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Pattern of Distribution and Adaptation to Different Irradiance Levels of Zooxanthellae in the Soft Coral *Litophyton arboreum* (Octocorallia, Alcyonacea)

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Abstract

Photoadaptation responses of endosymbiotic zooxanthellae exposed to different light intensity within the same colony of the soft coral *Litophyton arboreum* were studied. Differences in the ultrastructure, including number and total length of sections of thylakoids as compared to chloroplast and cell membrane perimeter were measured. Chlorophyll a is 2.5-fold higher in cells from low light intensity as compared with cells taken from high light intensity. Chlorophyll a to c ratio of algae under lower light intensity increases in comparison to high irradiance. All the results show higher light harvesting capacity in terms of ultrastructure and pigment content in the same shade-adapted algae as compared to the light-adapted ones.

Keywords: *Litophyton*, Octocorallia, zooxanthellae, light-shade adaptation, symbiosis, ultrastructure, Red Sea

1. Introduction

The existence of symbiotic algae within Coelenterata has been recognized as early as 1882 (Brandt, 1882; Entz, 1882) and various aspect of this association have been extensively studied since then. These studies have been reviewed, among others, by Droop (1963), McLaughlin and Zahl (1966), Trench (1971), Taylor (1973), Muscatine (1974), and Glider and Pardy (1982). Within the Coelenterata, the relationships between zooxanthellae and alcyonacean species has also been documented. Most studies describe

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the phenomenon of the occurrence of zooxanthellae in the organisms and the morphology of the animal tissues containing the algae (Ashworth, 1899, 1900; Bourne, 1900; Pratt, 1903, 1905a,b; Gohar, 1940a,b,; Rudman, 1981; Faure et al., 1984). Ciereszko (1962) examined the occurrence of antimicrobial terpenoid compounds in zooxanthellae of alcyonaceans and Drew (1972) discussed the algal density as a function of depth in the class. Some aspects of nutrition, including the extent heterotrophy (Schlichter, 1982a,b; Schlichter et al., 1983, 1984) and productivity (Mergner and Svoboda, 1977) were also investigated.

Litophyton arboreum Forskål from the Gulf of Eilat is a tall arborescent soft coral (up to 60–100 cm) forming dense colonies, where the uppermost and peripheral parts of the colony shade the lower and inner ones. Under such conditions, the upper polyps are exposed to considerably higher light intensity than the polyps at the bottom of the same colony. Hence, it is expected that associated algae found in the polyps throughout the animal will react by adapting to the light gradient within their host.

Photoadaptive responses of microalgae, known better as light-shade adaptation, have been studied extensively since the classical works of Steemann-Nielsen and Hansen (1959) and Steemann-Nielsen and Jorgensen (1962). The recent works of Falkowski (1980, 1981, 1983), Prezelin (1981) and Richardson et al. (1983) summarize various aspects of subsequent research in this field. The adaptation has been examined mainly in free living marine phytoplankton, since these organisms experience different light intensities within the euphotic zone due to their vertical transport in the water column (Falkowski and Owens, 1980).

Light-shade adaptations in algae include: (a) changes in ultrastructure and cell volume (Falkowski and Owens, 1980; Dubinsky et al., 1983, 1984); (b) optical characteristics (Dubinsky et al., 1984); (c) chemical modifications, such as in pigment content and the chemical composition (Falkowski, 1980; Post et al., 1985); (d) biophysical and physiological responses, such as changes in the characteristics of photosynthesis to irradiance relationship (P vs. I curves), enzyme activity, and changes in respiration and growth rate (Muscatine, 1980; Rivkin et al., 1982; Chang et al., 1983; Falkowski et al., 1984).

Aspects of photoadaptation in endosymbiotic algae have been studied in alcyonacean (Drew, 1972), in hermatypic coral (Dustan, 1979, 1982) and some large Foraminifera (Lee et al., 1982). The common feature of these studies is that they compare light-shade adaptation of endosymbiotic algae

within invertebrate populations distributed at various depths. It is to be expected that at various depths, other environmental parameters (besides the irradiance levels) are different, e.g., spectral distribution of light, pressure, water temperature and quality, and plankton availability.

