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Multiple scattering on coral skeletons enhances light absorption by symbiotic algae

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Abstract

The success of symbiotic reef-building corals is largely determined by the efficiency with which they collect solar energy. Using thin coral laminae from the Caribbean scleractinian *Porites branneri*, we characterize the absorption spectra of intact coral surfaces. Comparisons of absorption spectra from corals with a broad range of photosynthetic pigment densities, collected during a natural bleaching event, indicate that they are capable of collecting more than 85% of solar radiation with one order of magnitude less pigment density than terrestrial leaves. Measurements of the light-absorption efficiency as a function of pigment density reveal that symbiotic algae in intact *P. branneri* absorb between two and five times more light than freshly isolated symbionts. A theoretical model shows that multiple scattering by the skeleton can enhance the local light field, thus increasing absorption. As a result of this phenomenon, corals inhabiting high light environments can maximize their absorption capacity with low pigment investment while reducing self-shading in low-light environments. Local light field enhancements may have negative effects when corals are exposed to stressful conditions. During coral bleaching, increases in local irradiance associated with reductions in pigment density could exacerbate the negative effect of elevated temperatures. Symbiotic scleractinian corals are one of the most efficient solar energy collectors in nature, and the modulation of the internal light field by the coral skeleton may be an important driving force in the evolution of this group.

In coral reefs, scleractinian corals play a fundamental role as builders of the primary reef framework (Muscatine and

Weis 1992). The success of scleractinian corals in oligotrophic waters during the last 200 million years can be attributed to the establishment of obligate endosymbioses with photosynthetic dinoflagellates of the genus *Symbiodinium* (zooxanthellae) (Muscatine and Porter 1977; Muscatine and Weis 1992). Algal photosynthesis provides nutritional advantages to scleractinians, since the translocation of photosynthates may account for their entire metabolic needs while promoting rapid calcification (Goreau and Goreau 1959; Muscatine and Weis 1992). Therefore, symbiotic reef-building corals depend heavily on the efficiency with which they collect solar energy.

Considering the importance of symbiont photosynthesis on the ecology of reef corals, the photobiology of these organisms has attracted a great deal of attention (Dubinsky et al. 1990; Iglesias-Prieto and Trench 1994; Gorbunov et al. 2001). As a result of the application of measurement tech-

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niques developed for phytoplankton studies (Dubinsky et al. 1990; Iglesias-Prieto and Trench 1994) and the use of highly sensitive and nondestructive chlorophyll *a* (Chl *a*) fluorescence techniques (Hoegh-Guldberg and Jones 1999; Gorbunov et al. 2001; Warner et al. 2002; Iglesias-Prieto et al. 2004), coral photobiology has experienced significant developments over the last few decades. Despite this progress, not much work has been reported on the optical properties of intact corals. A major obstacle for the study of the optical properties of intact corals results from the complexity of the coralline structure, consisting of coelenterate tissue, symbiotic algae, and the intricate geometries of the aragonite coral skeleton (Falkowski et al. 1990).

Reflectance measurements of intact corals were first reported by Shibata (1969), then, more recently, by Hochberg and Atkinson (2000) and Minghelli-Roman et al. (2002), but no estimates of the fraction of incident flux absorbed by the symbiotic dinoflagellates were provided in those papers. Although the absorption properties of the symbionts and the specific absorption of Chl *a* have been measured for suspensions of freshly isolated dinoflagellates (coral “blastates”) (Dubinsky et al. 1984, 1990; Wyman et al. 1987; Lesser et al. 2000), the assessment of the optical properties of intact corals from such data is, at best, unclear. In a recent paper, Stambler and Dubinsky (2005) have reported absorption measurements of intact corals using an integrating sphere; we note, however, that their results and conclusions differ from those presented here.

In this paper, using a technique developed for absorption measurements of highly dispersive materials (Shibata 1959), we present direct measurements of the absorption spectra of intact corals and their respective Chl *a* specific absorption. For the study, we chose the Caribbean scleractinian *Porites branneri*, a relatively uncommon species, since its morphological characteristics (Wells 1973) permit the preparation of even and thin coral laminae with homogeneous pigmentation, which are suitable for spectroscopic transmittance analyses. This species experienced extensive bleaching—the loss of symbiotic algae—in the Mexican Caribbean in the summer of 1998. During the bleaching event we collected specimens exhibiting a broad variation in symbiont and Chl *a* densities, which allowed us to assess the effects of such variability on the optical properties of *P. branneri*.

