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Light absorption and utilization by colonies of the congeneric hermatypic corals *Montastraea faveolata* and *Montastraea cavernosa*

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Abstract

The congeneric species *Montastraea faveolata* and *Montastraea cavernosa* are important hermatypic corals on reefs throughout the Bahamas, Caribbean, and the Florida reef tract that have overlapping bathymetric distributions. However, these congeners differ in their respective abundance at similar depths. The underlying mechanism for these patterns may partly be because of their relative dependence on photoautotrophy versus heterotrophy. The dependence of these two corals on photoautotrophy was examined quantifying the optical properties and productivity of these two species of corals at two different depths in the Dry Tortugas. Maximum surface irradiances in the Dry Tortugas during this study varied from 1,900 to 2,100 μmol quanta m^{-2} s^{-1}. Spectral attenuation coefficients calculated from the 1995 and 1996 irradiance data differed by as little as 10% within the visible wavelengths (photosynthetically active radiation [PAR], 400–700 nm), suggesting year-to-year similarities in the optical properties of the overlying water column. Underwater irradiances of PAR were ~400 μmol quanta m^{-2} s^{-1} and 25 μmol quanta m^{-2} s^{-1} at 10 m and 18 m, respectively. Significantly lower rates of maximum photosynthesis were observed for samples of *M. cavernosa* compared with *M. faveolata* at 10 m and 18 m. For samples of *M. faveolata* from both depths, the mean chlorophyll-specific absorption (a^*) across all PAR wavelengths was greater than that of *M. cavernosa.* When spectrally corrected for the underwater light field and used to calculate the minimum quantum requirements ($1/\phi_m$) of these corals at each depth, we observed that *M. faveolata* always had higher $1/\phi_m$ than *M. cavernosa* (50 versus 18 quanta O_2^{-1} and 39 versus 15 quanta O_2^{-1} at 10 m and 18 m, respectively). *M. cavernosa,* with its greater pigment concentrations and lower a^*, exhibits a significant package effect that results in a smaller functional optical cross section and lower maximum photosynthetic capacities, whereas *M. faveolata* at the same depths, despite the greater minimum quantum requirements, has a larger functional optical cross section and enhanced absorption of available visible radiation, resulting in a greater maximum photosynthetic capacity. Based on polyp size, corallite structure, and surface area considerations, *M. faveolata* appears to depend on photoautotrophy versus heterotrophy to a greater extent than its congener, *M. cavernosa.* Recent data suggest, however, that polyp size alone may not be a good indicator for differences in trophic strategies and that coordinated studies on feeding and productivity in corals are needed to better understand their ecological distributions.

The light environment is an important component of the productivity, physiology, and ecology of corals (Dustan 1982; Dubinsky et al. 1984; Porter et al. 1984; Falkowski et al. 1990) that restricts the distribution of most species of coral to depths of 60 m or less. Although heterotrophy plays an important role in the feeding biology of many species of coral, the principal input of carbon comes from autotrophic processes with the closest coupling for the translocation of carbon-rich photosynthate between their dinoflagellate symbionts (= zooxanthellae) and host tissues (Muscatine 1990).

The underwater light field is modified by the angle of incident light, the absorption and scattering of light by dissolved and particulate materials in the water, and by the water itself (Kirk 1994). Additionally, incident irradiance is not attenuated uniformly across all wavelengths and corals in shallow waters are exposed to wave-focused light, so-called flashes or sunflecks, which can exceed 4,000 μmol quanta m^{-2} s^{-1} (Falkowski et al. 1990). After the effects of the overlying water column are accounted for, the incident irradiance that zooxanthellae are exposed to is further modified by the host tissues and carbonate skeleton (Kühl et al. 1995). Changes in the underwater light field, variations in polyp size and corallite architecture, the bathymetric distri-

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bution of corals, and their sessile lifestyle make them ideal systems for studying optical properties and productivity of the symbiosis as they relate to changes in spectral quantity and quality.

Productivity studies on *Montastrea annularis,* prior to the proposed recognition of sibling species within the genus (Knowlton et al. 1992), have shown a decline in chlorophyll-specific productivity that is highly correlated with the exponential decline of photosynthetically active radiation (PAR; Battey and Porter 1988). Despite this demonstrated decrease of productivity in corals with depth and therefore irradiance (Wethy and Porter 1976; Falkowski and Dubinsky 1981), there are few published studies that have examined the photoacclimatization strategies, productivity, and optical properties of corals as they change with either depth or between species (Dunstan 1982; Dubinsky et al. 1984; Wyman et al. 1987). However, there have been studies on the effect of spectral composition (visible) on photosynthesis (Kinzie et al. 1984; Kinzie and Hunter 1987) that have shown that corals do not exhibit complementary chromatic adaptation; they photoacclimate principally in response to changes in total irradiance.

Evidence for photoacclimatization to changes in visible radiation is well known. First, and most important in respect to the optical properties of corals, is the inverse relationship between the concentration of photosynthetic pigments contained within the zooxanthellae and total irradiance (Falkowski and Dubinski 1981). This light–shade acclimation is now known to reflect changes in the size and number of photosynthetic units (PSUs) resulting principally in an increase in the amount of chlorophyll (Chl) *a* cell^{-1} and per unit area. Changes in the photosynthetic apparatus with total irradiance does effect the shape of the photosynthesis–irradiance (*P-I*) curve. When maximum productivity (P_{max}) is normalized to chlorophyll or surface area, it usually exhibits a direct relationship with irradiance increasing to some asymptotic value once the photosynthetic apparatus is saturated with light, and rarely exhibits photoinhibition of photosynthesis, as commonly observed in phytoplankton (Falkowski et al. 1990). On theoretical grounds, Chang et al. (1983) used pigment ratios and photosynthetic responses to characterize changes in PSUs and the photoacclimation strategies of zooxanthellae in culture from three cnidarian hosts. Subsequently, Lesser and Shick (1989) used the methods described in Chang et al. (1983) to describe a mixed photoacclimatory response (changes in both the size and number of PSUs) for the cultured zooxanthellae of the sea anemone *Aiptasia pallida.* More recently, direct measurements of PSU size and number by Iglesias-Prieto and Trench (1994) showed that the photoacclimatory response of cultured zooxanthellae involves changes in both PSU size and numbers, that these changes are species specific, and that they reflect the ecological distribution of their respective hosts.

