ice and brine solution and returned to the lab for processing. The delay between termination of incubation and initiation of processing was less than 15 min.

Pieces of the 14C labelled coral were removed with a hammer and chisel, and their area determined by the aluminum wrap method of Marsh (1970). These pieces were then completely crushed in a mortar, and added to 33.3 ml of 0.2 micron Millipore

filtered seawater in a 250 ml capped Erlenmeyer flask. These flasks were vigorously hand agitated for 2 min. The resulting tissue slurry was decanted from the settled skeletal fragments, and the procedure carried out additionally two times. The resulting 100 ml of tissue homogenate were blended for 1 min. in a Waring blender. Replicate 1 ml aliquots were prepared for scintillation counting to determine rates of carbon fixation, translocation, biochemical fractionation, and percent recovery.

Zooxanthellae were separated from 30 ml of coelenterate tissue by centrifugation at 6,500 rpm for 5 minutes at 4°C using a RC-2B Sorvall centrifuge fitted with a Sorvall 5534 rotor (resultant centrifical force of 5090). This process was repeated once. Four ml aliquots of the combined supernatants and the washed zooxanthellae pellets were frozen at -15°C until biochemical fractionation. A 1 ml aliquot of the supernatant was prepared for scintillation counting, to be used in determination of translocation of photosynthetically fixed carbon (Muscatine and Cernichiari 1969). All tissue samples were acidified by addition of 100 µl 6N HCl to drive off unincorporated $NaH^{14}CO_3$.

Coelenterate and zooxanthellae tissue was separated into five biochemical fractions by a modification (Lenhoff and Roffman 1971; Method II) of Roberts et al. (1955) fractionation utilizing differential solubilities. The isolation and content of the biochemical fractions are as follows: Fraction 1 = filtrate from ethanol treatment of cold trichloroacetic acid (TCA) filtrate. This contains amino acids, monosaccharides and other water soluble metabolic intermediates. Fraction 2 = filtered particles retained on Whatman GF/F filters from ethanol treatment of cold-TCA filtrate. This contains oligosaccharides and oligonucleotides. Fraction 3 = filtrate from ethanol treatment minus Fraction 1, and contains lipids, lipid soluble compounds and small proteins. Fraction 4 = filtrate from hot-TCA treatment minus filtrate from cold-TCA treatment, and contains nucleic acids. Fraction 5 = filtered particles from hot-TCA treatment minus Fraction 3, and contains proteins. For a complete description of the fractionation, see Lenhoff and Roffman (1971) and Szmant-Froelich (1981). All samples were prepared for scintillation counting in Fischer Scinterverse fluor, and counted on a Beckman LSC-100. Quenching was corrected by counting all samples a second time after addition of 10 µl of [14C]-toluene (New England Nuclear, 4 x 10^5 dpm/ml).

Measurements of photosynthetically active radiation (PAR, 400-700 nm) were made in situ from the surface to 50 meters with a Licor LI-185A Quantum Photometer and Licor LI-190 cosine-corrected flat-head sensor. To allow comparison of incubations made on different days, all depth series incubations were made within 1 h. of solar noon. All depth series incubations were repeated until integrated surface irradiances over each of the two-hour incubations were within 10% of each other.

Protein content of the tissue homogenates was determined by the Coomassie blue dye binding assay of Bradford (1976) using crystallized and lyophilized bovine serum albumin as a standard. Chlorophyll a and c2 content of the zooxanthellae were determined and Beckman DU-2 spectrophotometer, after extraction by the methods of Strickland and Parsons (1972). Values were calculated by the equations of Jeffrey and Humphrey (1975). Zooxanthellae density was determined by counting algal cells in tissue homogenates with a Neubauer haemocytometer. Five fields were counted in each of the three replicates of the tissue homogenate.

RESULTS

The relationship between light intensity, time of day and carbon fixation of colonies incubated in situ at 10 m is graphed in Figure 1. $NaH^{14}CO_3$ uptake per unit chlorophyll rapidly increases in early morning and reaches its maximum rate in early afternoon. Production rates between 1100 h. and 1700 h. are not significantly different (Figure 1).