Material and methods

Sampling and manipulation—Small fragments of the stony coral *P. branneri* were collected with a hammer and chisel from the reef lagoon in Puerto Morelos, Quintana Roo, Mexico (2.5 m depth). Samples were transported immediately to the laboratory and maintained in a running seawater aquarium screened with several layers of netting to remove 75% of the natural illumination. Colony fragments ($n = 16$) were cut with a Moto Tool equipped with a mechanical extension into a rectangular shape (2.0×0.9 cm) to match the measuring area of the spectrophotometer. The internal parts of the skeletons were polished into laminae (3.0 ± 0.1 mm in thickness) with a grinding stone attached to the same instrument. These procedures were performed

inside a plastic container filled with seawater to prevent damaging the tissues by overheating. The laminae produced with this technique survived and are capable of growing indefinitely in the aquarium. Coral laminae were allowed to recover for 48 h in a running seawater aquarium before being used.

Spectroscopy: absorption spectra of corals and cell suspensions—Absorption spectra of *P. branneri* colonies and cell suspensions were determined using the opal glass technique developed by Shibata (1959). Absorption spectra of the coral laminae were recorded between 380 and 750 nm with an Aminco DW2 spectrophotometer controlled by an Olis data collection system. Bleached skeleton laminae were used as reference. The light beams of the spectrophotometer were baffled with black tape apertures to match the exact dimensions of individual samples. Absorption spectra were corrected by subtracting the apparent absorbance at 750 nm to exclude residual scattering. While it is possible that some small errors and even a bias were introduced in the determination of the absorbance, given the normalization procedure and the measurement geometry, the general tendency is to underestimate absorbance. The majority of the absorption spectra of coral laminae examined showed no absorption by Chl *b* characteristic of endolithic algae, indicating that the layer containing these organisms was successfully removed by the procedure described. The absorbance (A) was calculated from the absorbance (D) measurements given by the spectrophotometer in the visible region of the spectrum (between 400 and 700 nm), employing the relation $A = 1 - 10^{-D}$. The absorption spectra of dinoflagellates suspended in filtered seawater were measured in the same way, using as a reference a cuvette with filtered seawater.

Spectroscopy: reflectance spectra of corals and skeletons—Reflectance spectra of corals and skeletons were measured between 400 and 750 nm with 1 nm resolution using a 4800S Lifetime spectrofluorometer (SLM-Aminco) equipped with a red sensitive photomultiplier tube (R955, Hamamatsu). Coral samples were submersed in seawater in a small glass container with a black bottom. Homogeneous illumination was provided by an incandescent light source placed ≈ 25 cm above the coral surface, making a 45° angle. The reflected light was collected with a 2-mm diameter waveguide attached to the spectrometer. The detector waveguide was placed underwater, 1 cm away from the sample, making an angle of 45° with the coral surface. The field of view of the detector waveguide was ≈ 0.4 cm². Reflectance was expressed as the ratio of the radiance measured from the coral surface relative to the radiance obtained from a reference white diffusing surface.

Angular scattering distribution produced by the skeletons—The angular distribution of the light scattered by several coral skeletons was measured with the in-plane automated scatterometer described by Luna et al. (1995). A circular area (2.5 cm in diameter) of a flat slab of coral skeleton was illuminated using a linearly polarized collimated beam arising from a HeNe laser ($\lambda = 633$ nm). Angle-resolved scattering data were taken in 1° steps with a detec-

tion system that subtends an angle of approximately 2° , when viewed from the sample. With this geometry the speckle size is much smaller than the size of the detecting aperture, which leads to a good estimation of the mean intensity. The detection system consisted of a combination of an aperture, a lens, and a detector, arranged in such a way that the detector viewed the whole of the illuminated area of the sample for all angles of observation. This ensured that no artificial geometrical factors were introduced into the measurements. By placing a polarizer in the detection system, it was also verified that the scattered light was completely depolarized.