Another approach to understanding the photoacclimatization processes and changes in coral productivity is to quantify the optical properties of the coral with an attempt to obtain optical closure, that is, assessing which photons are absorbed, reflected, or re-emitted as fluorescence. This approach is not necessarily new; both Dubinsky et al. (1984) and Wyman et al. (1987) examined the chlorophyll-specific absorption coefficients and quantum yields for photosynthesis of corals from the Red Sea and the Caribbean. Their interpretation of these parameters suggested that differences in the efficiency of light utilization are correlated with the growth rates and bathymetric distribution of the corals examined. Our aim here is to gain an understanding of the variation in optical properties of corals (e.g., pigment concentrations, absorption spectra, and fluorescence emission spectra), with changes in the quantity and quality of the underwater light field (i.e., with depth). Changes in optical properties as a component of the photoacclimatization response are directly linked to differences in photosynthetic performance observed between coral species and also within a species of coral as a function of its physical environment. The objectives of this study are to elucidate differences in the optical properties of two ecologically important congeneric species of hermatypic coral in the Caribbean, *Montastraea faveolata* and *Montastraea cavernosa,* with respect to absorption spectra, pigment concentration, chlorophyll fluorescence, and productivity under varying in situ light regimes.

Materials and methods

Research sites—Two sites within the Dry Tortugas National Park were selected for study: a 10-m site consisting of a fringing reef with spur and groove formation on Long Key (24°37.4′N, 82°51.6′W) was used during the summer of 1995 (20 August–28 August) and an 18-m site consisting of a sandy bottom with isolated patch reefs adjacent to Loggerhead Key (24°38.5′N, 82°56.0′W) was used during the summer of 1996 (7 July–16 July). A detailed description of the area can be found in Jaap et al. (1989); quantitative photographic quadrats of these sites indicate no substantial difference in the percentage of cover of hermatypic corals and other functional groups since that earlier study (Lesser unpubl. data). All experimental sites were accessed by SCUBA diving.

Underwater light field—Visible and ultraviolet (UV) radiation (300–700 nm) were measured over several days during August 1995 at 10 m and July 1996 at 18 m, as well as simultaneous measurements of surface irradiance using a LiCor LI-1800UW scanning spectroradiometer calibrated with National Institute of Standards and Technology (NIST) traceable standards. At each deployment depth, hourly readings of three scans were taken and the mean reported in units of W m^{-2} nm^{-1}. The cosine-corrected collector and sensors were programmed to scan from 300–700 nm in 2-nm intervals. The sensor has a 50% detection range of $\pm$2 nm on either side of the wavelength measured and minimum excitation energies on the order of 10^{-8} W cm^{-2} nm^{-1}. Despite the 8-nm bandwidth of this instrument, which tends to smooth sharp peaks, comparison testing has shown very good agreement with radiative transfer models and other commercial underwater instruments for measurements in the visible and UV radiation portion of the spectrum (Kirk et al. 1994; Lesser unpubl. data). Vertical attenuation coefficients (K_d m^{-1}) for both visible and UV radiation were calculated as described by Kirk (1994).

Primary productivity (photosynthesis versus irradiance and respiration)—Colonies ($n = 6$) of *M. faveolata* and *M. cavernosa* were collected at their depth of occurrence (10 m and 18 m), cleaned of all epibionts, and allowed to heal for 48 h. These samples were then placed in a self-contained, multichambered, underwater respirometer at the depth of collection for 24–36 h to obtain oxygen flux and underwater irradiance data. Briefly, the chambers were approximately 15 cm in diameter and 20 cm tall, with a volume of 3.7 liters. The chambers and lids were made of UV-transparent Plexiglas (100% cutoff at 295 nm). All chambers were constantly stirred using hydraulically driven magnetic stirrers and flushed at 60-min intervals to prevent supersaturation of the seawater with oxygen during the day. Changes in oxygen concentration were measured using calibrated Cameron Instruments E101 polarographic electrodes. The oxygen electrode polarization and the pump and solenoid controls were provided on a custom-designed printed circuit (Pamunkey Engineering Associates) in an Ikelite U/W housing. Data were collected and stored using a LiCor 1000 datalogger, also located in the Ikelite U/W housing, then downloaded to a computer as a text file and converted to oxygen concentrations and fluxes. The oxygen flux within each chamber was corrected for the volume displacement of each individual coral. The incident PAR (400–700 nm) was recorded using an underwater cosine-corrected sensor (LiCor LI-192SA) simultaneously with the oxygen flux data. Temperatures at each depth were measured by thermistor strings (HOBO recording temperature thermistors; Onset Corporation). Photosynthesis and respiration were normalized to colony surface area determined immediately after removal from the respirometer using the aluminum foil technique (Marsh 1970). The oxygen flux data (net photosynthesis) was then modeled and described as a *P-I* curve. Initial plots of the normalized data showed no photoinhibition of photosynthesis at irradiances greater than saturation as commonly observed in phytoplankton. Consequently, the hyperbolic tangent *P-I* model [$P_i = P_s \tanh(\alpha I/P_s)$] of Jassby and Platt (1976), where P_i(μmol O_2 cm^{-2} h^{-1}) is the instantaneous rate of photosynthesis normalized to surface area at irradiance i; P_s (μmol O_2 cm^{-2} h^{-1}) is the maximum rate of photosynthesis; and α (μmol O_2 cm^{-2} h^{-1} (μmol quanta m^{-2} s^{1})$^{-1}$) is the initial slope of the *P-I* curve, was used to nonlinearly fit the oxygen flux data normalized to surface area and derive the maximum photosynthetic capacity, P_{max} (μmol O_2 cm^{-2} h^{-1}), for each coral. The photosynthetic parameters were statistically compared using an unpaired Student's t-test with species as the factor at a significance level of 5%. Additionally, coral plugs (1.8–1.95 cm^{-2}) were analyzed for Chl *a*. Each plug ($n = 3$) was placed overnight in 90% acetone at 4°C, and subsequently the absorbance was measured against acetone blanks at 630 nm and 663 nm. The trichromatic equations of Jeffrey and Humphrey (1975) were then used to calculate the concentrations of Chl *a*.

Mycosporine-like amino acids—For all coral samples, the extraction and analysis of UV radiation–absorbing compounds, or mycosporinelike amino acids (MAAs), were performed according to the procedures of Dunlap et al. (1986) as modified by Shick et al. (1992). For analysis by high-performance liquid chromatography (HPLC), coral plugs (1.8–1.95 cm^{-2}) from each species ($n = 6$) were cleaned of epiphytes, broken into small pieces, and extracted overnight in 5 ml of 100% HPLC-grade methanol at 4°C. The extracts were centrifuged and the supernatant used for MAA and protein analyses. Individual MAAs were separated by reverse-phase isocratic HPLC on a Brownlee RP-8 column (Spheri-5, 4.6 mm inner diameter × 250 mm) that was protected with an RP-8 guard column (Spheri-5, 4.6 mm inner diameter × 30 mm). The mobile phase consisted of 40 to 55% methanol (v : v) and 0.1% glacial acetic acid (v : v) in water and run at a flow rate of 0.6 ml min^{-1}. Detection of MAA peaks was by UV absorbance at 313 and 340 nm. Standards were available for seven MAAs (mycosporine–glycine, shinorine, porphyra-334, palythine, asterina-330, palythinol, and palythene). Identities of peaks were confirmed by cochromatography with standards and the ratios of 313–340-nm absorbances. Peaks were integrated and quantification of individual MAAs was accomplished using HPLC peak areas and calibration factors determined by analysis of the standards listed above. All MAAs were normalized to soluble protein from an aliquot of the methanol-extracted sample; concentrations are expressed in μg MAA mg protein^{-1}. Protein measurements were determined using the procedure of Bradford (1976). The MAA concentrations between species at the same depth were compared using an unpaired one-tailed Student's t-test at a significance level of 5%.