In the studies conducted on the hermatypic coral, *Stylophora pistillata* (Falkowski and Dubinsky, 1981; Dubinsky et al., 1983, 1984; Porter et al., 1984; Muscatine et al., 1984; Falkowski et al., 1984), the effects of irradiance levels were isolated by selecting colonies from similar depths, but from heavily shaded and fully exposed sites. Similarly, the endosymbiotic algae of *L. arboreum*, although under different light intensities, are found, even within the same colony, under otherwise similar physical and chemical conditions.

The objectives of this study is to reexamine with presently available techniques, the distribution of symbiotic algae in *L. arboreum* and to compare it to that reported for other coelenterates. It is also aimed at the expressions of light-shade adaptation in the ultrastructure and chlorophyll content of the algae, under natural conditions, located in *L. arboreum* tissues of the same colony exposed to different light intensities.

2. Distribution, Materials and Methods

Animal distribution

The soft coral, *Litophyton arboreum* (Octocorallia: Alcyonacea), belongs to the family Nephtheidae. Its zoogeographical distribution includes several localities in the Indo-Pacific region (Verseveldt, 1965, 1966). Among the five *Litophyton* species of the Red Sea, *L. arboreum* is the most common (Benayahu, 1985). In the Gulf of Eilat, colonies of this species abound (Fishelson, 1970), forming monospecific stands (Benayahu and Loya, 1977). Each stand consists of several colonies most probably resulting from colony fission. Such asexual colony propagation is a common feature of many soft corals, leading to space monopolization (Benayahu and Loya, 1977; Tursch and Tursch, 1982). *L. arboreum* is found in the northern Red Sea up to a maximal depth of 18 m (Benayahu, 1985). Their preferred bathymetric range is 1–10 m. Current studies indicate that *L. arboreum* is capable of successful competition with benthic reef organisms, such as hermatypic corals and several other soft corals, resulting in gradual exclusion (Benayahu, in prep.). In addition, these findings indicate a rapid growth rate of this soft coral.

The upper parts of the animal are light beige-brownish and change gradually to dark greenish and egg plant-violet in the most shaded parts of the coral. Small colonies hidden among large ones are also very dark. Samples

for this study were collected in the northern Gulf of Eilat, off the Heinz Steinitz Marine Biology Station from a depth of ca. 4m.

Light microscopy

Small clusters of polyps were fixed in Bouin and then decalcified in a mixture of equal volumes of formic acid (50%) and sodium citrate (15%). Sections of 8μ thickness were stained in Mallory Trichrome or hematoxylin-eosin and examined under a light microscope. Sections lightly stained by eosin were examined under an epifluorescence microscope.

Scanning electron microscopy (SEM)

Light and dark clusters of polyps and stems were prepared according to the GTGO procedure (Gamliel et al., 1983). Samples were examined by a JEOL JSM 840.

Transmission electron microscopy (TEM)

Small pieces of light and dark clusters of polyps and stems were fixed in Karnowsky's solution in phosphate buffer 0.1 M. After post fixation in osmium tetroxide, samples were block stained with uranyl acetate following serial dehydration in ethanol and propylene oxide and then embedded in Spurr's low viscosity medium (Spurr, 1969). Sections were cut with a diamond knife and stained with uranyl acetate (Stempak and Ward, 1964) followed by lead citrate (Reynolds, 1963). Sections were observed in a JEOL TEM 1200× operating at 80 kV.

The length of the thylakoids and chloroplast membranes was measured with a map distance reader on micrographs selected at random. The ratio between thylakoid length to chloroplast length was then calculated. The ratio of cross-sectional area of chloroplast to cell was measured by tracing the patterns from micrographs crossing, more or less, the cell's center, cutting and weighing the paper cutouts and comparing the weight to a known area.