Symbiont isolation and pigment analyses—Symbiotic dinoflagellates were isolated from coral fragments with a recirculating WaterPik (Teledyne). The coral slurry was centrifuged at 377 g for 3 min in a clinical centrifuge. Pellets containing the algae were resuspended in 15 ml of filtered seawater in a tissue homogenizer and concentrated by centrifugation. This procedure was repeated until most of the animal debris was removed. Cell densities were determined with triplicate counts in a hemocytometer (data not shown). Photosynthetic pigments were extracted in acetone : dimethyl sulfoxide (90 : 10, v : v) (Iglesias-Prieto et al. 1992), and the concentration of Chl a was determined spectroscopically using the equations of Jeffrey and Humphrey (1975).

Estimation of the Chl a specific absorption coefficient—We calculated the specific absorption coefficient of Chl a , $a_{\text{Chl } a}^*$ (Morel and Bricaud 1981; Kiefer and Mitchell 1983), through the relation $a_{\text{Chl } a}^* = (D/\rho) \ln 10$, where ρ is the pigment content per projected surface area (in mg m^{-2}) (Enrriquez and Sand-Jensen 2003). The specific absorption coefficient was calculated only for the absorbance value at 675 nm, to minimize the interference of accessory algal and animal pigments. For comparison, the specific absorption coefficients of freshly isolated symbionts of *P. branneri* were estimated from their absorption spectra in suspension.

Results and discussion

P. branneri specimens with Chl a densities above 20 mg m^{-2} and with skeleton thickness between 2.5 and 3 mm reflect a small fraction of the incident light ($5.23\% \pm 0.39\%$, $n = 8$) and transmit between 0.44% and 0.79% of it. A clean coral skeleton with 3 mm thickness transmits on average along the photosynthetically active radiation (PAR) range, 3.6% of the incident radiation. Spectroscopic determinations of the absorbance of *P. branneri* using the opal glass technique are shown in Fig. 1. A typical absorption spectrum of a thin lamina of *P. branneri* is shown in the top curve of Fig. 1A. As expected, the red part of the absorption spectra is dominated by absorption bands of Chl a and Chl c_2 , with a peak at 675 nm and a shoulder at approximately 639 nm. In contrast, in the blue part of the spectrum, the photosynthetic pigment bands of the symbiotic dinoflagellates are masked by other chromophore(s) of animal origin. The absorption spectra of a suspension of cultured *Symbiodinium pilosum* and a symbiont-free *P. branneri* homogenate are also presented in the figure for comparison.

As a result of bleaching, we had available a series of spec-

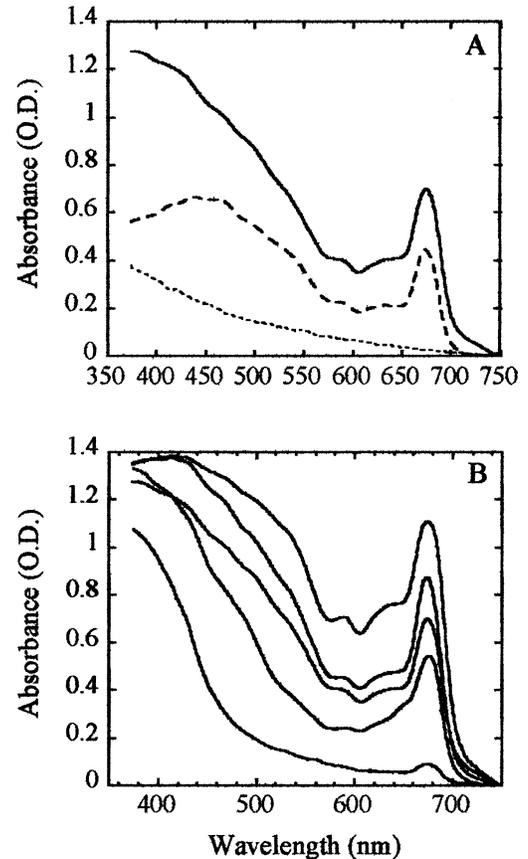


Fig. 1. Spectroscopic properties of intact *Porites branneri* surfaces. (A) Absorption spectra of a thin lamina (thickness = $3.0 \pm 0.1 \text{ mm}$) of *P. branneri* (upper solid line), a suspension of cultured *Symbiodinium pilosum* (dashed line), and a symbiont-free homogenate of *P. branneri* (lower dotted line). (B) Absorption spectra of *P. branneri* laminae with different Chl a densities (38.9, 19.2, 14.1, 7.5, 3.3 $\text{mg Chl } a \text{ m}^{-2}$ from top to bottom) obtained during a natural coral bleaching event.

imens whose Chl a density varied from 3.3 mg m^{-2} to 102.1 mg m^{-2} . Absorption spectra taken from corals with different Chl a densities are shown in Fig. 1B. The observed 30-fold variation in Chl a density resulted in an approximately five-fold variation in coral absorbance. The curves also show that as the density of Chl a is reduced, there is a relative increment in the concentration of unidentified animal chromophore(s).