The assimilation number, mg C mg Chl $a^{-1}h^{-1}$ at saturation, reaches a mean value of 3.5 between 1405 and 1605 hours. This is in the upper range of assimilation numbers, 1.0 to 3.9, reported for a variety of symbiotic scleractinian corals (Muscatine 1980). Carbon assimilation numbers increase with depth (Figure 2). Nonparametric statistical analysis of the data shows a significant positive relationship between increasing depth and increasing carbon assimilation number (Kendall's τ and Spearman's θ, $p < 0.05$). This clearly demonstrates photoadaptation by the zooxanthellae to lowered ambient irradiance.

Figure 3a demonstrates that the majority of photosynthetically fixed carbon in the zooxanthellae appears from 0730-1817 in Fraction 3, the lipid pool. Between 1820 and 2035 only 10% of the carbon appears as lipid, while close to 50% appears in Fraction 1, the water soluble small molecule pool which includes glucose.

The metabolic fate of fixed carbon that has been translocated to the coelenterate tissue throughout the day is shown in Figure 3b. Unlike the zooxanthellae, the majority of carbon appears in Fraction 1, the soluble small molecule pool, and secondarily in Fraction 3, the lipid pool. This pattern could be accounted for by translocation of both small water soluble molecules such as glycerol (Muscatine and Cernichiari 1969) and the translocation of lipid droplets (Kellog and Patton 1983; Patton and Burris 1983) but we have no way of knowing how much biochemical modification and or catabolism the organically translocated radiolabeled compounds have undergone.

Carbon fixation drops between 0.5 m and 50 m depth from 4.05 ± 0.14 to 0.27 ± 0.06 mgC mg Chl $a^{-1}h^{-1}$ (Table 1). Between 10 and 40 m, carbon fixation decreases more slowly than light intensity, indicating that the coral symbiosis is photoadapting to decreasing light intensity. When viewed on a per alga basis the rates of fixation in units of µgC 10^{-6}zoox h^{-1} falls from 4.5 to 0.9, a decrease of only 80% over this 50 m depth increase.

Table 1. Relationship between carbon fixation and depth during two-hour mid-day incubations in colonies of Montastraea annularis. Values shown are Mean ± one S.D. with N = 3.

Depth (m)	mgC mgChl $a^{-1}h^{-1}$	µgC $cm^{-2}h^{-1}$	µgC mg $protein^{-1}h^{-1}$	% Translocation
0.5	4.05 ± 0.14	11.2 ± 1.3	10.8 ± 0.5	42.0 ± 12.7
10	2.14 ± 0.59	8.1 ± 0.6	7.9 ± 1.1	51.5 ± 10.0
20	1.61 ± 0.67	5.2 ± 0.5	6.7 ± 0.5	32.7 ± 6.3
30	1.40 ± 0.98	4.4 ± 0.6	6.4 ± 0.9	34.5 ± 7.9
40	0.57 ± 0.12	2.6 ± 0.2	5.0 ± 1.2	28.3 ± 5.5
50	0.27 ± 0.06	1.6 ± 0.2	4.5 ± 0.3	39.0 ± 11.9

Table 2. Relationship of zooxanthellae density, chlorophyll concentration, and protein weight in Montastraea annularis colonies from different depths. Values shown are Mean ± one S.D. with number of samples in parentheses.

Depth (m)	10^6 zoox cm^{-2} (N = 6)	µg chl *a* cm^{-2} (N = 9)	µg Chl c_2 cm^{-2} (N = 9)	pg Chl *a* $cell^{-1}$ (N = 6)	pg chl c_2 $cell^{-1}$ (N = 6)	Chl a/c_2 (N = 6)	mg protein cm^{-2} (N = 6)
0.5	2.45 ± 0.96	2.72 ± 0.26	0.48 ± 0.19	1.21 ± 0.32	0.24 ± 0.15	5.67	0.97 ± 0.07
10	1.65 ± 0.36	3.78 ± 0.63	2.48 ± 1.15	2.43 ± 0.54	1.62 ± 1.10	1.52	1.04 ± 0.08
20	1.10 ± 0.48	4.20 ± 1.30	3.34 ± 2.45	3.32 ± 0.57	2.77 ± 1.79	1.26	0.78 ± 0.06
30	1.17 ± 0.46	4.47 ± 1.23	2.79 ± 2.66	3.28 ± 0.28	2.86 ± 2.71	1.60	0.68 ± 0.03
40	1.55 ± 0.35	5.06 ± 0.84	3.96 ± 0.83	3.06 ± 0.06	2.49 ± 0.30	1.28	0.54 ± 0.11
50	1.83 ± 0.05	5.95 ± 0.44	6.61 ± 2.67	2.62 ± 0.61	4.47 ± 0.86	0.90	0.37 ± 0.05