For the calculations of algal cell number and chlorophyll content per cell, clusters of dark and light polyps were dried in a paper towel and weighed following grinding in a blender containing a known volume of filtered sea water. Cell counts were made with an improved Neubauer haemocytometer.

Known volumes of algal suspension were filtered through glass fiber paper (Whatmann GF/C), which was then ground in 90% acetone in a glass Teflon homogenizer and then filtered. The filtrates were measured spectrophotometrically and chlorophylls a and c per cell were calculated according to Jeffrey and Humphrey (1975).

Light measurements

Light measurements were taken with a QSI-140 Integrating Quantum Scalar Irradiance Meter (Biospherical Instruments). Light levels were measured as photon fluency above the external upper polyps and in the internal polyps of the colony. Due to water turbulence and the resulting colony movement, the lower polyps were exposed to wide fluctuations in light intensity. All measurements were taken at noon.

3. Results

The colony is a profusely branching plant-like form that may reach the height of one meter (Fig. 1). The small polyps are arranged in clusters situated on a common branch (Fig. 2). Algae were found in the endodermis of the anthocodia and the antostele in grooves which are formed by two adjacent septa. No algae were seen within the septa. The short tentacles contained algae in the endoderm (Fig. 3). The endodermis of the polyps extends into the coenenchyme forming the endodermal canals (Fig. 4). In these canals the highest concentration of algae was found in the walls at the perimeter of the branch. The density of algae in the parts of the polyps extending towards the inner part of the coenenchyme is very low.

Table 1. Comparison between light adapted (HL) and shade adapted (LL) algae from *Litophyton arboreum* (n indicates sample size).

Parameter	HL	LL	LL/HL
Photon fluency (μmole·m^{-2}·sec^{-1})	835–390	25–51	0.03–0.57
Cell × gr of animal tissue ×10^8	2.142 (n=5)	1.87	0.873
Cell diameter (μm)	7.64±99	8.24±87	1.079
Cell volume (μm^3)	233.4	292.8	1.253
Chloroplast to cell cross-sectional ratio (%)	31.8±9.9 (n=27)	55.24±9.9 (n=40)	1.732
Thylakoid length per cell (μm)	65.4 (n=17)	198.9 (n=19)	3.041
Thylakoid to cell perimeter length ratio	3.38 (n=17)	9.7 (n=19)	2.87
Thylakoid membrane to chloroplast perimeter length ratio	3.06±1.06 (n=30)	7.33±2.55 (n=28)	2.438
Thylakoid number per chloroplast	12±4 (n=90)	23±6 (n=48)	1.917
Chlorophyll a per cell (pg)	0.871±.11 (n=47)	2.205±.49 (n=62)	2.532
Chlorophyll a to c (mole:mole)	2.474 (n=5)	2.032	0.821