Measurements of the absorption with the opal glass technique are not only laborious, but can be difficult to implement with corals of other morphologies. It is then relevant to consider alternative techniques for estimating coral absorption that can be implemented in situ. In Fig. 2A, we show the reflectance (R) spectrum of a coral colony with Chl a density of 52.3 mg m^{-2} . We point out that this represents the reflectance of the whole structure (algae and a thick skeleton). For comparison, the reflectance of a clean coral skeleton is also shown. The estimated absorbance ($D_e = \log[1/R]$) calculated from the coral reflectance data is shown in Fig. 2B. Assuming that the absorption by the skeleton is negligible, we can compare this curve with those obtained

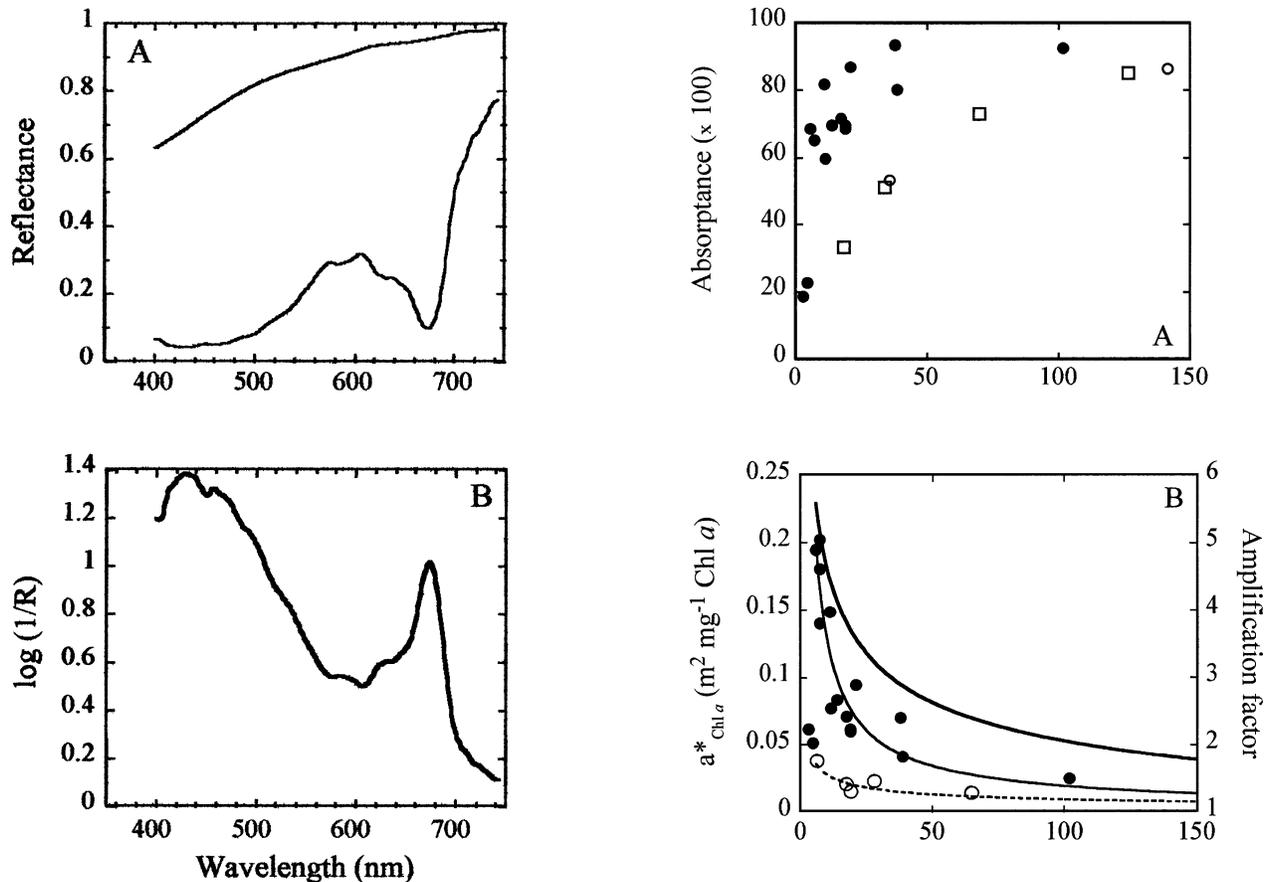


Fig. 2. Spectroscopic properties of intact *Porites branneri* surfaces and a coral skeleton. (A) Reflectance spectrum of an intact *P. branneri* surface (lower thick solid line) with 52.3 mg Chl *a* m⁻², and reflectance spectrum of a clean coral skeleton (upper thin solid line). (B) Absorption spectrum ($D_e = \log[1/R]$) of an intact *P. branneri* surface with 52.3 mg Chl *a* m⁻² estimated from reflectance measurements.

with the opal glass technique (Fig. 1B). One can see that the two techniques give similar results and that, owing to the high reflectivity of the skeleton, it is possible to estimate algae absorption solely from reflectance measurements. From these independent estimations of coral absorbance it is clear that endosymbiotic dinoflagellates in hospite absorb most of the incident light.

Coral absorbance depends primarily on pigment content. Determinations of absorbance as a function of Chl *a* density are shown in Fig. 3A. The palest coral examined (<5 mg m⁻²) absorbed 18.4% of the incident irradiance (absorbance

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Fig. 3. (A) Comparison of coral absorbance (fraction of the incident radiation captured by the coral surface) as a function of pigment density for intact *Porites branneri* specimens (solid circles) and for filtered freshly isolated symbionts of *Stylophora pistillata* (open squares and open circles) (Dubinsky et al. 1984, 1990). (B) Comparison of changes in Chl *a* specific absorption coefficient ($a_{\text{Chl } a}^*$) as a function of Chl *a* density of intact *P. branneri* laminae (solid circles, fitting function: $a_{\text{Chl } a}^* = 0.88 \pm 0.25 \times \text{Chl}$