The metabolic fate of fixed carbon of zooxanthellae and coelenterate tissue isolated from colonies incubated in situ at depths of 0.5 to 50 meters is shown in Figure 4. The only major depth-mediated variations in metabolic fate occurs in Fraction 3, the lipid pool, and Fraction 5, the protein pool in both the zooxanthellae (Figure 4a), and to a lesser extent in these same fractions of coelenterate tissue also (Figure 4b). The percentage of coelentrate tissue activity in the lipid pool decreases slightly in colonies incubated from 0.5 m to 30 m then increases significantly.

Zooxanthellae density in Montastraea annularis tissue did not vary significantly with depth in this study (Table 2). Both chlorophyll *a* and *c*2 were found to increase in concentration with depth when expressed as mass per cm^2 of surface area of Montastraea annularis skeleton or per algal cell (Table 2). The chlorophyll *a* : *c*2 ratio declines significantly with depth (Table 2) droping from 5.67 in 0.5 m of water to 0.90 in 50 m of water.

Protein concentration expressed as mg cm^{-2} surface (Table 2) decreases from 0.97 ± 0.07 at 0.5 m to 0.37 ± 0.05 at 50 m a 62% decrease in the amount of biomass.

DISCUSSION

Our results, demonstrating uniform production rates throughout the mid-day, are consistent with in situ production studies utilizing polaragraphic oxygen electrodes. For instance, Acropora cervicornis, (Porter 1980) and Montastraea annularis (Porter et al. in review) show no mid-day depression in the generation of photosynthetically evolved oxygen. Other studies using radiotracer techniques on laboratory specimen (Barnes and Crossland 1978) do exhibit a mid-day depression. Due to the non-significance in our data, we suggest that larger sample sizes may be required to resolve this potentially subtle photosynthetic pattern.

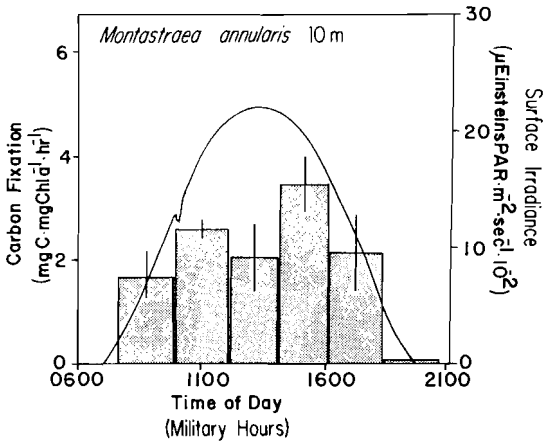

Figure 1. In situ carbon fixation (NaH14CO3 incorporation) by Montastraea annularis colonies at 10 m depth. Stippled rectangles and error bars represent mean ± one standard deviation (N = 3) incubated for two hours at each time period. Surface irradiance during the incubation is plotted on the right ordinate.