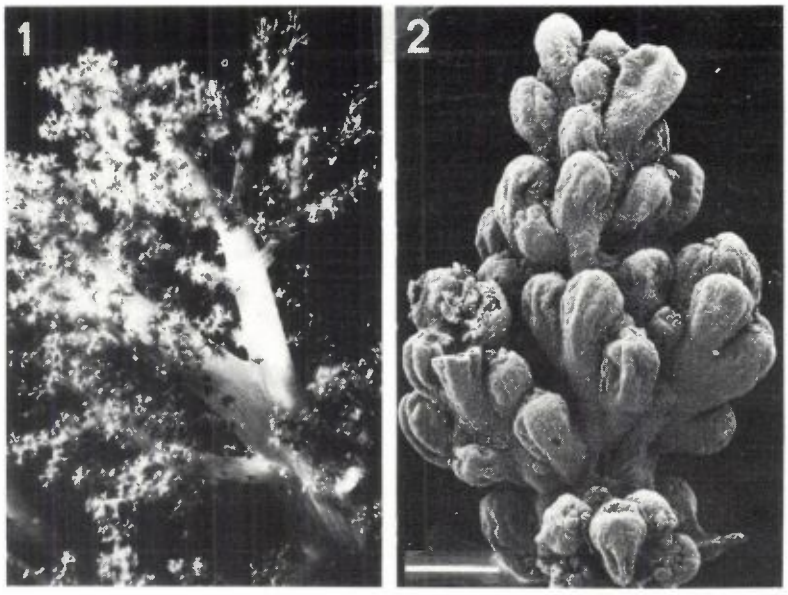


Figure 1. *Litophyton arboreum*, general view of a colony

Figure 2. *Litophyton arboreum*, SEM micrograph showing a group of polyps. The tentacles are contracted. (Bar = 1 mm).

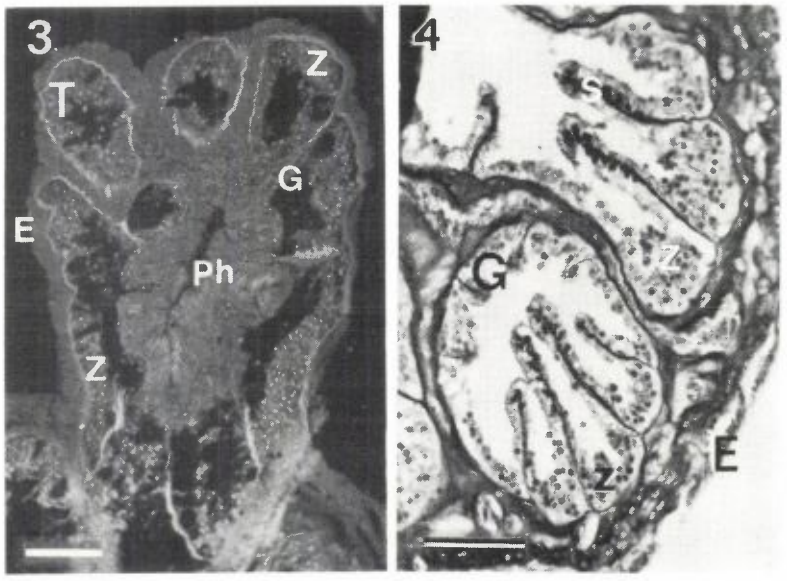


Figure 3. Histological section through a polyp examined under epifluorescent microscope showing the zooxanthellae in the tentacles and in the endodermis of the anthocodium and anthostele. G = endodermis, E = ectodermis, Ph = pharynx, T = tentacle, Z = zooxanthellae. (Bar = 100μm).

Figure 4. Histological section in a common branch showing endodermal tube. Algae are found at the perimeter of the branch. G = endodermis, E = ectodermis, S = septum, Z = zooxanthellae. (Bar = 100μm).