$a^{-0.83 \pm 0.12}$, $R^2 = 0.85$, $p < 0.01$) and its isolated symbionts (open circles; fitting function: $a_{\text{Chl } a}^* = 0.08 \pm 0.03 \times \text{Chl } a^{-0.47 \pm 0.14}$, $R^2 = 0.72$, $p < 0.05$). The amplification factor (upper solid line) was calculated as the ratio of the estimated absorption efficiency of intact corals relative to values estimated for isolated symbionts in suspension (lower thin lines). (C) Comparative analysis of changes in the $a_{\text{Chl } a}^*$ as a function of Chl *a* density for several species of phytoplankton (solid circles) (Morel and Bricaud 1981), and isolated symbionts from six species of Caribbean corals (open inverted triangles) (Wyman et al. 1987), *Montastraea cavernosa* and *Montastraea annularis* (solid squares) (Lesser et al. 2000), *S. pistillata* (open squares and open circles) (Dubinsky et al. 1984, 1990) and *P. branneri* (open squares with an inner cross). The dotted line represents the fitting function ($a_{\text{Chl } a}^* = 0.036 \pm 0.003 \times \text{Chl } a^{-0.23 \pm 0.03}$, $R^2 = 0.53$, $p < 0.05$).

= 0.18), while a specimen with a Chl *a* density of 38.9 mg m⁻² showed an absorbance of 0.93 (Fig. 3A). The light-harvesting capacity of *P. branneri* decreases abruptly only for Chl *a* densities below 20 mg m⁻², remaining practically constant for Chl *a* densities above this threshold. These results differ from former estimations based on filtered coral slurries (Dubinsky et al. 1984, 1990; Wyman et al. 1987; Lesser et al. 2000). Measurements on tissue slurries from *Stylophora pistillata* (Dubinsky et al. 1984, 1990) predict that coral absorbance would reach a maximum value of 0.85 at 105 mg Chl *a* m⁻². Consequently, *S. pistillata* would experience a monotonous reduction in energy harvesting for Chl *a* densities below this value. Our results suggest that reflectance-based remote sensors (Clark et al. 2000; Mumby et al. 2004) would have limited use for early detection of coral bleaching, since coral reflectance would be independent of pigment densities above a threshold value of 20 mg Chl *a* m⁻².