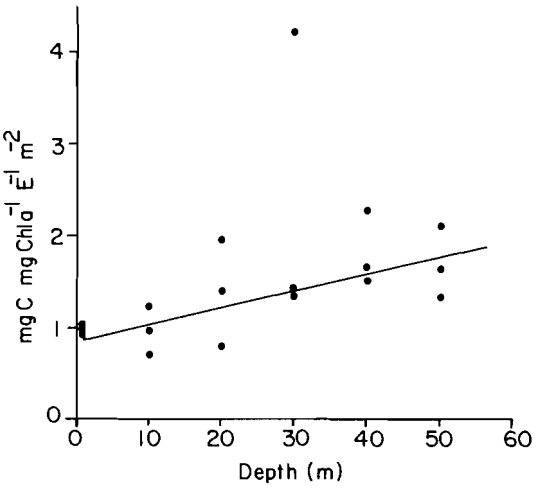

Figure 2. The efficiency of light utilization in photosynthesis increases with increasing depth in Montastraea annularis. Each point represents measurements from a single colony.

Our data (Figure 3) suggest that lipid synthesis by the zooxanthellae is light stimulated. In the early part of the evening (1820 h - 2035 h) when light intensity decreases, lipid synthesis also decreases. Build up in the small molecule pool at this time (Fraction 1) may reflect the accumulation of radio-labeled precursors of lipid synthesis. Light is known to stimulate lipid synthesis by zooxanthellae in other symbiotic associations such as in the scleractinian corals Pocillopora damicornis (Patton et al. 1977), Stylophora pistillata, (Patton et al. 1983), and Acropora acuminata (Crossland et al. 1980). The sea anemone, Anthopleura elegantissima, and the zoanthid Palythoa townsleyi, both symbiotic with zooxanthellae, also show light stimulation of lipid synthesis, and an increase in the soluble small molecule pool activity at sunset (Trench 1971a and b).

Due to respiration during the incubation, 14C bicarbonate measurements of productivity should estimate carbon fixation somewhere between actual net or gross production; oxygen measures of production will assess net production, and, if respiratory values can be added back in, can calculate gross production as well. Assuming a PQ value of 1.1, and a conversion factor of 0.375, oxygen studies on this species (Porter et al. in review) demonstrate that net asssimilation numbers drop from 2.89 mg C mg Chl $a^{-1}h^{-1}$ at 1 m to 1.90 at 30 m; gross values drop from 3.84 to 2.76. These values are similar in magnitude and change in a similar direction to the values reported in Table 1.

Analysis of total retrievable radioactivity in zooxanthellae and host coelenterate tissue shows that approximately 40% of the activity in the symbiotic association was located in the 10 m coelenterate tissue regardless of when the 2 h incubation occurred throughout the day. The remaining 60% of the activity resides in the zooxanthellae cells. In the past this would have been called 40% translocation of photosynthetically fixed carbon. The measurement of translocation monitoring distribution of photosynthetically fixed 14Carbon has recently been questioned (Muscatine et al. 1984). They propose that some of the carbon translocated from zooxanthellae to coelenterate is not radio-labeled, resulting in an underestimation of carbon transfer.

Measurement of instantaneous light utilization efficiency at saturating irradiance demonstrates an increasingly efficient use of ambient irradiance with increasing depth (Figure 2). These instantaneous carbon fixation measures are consistent with integrated oxygen flux measurements of production and irradiance from this species (Porter et al. in review) and its isolated zooxanthellae (Dustan 1982). Similar trends towards increasingly efficient light utilization with increasing depth have also been shown for other species (Wethey and Porter 1976; Falkowski and Dubinsky 1981; Dubinsky et al. 1984). Our carbon data are among the clearest demonstrations of the photoadaptive response of Montastraea annularis to reduced light intensity. They show that one of the responses to lowered ambient irradiance is to increase the efficiency with which both saturating as well as integrated total light is utilized.

Two alternative explanations exist to our demonstration of increased light utilization efficiency with increased depth. (1) The increased efficiency could be due to a decrease in UV light associated with an increase in depth. (2) The increased efficiency might relate to the decrease in red light associated with an increase in depth. We