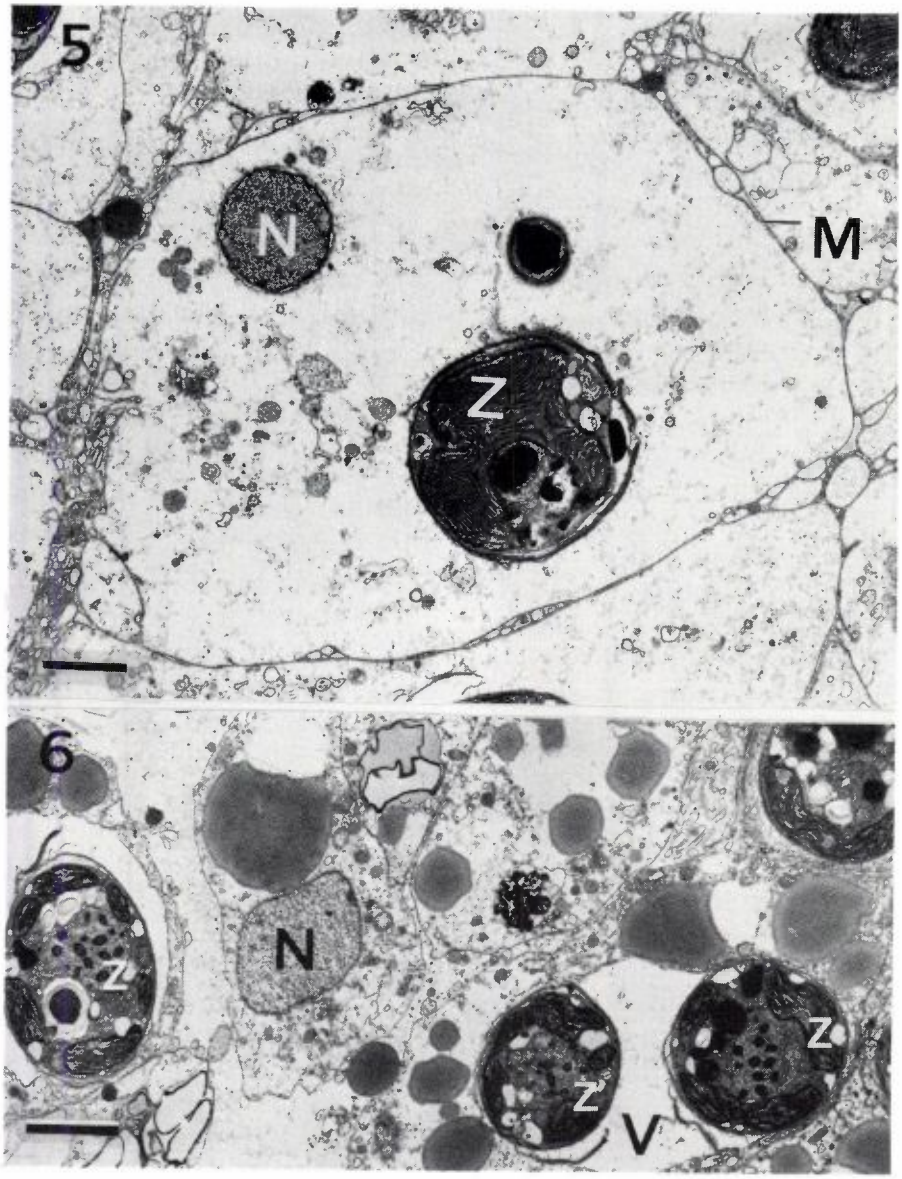
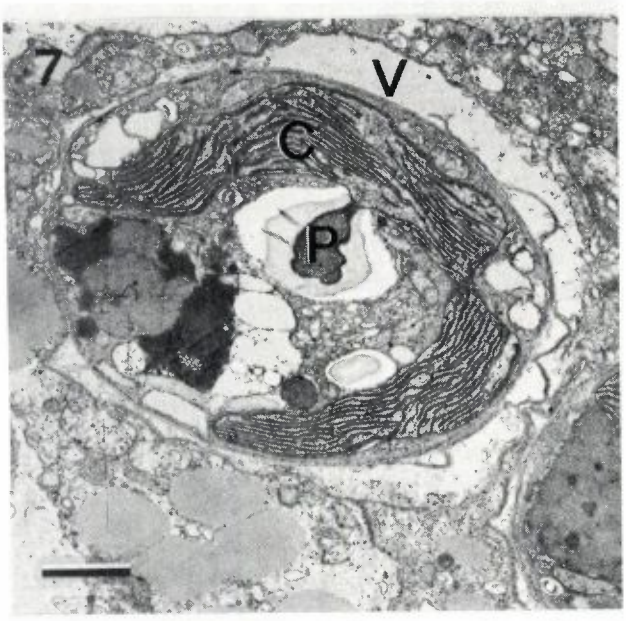


Figure 5. TEM micrograph of an endodermal cell of a polyp. N = coral's cell nucleus, M = coral's cell membrane, Z = zooxanthella. (Bar = 1μm).