Our estimations of the absorbance of intact corals are similar to those reported for leaves of terrestrial plants (Gabrielsen 1948; Björkman and Demming 1987), although terrestrial leaves have between three and six times higher Chl *a* density than corals. Intact *P. branneri* surfaces absorb the same fraction of incident light as terrestrial leaves (0.84) with only 20 mg of Chl *a* m⁻²; that is 2.6 times less Chl *a* density than that predicted from *S. pistillata* tissue slurries (Fig. 3A). The observed coral absorbance maximum (0.93) was 10% higher than the estimated maximum from *S. pistillata* (Fig. 3A).

To quantify the variations in pigment light-absorption efficiency, we estimated the changes in the Chl *a* specific absorption coefficient ($a_{\text{chl } a}^*$) as a function of Chl *a* density. The analysis of this variation shows that the values of $a_{\text{chl } a}^*$ estimated for intact corals are between two and five times higher than those estimated from suspensions of freshly isolated symbionts with similar pigment density (Fig. 3B). The $a_{\text{chl } a}^*$ of *P. branneri* laminae varied from a minimum of 0.025 m² (mg Chl *a*)⁻¹ for a highly pigmented colony to a maximum of 0.202 m² (mg Chl *a*)⁻¹ for a specimen with a Chl *a* density of 7.5 mg Chl *a* m⁻² (Fig. 3B). The differences in the effective absorption cross section between intact corals and cell suspensions were extraordinarily large for the colonies with low pigment density. Laminae of *P. branneri* absorb light up to five times more efficiently than a suspension of its freshly isolated symbionts (Fig. 3B). These a^* values differ significantly from those reported by Stambler and Dubinsky (2005).

On the other hand, the a^* values obtained in our study for a suspension of freshly isolated symbionts are consistent with measurements of the absorption of filtered "blastates" (Dubinsky et al. 1984, 1990; Wyman et al. 1987; Lesser et al. 2000) and with values reported for phytoplankton (Morel and Bricaud 1981) (Fig. 3C).

The increased absorption capacity by algal pigments can be understood in terms of the multiple scattering processes that take place in the coral structure. Multiple scattering by the skeleton produces diffuse light, reducing pigment self-shading and increasing the probability of light absorption. These processes lead to an enhancement of the local irradiance within the tissue. Evidence of the modification of the

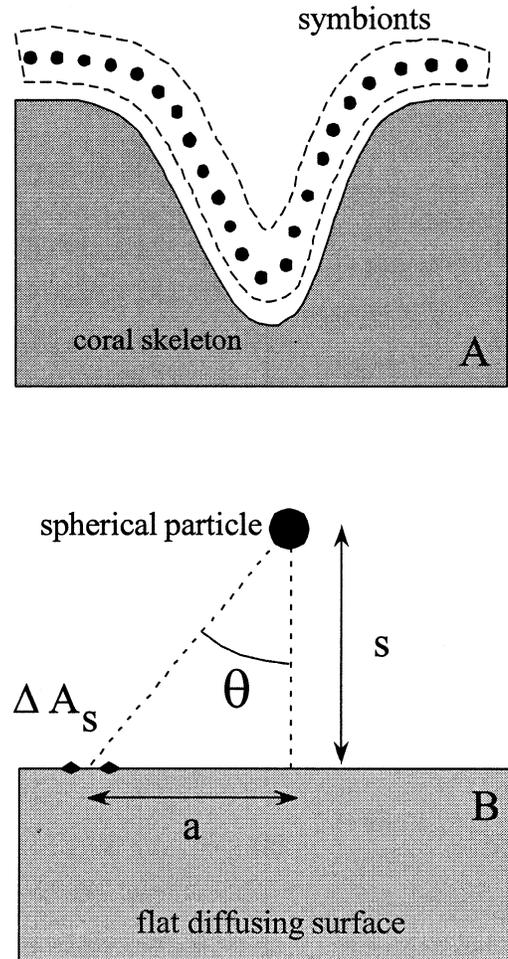


Fig. 4. (A) Schematic representation of the distribution of the symbiotic dinoflagellates above the coral skeleton. (B) Schematic diagram of the geometry considered for the estimation of the absorption by a particle in the presence of the coral skeleton. The distance from the particle to the surface along its normal is denoted by s , and the distance from this intersection to the surface elements ΔA_s is denoted by a .