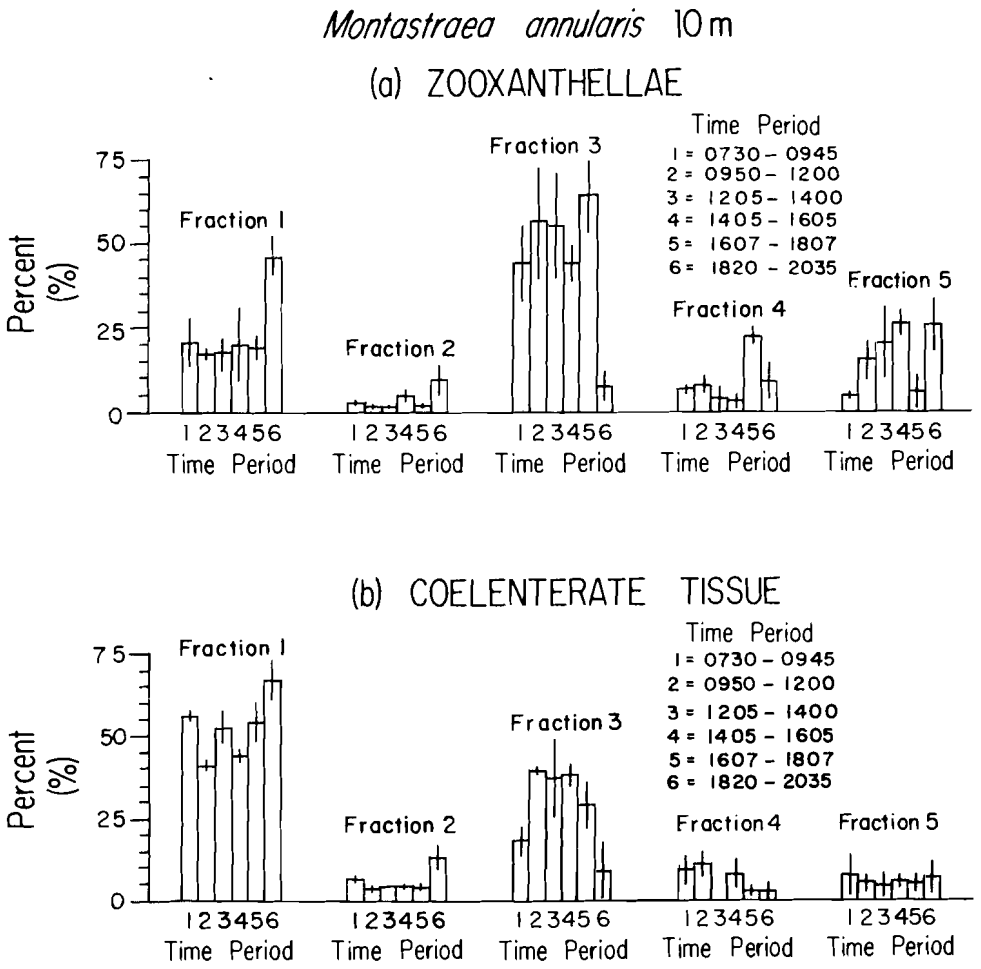

Figure 3. Biochemical fate of photosynthetically fixed carbon during two hour in situ incubations at 10 m of Montastraea annularis in a NaH14CO3 spiked seawater. Each cell of the histogram represents the percentage (mean ± one standard deviation of 3 colonies) of photosynthetically fixed carbon in the biochemical fractions of separated zooxanthellae tissue (Figure 3a) and coelenterate host tissue (Figure 3b). Values for total carbon fixation throughout the incubation period are shown in Figure 1.

have not tested these alternative hypotheses directly.

The percentage of fixed carbon appearing in the protein pool (Fraction 5) of the zooxanthellae decreases with increasing depths of incubation (Figure 4a). This is consistent with an observed reduction in the amount of tissue protein per unit area with increasing depth (Table 2), but the opposite of what would be predicted from the data of Morris (1981) correlating decreasing light intensity with an increase in the proportion of fixed carbon appearing as protein in laboratory experiments on unicellular algae. Morris et al. (1974) also showed that cultures of Phacodactylum tricornutum increased the proportion of 14C flowing into the protein pool under conditions of decreasing light intensity. However, when they performed the experiments in situ, from the surface to a depth of 25 m there was no depth-related increase in the proportion of fixed carbon appearing in protein, even though light intensity at 25 m was only 5% of surface intensity. Spectral shifts experienced under field conditions were not mimicked in the laboratory experiment.