Figure 6. TEM micrograph of an endodermal cell of a polyp showing two algal cells within a coral cell. N = coral's cell nucleus, V = vacuole, Z = zooxanthella. (Bar = 1μm).



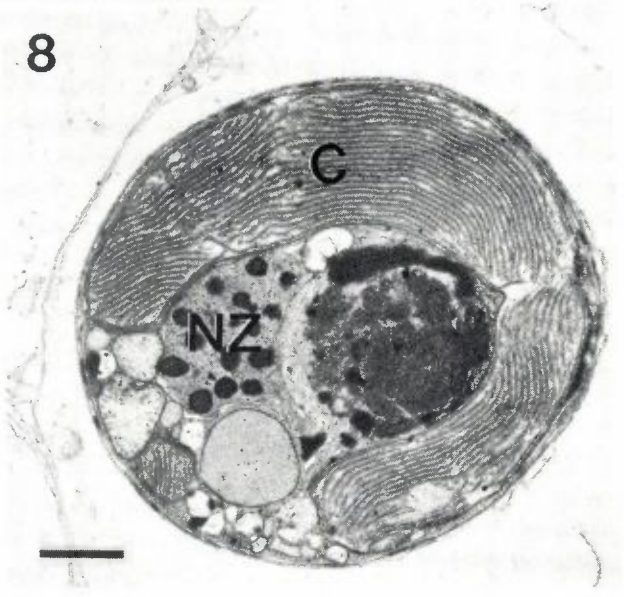


Figure 7. TEM micrograph of light-adapted zooxanthella. C = chloroplast with tylakoids, P = pyrenoid enveloped by starch, V = vacuole. (Bar = 1μm).

Figure 8. TEM micrograph of shade-adapted zooxanthella. C = chloroplast with tylakoids, NZ = nucleus of zooxanthella. (Bar = 1μm).

Figure 5 represents a section through an endodermal cell of a polyp showing the cell's nucleus and the algae within the same cell, illustrating the intracellular location of the symbiotic algae.

One or two algal cells are usually found within the same animal cell and in most cases they appear to be contained within a vacuole (Fig. 6).

The ultrastructure of algae taken from the upper (Fig. 7) and lower parts (Fig. 8) of the soft coral *L. arboreum* clearly shows the morphological differences between light-adapted and shade-adapted algae, respectively.

The difference between algae from high light (HL) and low light (LL) polyps, including ambient light intensity, are summarized in Table 1.

4. Discussion

The TEM micrographs reveal a metacaryon typical of the Dinophyceae. In general, the alga seems to be *Symbiodinium* sp., the zooxanthellae commonly found in most marine symbiont harbouring coelenterates (Blank and Trench, 1986).

Except for very few samples of extracellular location of zooxanthellae among coelenterates (Kawaguti, 1964; Kawaguti and Ogasawara, 1967; Kevin et al., 1969), members of this phylum harbour algal symbionts intracellularly.

This is also the situation in *L. arboreum*. The TEM micrographs provide evidence of the intimate physical contact between algal and host cell, allowing mutual physiological interactions.

Very little is known about the number of zooxanthellae within animal cells. The numbers cited are between 4 to 6 in sea anemone (Glider et al., 1980) to several hundreds in Foraminifera per animal cell (Be and Hudson, 1977). From our micrographs it is quite obvious that most cells harbour at least 1 to 2 zooxanthellae.