Photosynthetic pigments—Extraction and quantification of zooxanthellae photosynthetic pigments were conducted as described by Wright et al. (1991). Coral plugs ($n = 3$) were collected from colonies of *M. faveolata* and *M. cavernosa* at 10- and 18-m depths, respectively. These plugs were extracted in 10 ml 100% acetone and aliquots centrifuged (1,000 × g), diluted to 66% acetone with distilled water, and 150 μl injected. Pigments were separated using a gradient system of 80 : 20 methanol : ammonium acetate, 90 : 10 acetonitrile : water, and ethyl acetate with a Spheri-ODS, 25 cm × 4.6 mm–inner diameter, 5-μm particle size column at a flow rate of 1.0 ml min^{-1} with detection at 436 nm, as described by Wright et al. (1991). Authentic standards were obtained from Sigma (Chl *a*, β-carotene) and VKI Water Quality Institute (Chl c_2, peridinin, diadinoxanthin, diatoxanthin) as described by the SCOR Carotenoid Workshop (Wright et al. 1991). Peaks were integrated, and quantification of individual pigments was accomplished using HPLC peak areas and calibration factors determined by analysis of the standards listed above. Concentrations are expressed in ng cm^{-2}.

Fluorescence measurements—A diver-operated spectrofluorometer (Mazel 1997) was used during the 1995 field season to measure fluorescence emission spectra in situ. The unit contained a model S1000 spectrometer (Ocean Optics Inc.) controlled by a Tattletale model 7 data logger (Onset Computer Inc.). Light reached the spectrometer via a 600-μm-diameter fiber optic cable and a 100-μm entrance slit, resulting in a nominal 10-nm spectral resolution. The spectrometer was fitted with a grating/detection combination that

recorded 1,024 spectral bins covering the wavelength range ca. 250–750 nm. Fluorescence excitation energy was provided by a 50-W halogen lamp. The lamp output was focused through one of four user-selectable filters onto the end of a 3-mm-diameter liquid light guide. The probe head holds the excitation and receiving fibers at a 45-degree angle and excludes ambient light. Data were saved to a hard disk for shipboard download via an infrared optical link. Where the data were excessively noisy, a simplified least-squares smoothing algorithm was utilized (Savitzky et al. 1964; Steinier et al. 1972).

During the 1996 field season, fluorescence emission spectra were obtained using a SPEX FluoroMax-2 fluorescence spectrofluorometer with a fiber optic probe. Emission spectra ($n = 6$) for each species of coral were collected from 460 nm to 750 nm using an excitation wavelength of 450 nm.

During both the 1995 and 1996 field seasons, shipboard measurements of excitation/emission fluorescence spectra on isolated zooxanthellae were made on each species of coral. These spectra are useful for identifying the dominant pigment groups within natural samples. In 1995 and 1996, measurements were made on freshly isolated zooxanthellae gently vacuumed onto GF/F filter pads ($n = 3$) as described below. The excitation and emission spectra were obtained using the techniques described by Yentsch and Yentsch (1979) with a spectrofluorometer consisting of two double-beam monochromators, a xenon light source, and a red-sensitive photomultiplier. The output from the photomultiplier is fed to a recorder with excitation spectra measured at 680 nm and emission spectra measured at 470 and 530 nm.

Light absorption and utilization by corals—The chlorophyl-specific spectrally corrected absorption coefficient was determined by filtering volumes ($n = 3$ for each species) of coral homogenate, obtained by air-brushing the host tissue and zooxanthellae free from the coral skeleton using filtered (0.45 μm) seawater, onto GF/F (4.5 cm) filters. These filtered volumes had chlorophyll concentrations approximating the in situ areal chlorophyll concentrations of the corals. Optical density was measured using a dual-beam spectrophotometer (290–700 nm) against seawater-wetted GF/F filters. Spectra were measured on the filter before and after a hot methanol extraction to remove chlorophylls and carotenoids (Kishino et al. 1985) and to estimate the absorption from nonalgal material. The spectral absorption coefficient was calculated from the optical density spectra using the following equation:

$$a(\lambda) = 2.303\ \mathrm{OD}(\lambda)/L \times 100$$
$$L = V/A \times \beta,$$

where 2.303 is a transform from $\log_{10}$ to $\log_e$, OD(λ) is the baseline-corrected optical density for each wavelength, L is the optical path length, 100 is the conversion from centimeters to meters, V is the volume of filtered sample in milliliters, A is the effective area of the filter in square centimeters, and β is the path length amplification factor associated with the multiple scattering by the filter pad (Bricaud and Stramski 1990). A β value of 2 was chosen for all calculations based on the work by Bricaud and Stramski (1990) that described amplification factors as being largely invariant at high optical densities (>0.2). The measurement of optical densities on a filter pad with high pigment concentrations and significant scattering more likely approaches the *in hospite* conditions of zooxanthellae. There is no attempt here to use amplification factors that better represent a dilute suspensions of cells. The spectral absorption coefficient was then divided through by the chlorophyll concentration on the filter pad, which was calculated after the filter pads were placed overnight in 90% acetone at 4°C, and the absorbance measured against acetone blanks at 630 nm and 663 nm. The trichromatic equations of Jeffrey and Humphrey (1975) were then used to calculate the concentrations of Chl *a* to obtain a spectral chlorophyll-specific absorption coefficient. This spectral chlorophyll-specific absorption coefficient was then multiplied by the underwater spectrum from midday at the depth of collection for that sample. This provided a spectrally corrected chlorophyll-specific absorption coefficient ($a^{*\prime}$). Using the mean $a^{*\prime}$ (400–700 nm), together with the productivity measurements and areal chlorophyll values, the maximum quantum yield (ϕ_m, O_2 per quantum) and the minimum quantum requirements ($1/\phi_m$, quanta O_2^{-1}) for photosynthesis were then calculated as described in Wyman et al. (1987).