Wallen and Geen (1971 a, b, and c), however, showed that the proportion of fixed carbon appearing as protein does increase with depth in natural phytoplankton assemblages, and claim that the increase is related to spectral composition rather than light intensity. When light is transmitted through seawater red wavelengths are attenuated more rapidly than green and blue, so that the proportion of total light energy in the blue range increases with depth (Jerlov 1976; Dustan 1982). Blue light does stimulate protein synthesis in

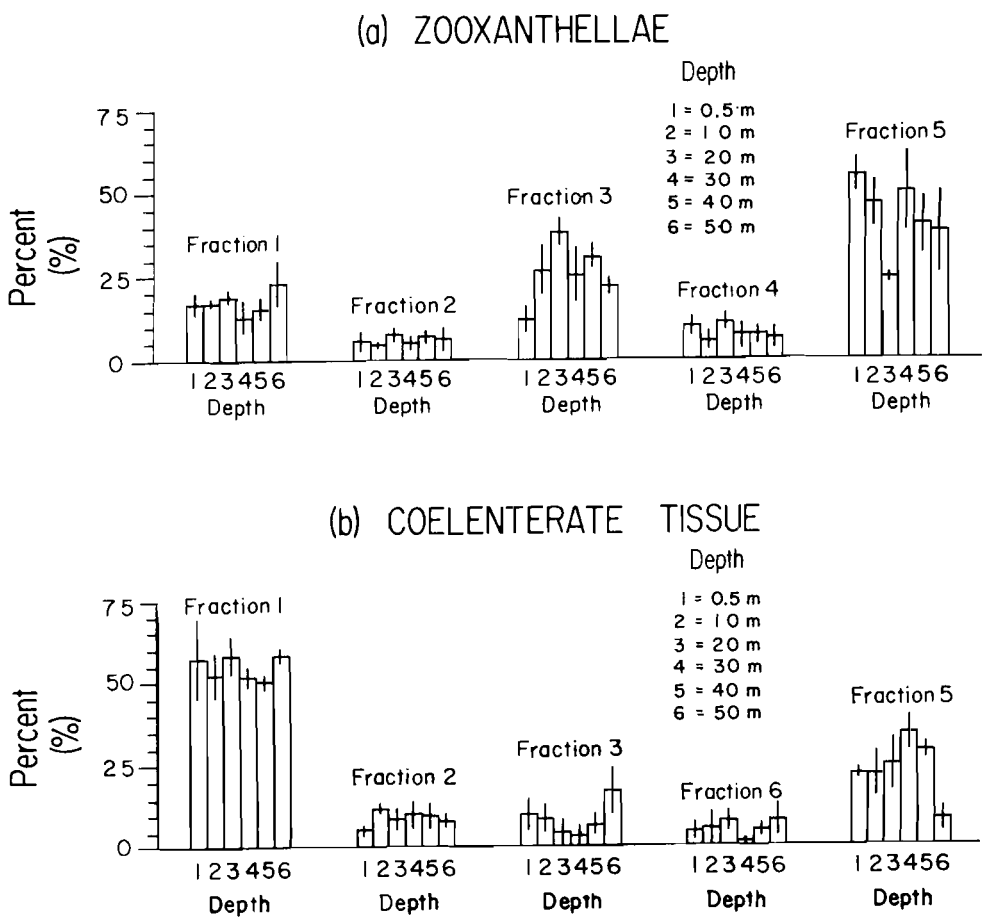

Figure 4. Biochemical fate of photosynthetically fixed carbon in Montastraea annularis at six different depths (0.5, 10, 20, 30, 40, and 50 m). Each cell of the histogram represents the percentage (mean ± one standard deviation of three colonies) of photosynthetically fixed carbon in the biochemical fractions of separated zooxanthellae tissue (Figure 4a) and coelenterate tissue (Figure 4b). Values for total carbon fixation throughout the incubation period are shown in Figure 1.