Depth-related changes in algal density in the animal tissue are discussed in the literature by several authors, though in some of these studies the influence of changes in irradiance from other depth-related factors are not separated. Some hermatypic corals show a reduction in algal cell density with depth (Drew, 1972; Porter, 1986; Porter et al., 1986). No significant difference in algal density has been found in the response of the hermatypic coral *Stylophora pistillata* to decreasing light (Falkowski and Dubinsky, 1981; Porter et al., 1984), whereas other investigators found an increase in cell density with shade (Zvalinski et al., 1978, 1980; Titlyanov et al., 1980). Our

results (Table 1) show a slight decrease in algal density in the lower parts of the soft coral colony, which is a shade, rather than depth response, since the distance within the colony does not exceed 40–50 cm. This result does not agree with Porter's conclusion (1986) that "zooxanthellae density lowers with increasing depth and remains constant with increasing shade."

Zooxanthellae of *L. arboreum* show a trend towards an increase in cell diameter in the shade, a result which is in contrast to that found for *Dunaliella tertiolecta* and *Skeletonema costatum* (Falkowski and Owens, 1980). It is possible that algae from different systematic groups will respond in different ways. Yet, a larger diameter is an advantage in enabling higher pigment content while algal density is lower.

Photosynthetic pigments per algal cell increase as light intensity decreases. This trend continues, up to an irradiance level below which pigment bleaching sometimes occurs (Falkowski and Owens, 1980; Lee et al., 1982). *L. arboreum* follows this trend by increasing chlorophyll content per zooxanthella cell by 2.5-fold as light intensity decreases 17- to 35-fold. It is interesting to see that the values of chl a per cell from the upper parts of the soft coral are at least 2.5 times lower than those reported in the literature for shallow water hermatypic corals (Dustan, 1979, 1982; Falkowski and Dubinsky, 1981; Porter et al., 1986).

Both chl a and c content in the *Litophyton* algae increase with lower light intensity; nevertheless, chl c concentration increases disproportionately to chl a so that the a/c ratio decreases. These data resemble those measured in chlorophytes and diatoms with reduction of a/b and a/c ratios, respectively (Myers and Graham, 1971; Falkowski and Owens, 1980). The same trend has been found for *Symbiodinium microadriaticum* from different hosts grown freely in culture (Chang et al., 1983). Our results are in contrast to those found in hermatypic-coral zooxanthellae (Porter et al., 1986) and in symbiotic diatoms (Lee et al., 1982), demonstrating no consistent trend for a/c ratio with depth or shade. The increase in chlorophyll content with shade or depth is expected to be accompanied by changes in the ultrastructure. Such results have been documented briefly for the algae of some hermatypic corals (Meshansky et al., 1980; Dubinsky et al., 1983; 1984). Some measurements of thylakoid/cell membrane in shade-grown cyanobacteria show relatively low values: 2.21 (Allen, 1968) and 4.68 (Berner and Jensen, 1982). These results are much lower than ours (9.7), probably resulting from the fact that in the eukaryotic dinoflagellates the thylakoids are packed in chloroplasts as compared to the loosely arranged thylakoids in the cyanobacteria. Our

results show significant differences between algae found in the upper polyps of *L. arboreum* to those found in the lower parts. Zooxanthellae from the shade contain more densely packed thylakoids and higher chloroplast volume, as seen in the cross sections. This increase in the thylakoids area allows the concomitant increase in cellular chlorophyll. The discrepancy between chl a/cell ratio in shade and light algae (2.53) as compared to other parameter ratios (i.e. thylakoid number/chloroplast (1.92), and chloroplast/cell cross section (1.7), might result from a denser packing of photosynthetic units in the shade cells.

The higher cellular levels of photosynthetic pigments with increased thylakoid area in the shade-adapted zooxanthellae of *L. arboreum* all add up to the increased light-harvesting capability under reduced irradiance levels. It may be worth noting that the decrease of more than 20 times cannot be offset by a 2.5-fold pigment increase. On the other hand, further increases in cellular pigment concentration would be self-defeating, since the cells become optically dense whereby the probability of additional pigment molecules to harvest light is greatly reduced (Dubinsky et al., 1984).

Further work aimed at elucidating the functional consequences of the different irradiance levels to which fully exposed and shaded parts of the same colony are subjected, is at present in progress in our laboratory.

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