Results

Daily measurements of visible and UV radiation on Long Key in 1995 and Loggerhead Key in 1996 showed little variability during the experimental period. Figure 1a shows a typical measurement of surface and 10-m spectral scans from 300 to 700 nm on Long Key on a cloudless day on 21 August 1995 at midday (~1300 h). The maximum surface PAR irradiance (integrated from 400 to 700 nm) on that day was 1,972 μmol quanta m^{-2} s^{-1}, while the maximum PAR irradiance at 10 m was 407 μmol quanta m^{-2} s^{-1}. Both the irradiance data and spectral attenuation coefficients at midday varied by less than 10% during the experimental period, suggesting that the optical properties of the water column changed very little during this time. Figure 1b shows a typical measurement of surface and 18-m spectral scans from 300 to 700 nm on Loggerhead on a cloudless day during July 1996 at midday. The maximum surface PAR irradiance on that day was 2,072 μmol quanta m^{-2} s^{-1}, while the maximum PAR irradiance at 18 m was 25 μmol quanta m^{-2} s^{-1}. Again, as in 1995, the irradiance and spectral attenuation coefficients at midday varied by less than 10% during the experimental period. The spectral attenuation coefficients in 1995 and 1996 are remarkably similar (Fig. 1a,b). Additionally, for both years, the higher attenuation of the underwater light field in the short- and long-wavelength portions of the spectrum is a consistent feature typical of coastal (Case II) waters. For comparison, the attenuation coefficient [K_d (m^{-1})] for the UVB (290–320 nm) portion of the spectrum for Long Key in 1995 (0.49 at 320 nm) and Loggerhead Key in 1996 (0.34 at 320 nm) is less than observed in Kaneohe Bay, Hawaii, a tropical estuary—a [K_d (m^{-1})] of 1.0 at 320 nm—and more than Moku Manu, an offshore Hawaiian reef, which had a [K_d (m^{-1})] of 0.20 at 320 (Shick et al. 1996).

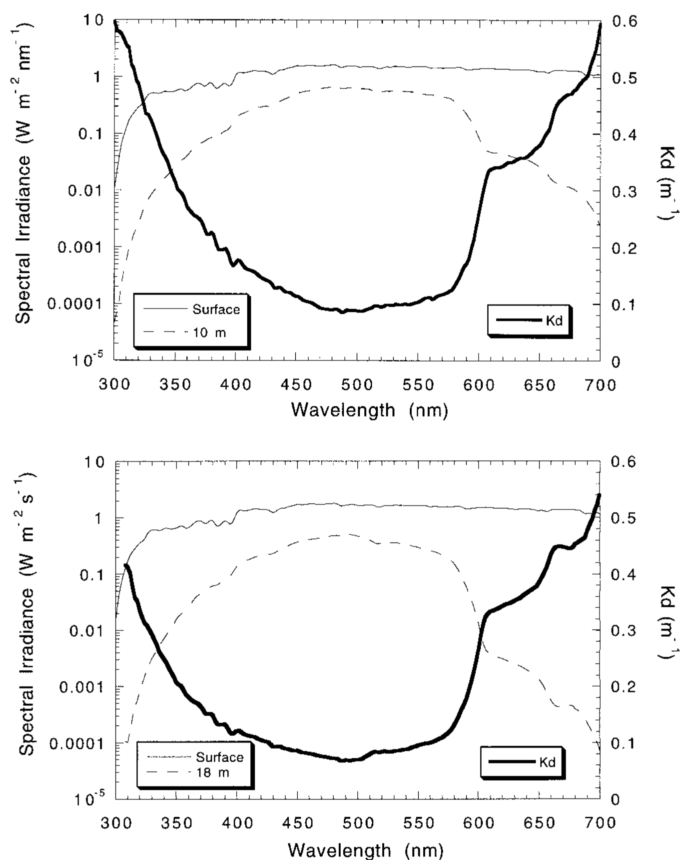

Fig. 1. (a) Surface (solid line) and 10-m (dashed line) spectral data (300–700 nm) recorded on Long Key, Dry Tortugas, August 1995 (~1300 h). Calculated spectral attenuation coefficients [K_d (m^{-1})] using the surface and 10-m data (dark solid line). (b) Surface and 18-m spectral data (300–700 nm) recorded on Loggerhead Key, Dry Tortugas, July 1996 (~1300 h). Calculated spectral attenuation coefficients [K_d (m^{-1})] using the surface and 18-m data (dark solid line).

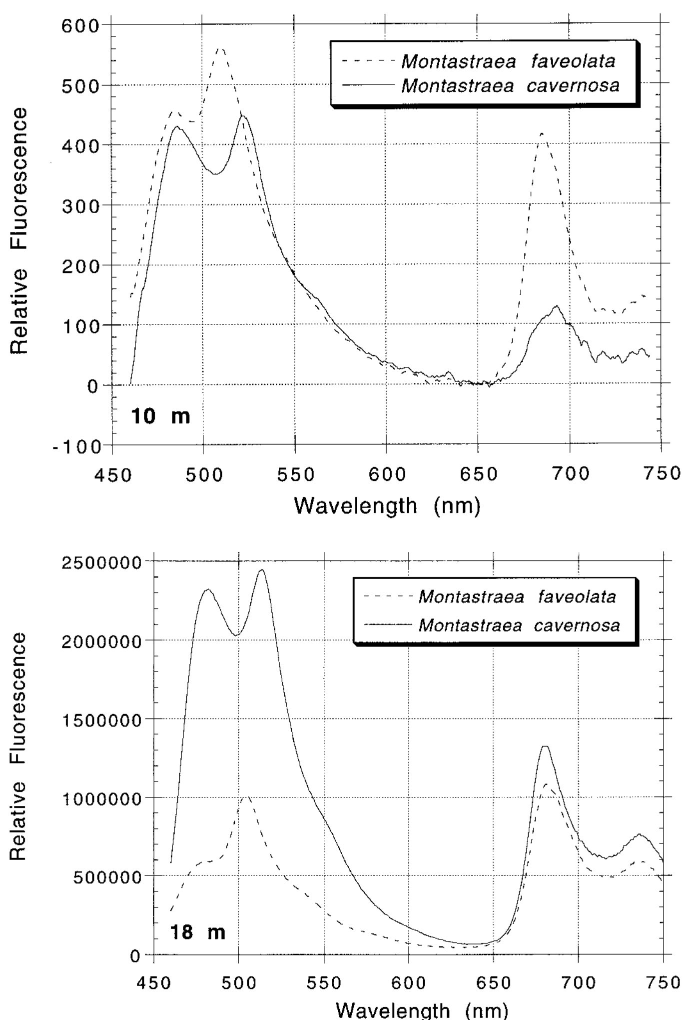

Fig. 2. (a) Representative in situ fluorescence emission spectra for the corals *M. faveolata* and *M. cavernosa* on Long Key at a depth of 10 m in August 1995. (b) Representative fluorescence emission (SPEX Fluoromax) spectra for the corals *M. faveolata* and *M. cavernosa* on Loggerhead Key at a depth of 18 m in July 1996.

Continuous measurements of temperature at discrete depths at the 10-m site in 1995 showed that temperatures at depths below 3 m ranged from ~29.5°C to ~30.5°C, with surface (~1.5 m) temperatures being higher (~30.0°C to >32.0°C), reflecting the greater heat transfer at the surface during the day and night (Fig. 2a). Temperatures at the 18-m site in 1996 for all depths ranged from ~28.5°C to ~29.8°C (Fig. 2b).