algae (Vokresenskaya 1972). Protein synthesis in Cyclotella nana and Dunaliella tertiolecta is stimulated by blue light (Wallen and Geen 1971 a, b, and c) but other algal species such as Gracilaria verrucosa (Bird et al. 1981) show no blue light stimulation. The percentage of coelenterate tissue activity in the lipid pool decreases in colonies incubated from 0.5 m to 30 m then increases (Figure 4b). Zooxanthellae density (Table 2) shows the same relationship with depth as the percentage activity in the lipid pool, suggesting that when more zooxanthellae are present, more lipid is translocated to host tissue. When evaluating the effect of spectral composition of light on the proportion of fixed carbon entering the protein pool of zooxanthellae, the effect of coelenterate tissue on spectral quality must be considered. Light must pass through the epidermis and mesoglea before striking the zooxanthellae in the gastrodermal cells, giving a spectrum of light of unknown composition for photosynthesis.

Zooxanthellae densities reported in Table 2 compare well with densities reported elsewhere for this species (Titlyanov et al. 1980; Porter et al. in review) except at the 40 m station where Porter et al. (in review) report significantly fewer zooxanthellae cells per unit area. Data reported here suggests that, within the errors of the counting method, zooxanthellae density is independent of depth. This trend will be an important one to sort out in future research since so many other biomass factors are changing with depth (see below) that the relationship between photosynthetic cell number and coelenterate host cell number could prove to be of great interest. The size as well as the number of each algal cell will also be of importance in determining the overall effect of

cell number on productivity or zooxanthellae respiratory demand.

An additional point of difference is a mid-depth depression in zooxanthellae density reported by Dustan (1979) for Montastraea annularis and for Favia pallida by Drew (1972). Our data (Table 2) are equivocal on this latter point, showing a non-significant mid-depth reduction.

The zooxanthellae in M. annularis utilize several mechanisms to compensate for the decreasing light and to increase absorbtion of the blue proportion of photosynthetically active radiation. The concentration of chlorophylls a and c2 per algal cell increases significantly with increasing depth (Table 2). Our increase in chlorophyll a content per algal cell with increasing depth is in agreement with Porter et al. (in review) but is disagreement with Dustan (1982) who found no significant increase between the surface and 50 m. A continuous increase with depth in chlorophyll c2 concentration (Table 2) allows more effecient utilization of the light available at depth. Chlorophyll c2 absorbs ten times as much blue light as red (Jeffrey 1969), partially filling the absorption window left by chlorophyll a (Prezelin and Sweeney 1978). Therefore, as chlorophyll c2 concentration in zooxanthellae increases with depth, they can utilize the blue proportion of the light spectrum more efficiently. Dustan (1982) found no significant difference in chlorophyll c2 concentration between the sufrace and 50 m.

Chlorophyll a : c2 ratios decline significantly with depth reflecting an increase in chlorophyll c2 concentration (Table 2). Other studies did not show this variation in a : c2 ratio (Dustan 1982) but are in agreement on the value of the ratio between 10 and 30 m. The extremely low values of c2 concentration at 0.5 m and high values at 50 m must be confirmed by additional data before this observation can be firmly established.

We have shown that in M. annularis the protein concentration per cm^2 surface area decreases by 62% between 0.5 and 50 m (Table 2), representing a large decrease in the amount of biomass to be supported by the decreasing amount of photosynthetic carbon fixation. Concomitant to this depth reduction in tissue biomass in Montastraea annularis is a significant reduction in respiration rate from 30.6 at 1 m to 14.0 $\mu gO2\ cm^{-2}h^{-1}$ at 10 m (Porter et al. in review). Within the limits of the experimental replication, respiration rates calculated on the basis of either tissue protein (Table 2) or Kjeldahl nitrogen (Porter et al. in review), do not change significantly with depth. These data are in apparent contradiction to the data of Davies (1980) which suggest that respiration rate per unit protein decreases with increasing depth.

The sum of the adaptations of the zooxanthellae, skeleton and coelenterate tissue result in a "photoadaptation" of the entire symbiotic complex. This whole organism response allows Montastraea annularis the broadest depth distribution of any known symbiotic scleractinian coral.

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