In both 1995 and 1996, there were consistent differences in the calculated photosynthesis–irradiance parameters between *M. faveolata* and *M. cavernosa* at each depth (Table 1), with *M. faveolata* exhibiting significantly higher rates of photosynthesis, a requirement for higher photon fluxes to saturate the photosynthetic apparatus as suggested by the significantly lower α value or light-limited portion of the *P-I* curve, and lower rates of respiration when compared with *M. cavernosa.* In 1995, P_{max} (Student's *t*-test, $P < 0.0001$, *n*

Table 1. Summary of calculated area-specific photosynthesis-irradiance parameters for *Montastraea faveolata* and *M. cavernosa* from Long Key (10-m depth) in 1995 and Loggerhead Key (18-m depth) in 1996.

Species	Depth (m)	P_{max} ± SD*	α ± SD†	R ± SD*
M. faveolata	10	1.923 ± 0.044	0.007 ± 0.0003	−0.021 ± 0.19
M. cavernosa	10	1.089 ± 0.042	0.032 ± 0.004	−0.105 ± 0.40
M. faveolata	18	1.827 ± 0.042	0.006 ± 0.0002	−0.021 ± 0.017
M. cavernosa	18	0.925 ± 0.035	0.027 ± 0.003	−0.090 ± 0.034

* Measured in μmol O_2 cm^{-2} h^{-1}.
† Measured μmol O_2 cm^{-2} h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$.

Table 2. Concentration (mean ± SD, nmole mg^{-1} protein) of individual mycosporine-like amino acids (MAAs) in the corals *Montastraea faveolata* and *M. cavernosa* on Long Key at 10 m in August 1995 and concentration (mean ± SD, nmole mg^{-1} protein) of individual mycosporine-like amino acids (MAAs) in the same corals on Loggerhead Key at 18 m in July 1996.

Species	Mycosporine–glycine	Shinorine	Porphyra-334	Palythine	Asterina-330	Palythene
10-m depth						
M. faveolata	1,399 ± 1,791	151 ± 341	219 ± 453	638 ± 1,259	264 ± 640	24 ± 49
M. cavernosa	1,292 ± 1,302	125 ± 165	940 ± 1,011	248 ± 288	228 ± 181	401 ± 938
18-m depth						
M. faveolata	207 ± 1,791	137 ± 21	283 ± 27	0 ± 0	0 ± 0	355 ± 54
M. cavernosa	108 ± 57	68 ± 5	696 ± 89	53 ± 5	0 ± 0	726 ± 135

= 6), α (Student's *t*-test, $P = 0.0003$, $n = 6$), and respiration (Student's *t*-test, $P = 0.029$, $n = 6$) were all significantly different between the two species at 10 m, whereas in 1996, P_{max} (Student's *t*-test, $P < 0.0001$, $n = 6$), α (Student's *t*-test, $P = 0.0003$, $n = 6$), and respiration (Student's *t*-test, $P = 0.034$, $n = 6$) were also all significantly different between the two species at 18 m.

In both *M. faveolata* and *M. cavernosa,* six MAAs were quantified (Table 2). No significant differences (unpaired one-tailed Student's *t*-test, $P > 0.05$, $n = 6$) were detected between these two species at 10 m in 1995. Both species at 10 m had very high and highly variable individual and total concentrations of MAAs compared with their conspecifics at 18 m. Only five MAAs were detected in *M. cavernosa* and four in *M. faveolata* at 18 m. Significant differences (unpaired one-tailed Student's *t*-test, $P < 0.05$, $n = 6$) were observed for all MAAs, when present in both species of coral, between species at 18 m, with *M. cavernosa* having higher concentrations in three of five detected MAAs. Additionally, *M. cavernosa* had a significantly higher total concentration of MAAs ($P = 0.003$).

In both 1995 and 1996, six photosynthetic pigments were observed and quantified. They were Chl *a,* Chl c_2, peridinin, diadinoxanthin (DD), diatoxanthin (DT), and β-carotene (Table 3). In 1995, samples of *M. faveolata* and *M. cavernosa* at 10 m exhibited significant differences (unpaired one-tailed Student's *t*-test, $P < 0.05$, $n = 3$; ratios were log transformed for analysis and back transformed for reporting) between species for all pigments, with *M. cavernosa* always having higher concentrations of each pigment, with the exception of β-carotene, in which no significant differences were observed. No significant differences were detected for Chl *a* or Chl c_2 and DD:DT ratios. For total DD+DT, however, significantly higher concentrations of these xanthophylls was observed in *M. cavernosa.* In 1996, the concentrations of all light-harvesting pigments (Chl *a,* Chl c_2, and peridinin) were greater in corals harvested from 18 m than those harvested from 10 m. Significant differences in these photosynthetic pigments and the Chl *a*:Chl c_2 ratios (unpaired one-tailed Student's *t*-test, $P < 0.05$, $n = 3$) between species at 18 m was only observed for peridinin, with *M. cavernosa* having higher concentrations. Pigments involved in photoprotection—diadinoxanthin, diatoxanthin, and β-carotene—exhibited lower concentrations in corals from 18 m than conspecifics from corals from 10 m. Significant differences in these photoprotective pigments between species from 18 m was observed for DD:DT ratios and β-carotene (unpaired one-tailed Student's *t*-test, $P < 0.05$, $n = 3$).

In situ fluorescence emission spectra (excitation at 440 nm) were measured on *M. faveolata* and *M. cavernosa.* Three principal emission peaks dominate the emission spectrum (Fig. 2a), one that occurs at approximately 486 nm and another within the range 510–520 nm. These first two peaks are believed to be from host-associated chromophores (Mazel 1995). The last peak at 685 nm is associated with zooxanthellae photosystem II (PSII) fluorescence (Fig. 2a). The 685-nm peak is variable from one coral to another and within species, but the mean relative fluorescence at 685 nm was generally greater in *M. cavernosa* (595 ± 381 nm, n= 13) than in *M. faveolata* (468 ± 152 nm, $n = 9$) but not statistically different (unpaired one-tailed Student's *t*-test, $P > 0.05$, $n = 6$). Because of equipment problems in 1996, no usable data from the Benthic SpectroFluorometer were available. In 1996, we collected samples and returned them to the laboratory to obtain emission spectra (excitation at 450 nm) using the SPEX spectrofluorometer (Fig. 2b). We observed the same three principal peaks in emission spectra from corals from 18 m that we observed in corals from 10 m (Fig. 2b). The 685 peak is less variable from one coral to another and within species in 1996 at 18 m, but the mean relative fluorescence at 685 nm is still greater in *M. cavernosa,* although not statistically different from *M. faveolata* (unpaired one-tailed Student's *t*-test, $P = 0.07$, $n = 5$).

In both 1995 (Fig. 3a,b) and 1996 (Fig. 3c,d), the average ($n = 3$) excitation and emission spectra for the isolated zooxanthellae of *M. faveolata* and *M. cavernosa* exhibits a typical pattern commonly observed for dinoflagellates. The excitation spectra shows wavelengths of peak excitation, measured as 680 nm emission, in the 440–450-nm range, indicative of Chl *a* excitation, and the 520–530 nm range, indicative of peridinin excitation and transfer of energy to PSII, resulting in higher, 685-nm emission. The interpretation of these excitation spectra are further supported by the emission spectra when excited at 470 nm and 530 nm, which showed an emission peak at 680–685 nm.

The chlorophyll-specific absorption for *M. faveolata* and *M. cavernosa* at 10 m was double the values of corals from 18 m, with *M. faveolata* having higher absorption values across the spectrum at both 10 m and 18 m (Fig. 4a,b). The mean a^* value for *M. faveolata* and *M. cavernosa* from 400–700 nm at 10 m was 0.0193 and 0.0175 m^{-2} mg Chl a^{-1}, respectively. At 18 m, the respective mean a^* values were

Table 3. Concentration (mean ± SD, μg cm²) of individual photosynthetic pigments and pigment ratios in the corals *Montastraea faveolata* and *M. cavernosa* on Long Key at 10 m in August 1995. Concentration (mean ± SD, μg cm²) of individual photosynthetic pigments and pigment ratios in the same corals on Loggerhead Key at 18 m in July 1996.

Species	Chl a	Chl c_2	a/c_2 ratio	Peridinin	Diadinoxanthin (DD)	Diatoxanthin (DT)	DD/DT ratio	DD+DT	β-Carotene
10 m									
M. faveolata	5.44 ± 0.1	2.34 ± 0.01	2.32 ± 0.01	6.44 ± 0.24	4.51 ± 0.29	1.14 ± 0.03	3.95 ± 0.01	5.66 ± 0.49	0.75 ± 0.007
M. cavernosa	6.8 ± 0.41	3.15 ± 0.015	2.19 ± 0.19	7.46 ± 0.02	6.65 ± 0.04	1.82 ± 0.13	3.72 ± 0.21	8.46 ± 0.98	0.84 ± 0.004
18 m									
M. faveolata	12.11 ± 0.87	4.47 ± 0.058	2.71 ± 0.061	7.87 ± 0.277	3.07 ± 0.01	0.64 ± 0.009	4.88 ± 0.28	3.71 ± 0.04	0.5 ± 0.002
M. cavernosa	14.01 ± 0.63	4.68 ± 0.013	3.00 ± 0.053	8.84 ± 0.055	3.41 ± 0.053	0.49 ± 0.002	7.05 ± 0.77	3.89 ± 0.046	0.75 ± 0.001

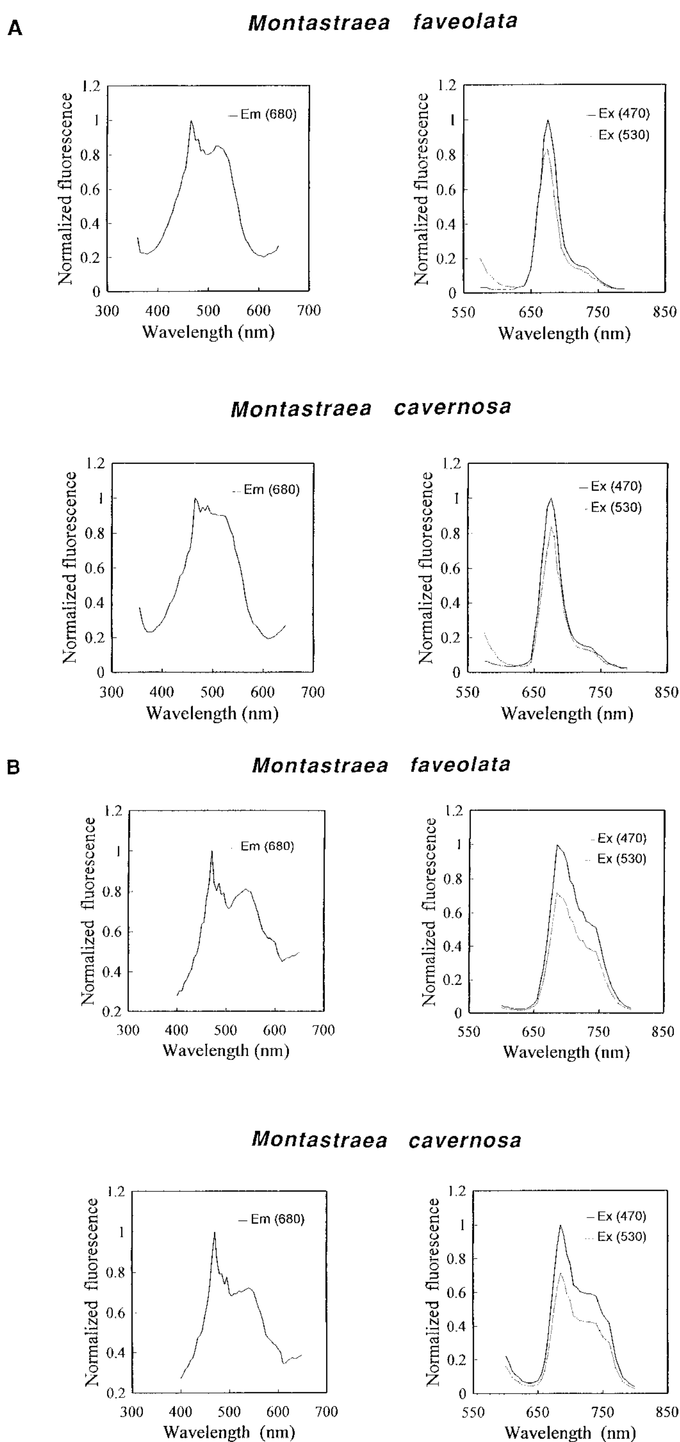

Fig. 3. (a) Fluorescence excitation and emission spectra for the isolated zooxanthellae from the corals *M. faveolata* and *M. cavernosa* on Long Key at a depth of 10 m in August 1995. (b) Fluorescence excitation and emission spectra for the isolated zooxanthellae from the corals *M. faveolata* and *M. cavernosa* from Loggerhead Key at a depth of 18 m in July 1996.

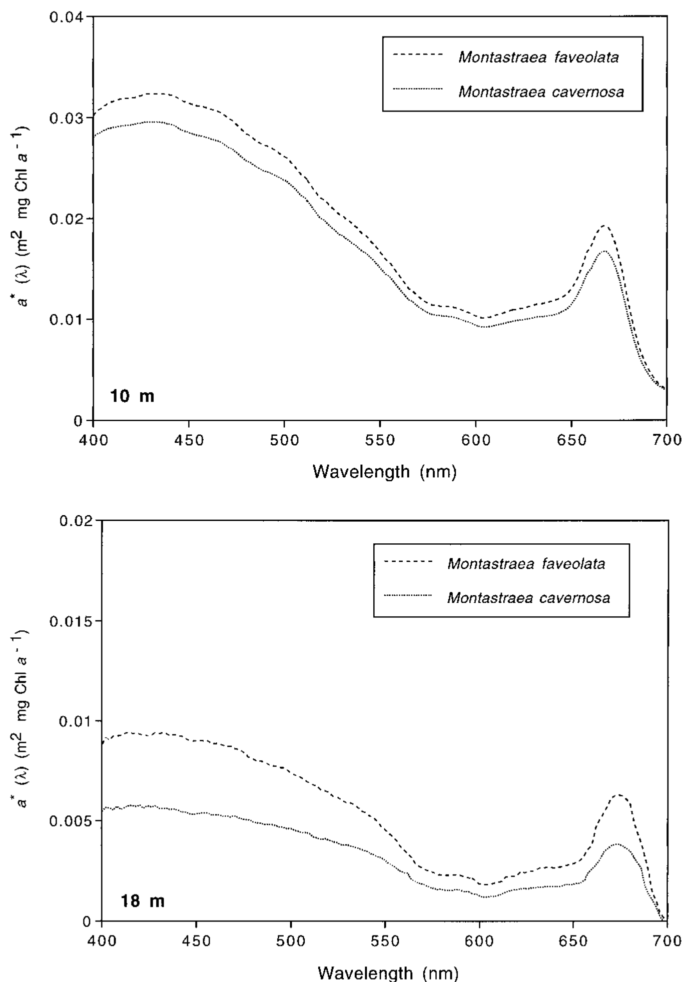

Fig. 4. (a) Chlorophyll-specific spectral absorption spectra (400–700 nm) for the isolated zooxanthellae from the corals *M. faveolata* and *M. cavernosa* on Long Key at a depth of 10 m in August 1995. (b) Chlorophyll-specific spectral absorption spectra (400–700 nm) for the isolated zooxanthellae from the corals *M. faveolata* and *M. cavernosa* from Loggerhead Key at a depth of 18 m in July 1996.

0.0055 and 0.0034 m^{-2} mg Chl a^{-1}. Nonalgal, or detritus, contributions to the optical density measurements were not detected after hot methanol extraction. When these absorption spectra are spectrally corrected ($a^{*\prime}$) for the spectral irradiance at 10-m and 18-m depths, the mean values from 400 nm to 700 nm for *M. faveolata* and *M. cavernosa* from 10 m are 0.0393 and 0.0356 m^{-2} mg Chl a^{-1}; for those from 18-m depths, they are 0.0109 and 0.0068 m^{-2} mg Chl a^{-1}.

The mean $a^{*\prime}$ values and the mean α values from the calculated *P-I* parameters for each species at each depth were then used to calculate the maximum quantum yield (ϕ_m) and the minimum quantum requirements ($1/\phi_m$) for photosynthesis using the following formula from Wyman et al. (1987):

$$\phi_m = \alpha/a^{*\prime} = 1/(1/\phi_m)$$

The $1/\phi_m$ for photosynthesis in *M. faveolata* and *M. cavernosa* from 10 m were 50 ($\phi_m = 0.0198$ O_2 per quantum) and 18 ($\phi_m = 0.0552$ O_2 per quantum) quanta O_2^{-1}, respectively, and for these species of coral at 18 m, the $1/\phi_m$ value for photosynthesis was 39 ($\phi_m = 0.0255$ O_2 per quantum) and 15 ($\phi_m = 0.0676$ O_2 per quantum) quanta O_2^{-1}, respectively.

Discussion

For these congeneric species of coral, at the same depth of occurrence, there are significant differences in several measured and calculated parameters directly related to light absorption and utilization. Differences between depths are also readily apparent. Why do congeneric species, with a bathymetric distribution that overlaps from 1 to 60 m, exhibit significant differences in their respective optical properties and photosynthetic capacities at the same depth of occurrence? Additionally, although their bathymetric distribution is similar, their abundance over that range in the Dry Tortugas is significantly different (Jaap et al. 1989). The Jaap et al. (1989) study showed that *Montastrea annularis,* based on previous taxonomy where all sibling species of the *Montastraea* complex (Knowlton et al. 1992, 1997) were grouped as *M. annularis*, had a greater abundance than *M. cavernosa* in all transect surveys from 1 to >15 m in depth, a pattern also observed in other parts of the Caribbean (Edmunds et al. 1990). Even when only *M. faveolata* is considered, the abundance differences are significant, with *M. faveolata* more abundant than *M. cavernosa* at 10 m and 18 m in the Dry Tortugas (Lesser unpubl. data). What is the role of optics in the ecology of these corals?

The differences in optical properties and photosynthetic capacities could be the result of different species of zooxanthellae within these coral hosts. It is now recognized that different genotypes of zooxanthellae within corals show a distinct ecological zonation with depth (Rowan and Knowlton 1995). The zooxanthellae within the congenerics used in this study from both depths have all been identified as belonging to clade C (Rowan and Powers 1991; Rowan and Knowlton 1995) by restriction fragment length polymorphisms of 24s rDNA (Lesser unpubl. data). Within-clade differences could still be large enough to warrant species-level assignment for these zooxanthellae (Rowan pers. comm.) and therefore does not eliminate the possibility that species differences contributed to the observed differences in optical properties and photosynthetic capacities.

Based on biophysical models, the relationship between photosynthesis and PSII fluorescence at 685 nm is ideally inverse. This, however, is rarely the case because of the control of fluorescence yields by two processes, photochemical and nonphotochemical quenching (Falkowski and Kolber 1993). Many physiological processes and recent light history contribute to changes in fluorescence yield through photochemical and nonphotochemical quenching. In this study, *M. cavernosa* exhibited higher mean PSII fluorescence yields than *M. faveolata,* although the differences were not statistically different, and lower rates of photosynthesis that are consistent with the biophysical model at a depth of 10 m.

Are there differences in pigments that may have contributed to the differences in optical properties and photosynthetic capacities? The UV-absorbing compounds, or MAAs, in *M. faveolata* and *M. cavernosa* at 10 m were not signif-

icantly different from one another, although significant differences between the two species were observed at 18 m, with *M. cavernosa* having significantly more total MAAs. Differences between depths were observed and probably reflect the attenuation of UV radiation that contributes to changes in MAA concentration (Dunlap et al. 1986; Jokiel et al. 1997). The differences between the two species at 18 m could potentially represent a strategy to absorb and utilize as much of the available underwater spectrum of UV and visible radiation as possible. It has been suggested that fluorescence by UV-absorbing compounds might be used for photosynthesis (Sivalingham et al. 1976) as the excitation of mycosporinelike amino acids at 340 nm causes the emission of fluorescent light that could potentially be absorbed by Chl *a* (Sivalingham et al. 1976). Although *M. cavernosa* has greater MAA concentrations at 18 m, the overwhelming majority of MAAs in all corals are located in the host tissues. The location of MAAs in host tissues should result in longer path lengths for the refluoresced photons and decreased efficiency of absorption by the photosynthetic apparatus. Additionally, work on dinoflagellates in culture by Yentsch and Yentsch (1982) demonstrated no stimulation of photosynthesis (PSII fluorescence) when short-wavelength UV radiation is absorbed. It is highly unlikely that the observed differences in the concentration of UV-absorbing compounds with depth or between species are a result of any photoacclimatization strategy to capture photons in the UV portion of the spectrum to drive photosynthesis.

Differences in photosynthetic pigments between depths reflect photoacclimatization processes (Falkowski et al. 1990; Iglesias-Prieto and Trench 1994, 1997). Additionally, the variation in the concentrations of diadinoxanthin and diatoxanthin with depth suggests that a xanthophyll cycle is present in these symbiotic dinoflagellates and is involved in photoprotection, as described for free-living dinoflagellates (Demers et al. 1991). Differences in pigments between species at the same depth observed in this study demonstrate different mechanisms for acclimatizing to the same underwater light field. *M. cavernosa* has significantly higher aerial pigment concentrations than *M. faveolata* at 10 m for all light-harvesting pigments, but only for peridinin at 18 m. The greater pigment concentrations in *M. cavernosa* result in significantly higher α values and lower chlorophyll-specific spectral absorption. The lower chlorophyll-specific absorption is probably a result of a significant package effect (Wyman et al. 1987), since the absorption of light is not a linear function of pigment concentration in living cells. This is clearly observed in the flattening of the absorption spectra for both species at 18 m (Fig. 4a,b). The photoacclimatization response of individual cells results in changes in the architecture of the thylakoids. Thylakoid surface area increases significantly when cells are exposed to lower irradiances (Lesser and Shick 1990), with the result that not all chlorophyll molecules participate in primary photochemistry. These differences in pigments and light absorption also supports an interpretation of a smaller functional optical cross section (probability of absorbing a photon; Falkowski et al. 1990) for *M. cavernosa* at 10 m and 18 m.

For *M. cavernosa* at both depths, the rate of light absorption in the light-limited portion of the *P-I* relationship (α) is greater than *M. faveolata* at low irradiances and quickly saturates the photosynthetic apparatus at higher irradiances because of package effects and a smaller functional optical cross section. These differences would likely be even greater if the curves were normalized to chlorophyll versus surface area. This results in lower maximum photosynthetic capacities (P_{max}) for *M. cavernosa.* Despite these differences, when we combine the photosynthetic responses and pigment concentration data, we observe that the minimum quantum requirements are higher for *M. faveolata* at both 10 m and 18 m than for *M. cavernosa* and decrease with depth for both species as previously described (Wyman et al. 1987). The photosynthetic advantage of one species versus another at the same depth is related to both the total amount of absorbed light and the quantum efficiency of light utilization. Although *M. faveolata* has greater minimum quantum requirements, its capacity for light absorption is greater (that is, it has a larger functional optical cross section), which results in higher photosynthetic capacities than those measured for *M. cavernosa* at the same depth. The slight year-to-year variation and within-site variation in temperature should have had little effect on the metabolic rates of the experimental corals or the optical properties of those corals.

It appears that *M. faveolata* absorbs more light and is less efficient with that light, but light is available in such excess that it makes little difference at 10 m. At 18 m, there is less visible radiation for *M. faveolata* to absorb, but the larger functional optical cross section of this species allows for absorption of more photons than *M. cavernosa.* The utilization efficiencies at 18 m are fairly similar compared with the differences at 10 m. On the other hand, *M. cavernosa* at 10 m and 18 m appears to exhibit a significant package effect resulting in a smaller optical cross section. *M. cavernosa* compared with *M. faveolata* at the same depth exhibit characteristics of being light limited. The significant differences in optical properties and photosynthetic rates in these congeneric species (Wyman et al. 1987; this study) are paralleled by the differences in growth rates observed at shallow depths (9–12 m) but not at deeper depths (15–20 m) between *M. annularis* (prior to recognition of sibling species) and *M. cavernosa* (Hubbard and Scaturo 1985), with *M. annularis* having faster growth rates at shallow depths. The growth rates of corals would also be affected by differences in whole-colony respiration. Rates of respiration, and therefore maintenance costs, were significantly lower (Table 1) in *M. faveolata* versus *M. cavernosa.* Lower rates of respiration in *M. faveolata* would tend to favor more energy going into growth and reproduction which may afford significant ecological advantages.

Why is *M. faveolata* a better plant than *M. cavernosa*? Polyp and corallite differences may play a role. *M. cavernosa* is a large, fleshy, tentacular polyp supported by a large corallite. It is now known that multiple scattering within the corallite makes a significant contribution to the maximum scalar irradiance, which can reach 180% of incident irradiance, within the polyp (Kühl et al. 1995). Scattering increases the path length of photons and is equivalent to a longer residence time and enhanced absorption efficiency within a layer of coral tissue (Kühl et al. 1995). Initially, this would appear to benefit *M. cavernosa* with its larger polyp size.

But *M. cavernosa* also has a decreased amount of skeletal ridges per unit surface area compared with *M. faveolata.* Since most of the enhanced scalar irradiance appears to occur on skeletal ridges (Kühl et al. 1995), we hypothesize that not only does *M. cavernosa* have less skeletal ridge per unit area, but the greater tissue thickness and package effect in *M. cavernosa* allows fewer photons to actually reach the corallite and participate in this phenomenon. Finally, it has been suggested than *M. faveolata* is a better plant because it depends upon photoautotrophy to a larger degree than *M. cavernosa* because of its greater surface area. Porter (1976) hypothesized that large tentacular polyps were better at, and dependent upon, zooplankton capture to a greater degree than corals with small polyps. This suggests a greater degree of dependence on heterotrophy in corals with large polyps and could explain a portion of the interspecific differences in optical properties and photosynthetic performance observed during this study. Recent work, however, suggests that corals having either small or large polyps are equally efficient at prey capture and capture prey items in the same size range (Sebens 1997). Additionally, corals with small polyps appear to present a greater tentacular surface area for feeding (Sebens 1997). Dissecting the respective contributions of photoautotrophy versus heterotrophy in corals will require measuring the simultaneous in situ contribution of feeding and photosynthesis to total carbon and energy budgets for these and other species of corals. Then the role of photoautotrophy versus heterotrophy in the ecology of one species versus another over their overlapping bathymetric distribution can be better assessed.

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