local light field within the coral tissue has been found in measurements carried out with irradiance microprobes (Kühl et al. 1995). The reported values of the spectral scalar irradiance on the tissue surface were 1.8 to 2 times larger than those observed in the external environment. The estimated differences between the specific absorption of intact coral surfaces of *P. branneri* and freshly isolated symbiont suspensions (Fig. 3B) are consistent with those estimated using irradiance microprobes on a normally pigmented coral (Kühl et al. 1995), since we found local enhancement factors of 5.6 for the specimens with low pigment content (≈ 6 mg Chl *a* m⁻²) and between 1.7 and 2.2 for Chl *a* densities between 80 and 160 mg m⁻² (Fig. 3B).

The increase in the absorption capacity may be understood through simple physical considerations. In simplified form, a coral structure may be visualized as a thin layer of small, pigmented particles above the coral skeleton (see Fig. 4A). Coral skeletons are efficient bulk scatterers with low ab-

sorption. Angular scattering measurements with flat portions of skeleton revealed that, as expected, the skeletons scatter equally well in all directions and constitute good Lambertian diffusers (Smith 1966). The skeleton also permits the diffusive propagation of light over relatively long distances, homogenizing the illumination of the symbionts. As the illumination reaches the pigment layer, a fraction of the incident light is absorbed. Part of the light transmitted through the layer is backscattered by the skeleton and passes again, as diffuse light, through the layer of pigment, thus increasing the absorption by the particles. The intricate geometry of the skeleton favors the multiple passing of scattered light through the pigmented tissue.

For simple geometries it is possible to quantify the absorption increase due to the presence of the skeleton. For reference, let us first consider an isolated spherical particle illuminated by a collimated beam of light. The particle has absorption cross section C_{abs} and, thus, the radiant flux (power) it absorbs from the incident beam is $\Phi_{\text{abs}}^{(i)} = C_{\text{abs}}E_{\text{inc}}$, where E_{inc} is the incident irradiance (power per unit area). When the particle is placed above a flat diffusely scattering surface (see Fig. 4B), it will also absorb light that is backscattered by the surface. Angle-resolved scattering measurements carried out with specially prepared skeleton slabs show that, for all angles of incidence, the diffuse scattering distribution they produce is isotropic (i.e., rotationally symmetric about the normal to the surface), completely depolarized, and well described by the Lambertian cosine law (Smith 1966). This behavior is characteristic of samples that scatter equally well in all directions and is to be expected from the complex, highly disordered microscopic nature of coral skeletons. Then, the scattering surface, viewed as a secondary source, has a radiance (power per unit area and solid angle) or brightness distribution of the form $L_s = L_0 \cos \theta$, where the constant L_0 is yet to be determined. In terms of the radiance, the radiant intensity I_s (power per solid angle) produced by a small element of area ΔA_s of the scattering surface in the direction of the particle is given by

$$I_s(\theta) = \Delta A_s L_0 \cos \theta \quad (1)$$

With reference to Fig. 4B, the flux absorbed by the particle due to scattering from this surface element will be

$$\Delta \Phi_{\text{abs}}^{(s)} = I_s(\theta) \Delta \Omega_{\text{abs}} \quad (2)$$

where $\Delta \Omega_{\text{abs}}$ is the solid angle subtended by the absorption cross section of the particle. Since the distance from the surface element to the particle is $s/\cos \theta$ (where s denotes the distance from the particle to the surface along its normal), substitution of $I_s(\theta)$ and $\Delta \Omega_{\text{abs}}$ in Eq. 2 gives

$$\Delta \Phi_{\text{abs}}^{(s)} = L_0 \Delta A_s \cos^3 \theta \frac{C_{\text{abs}}}{s^2} \quad (3)$$

This represents the flux absorbed by the particle due to radiation from the surface element ΔA_s . To obtain the total power absorbed by the particle we must add the contributions from all the elements of the surface. Owing to the isotropy of the scattering pattern produced by the elements of the surface, the contribution from a ring of radius a and width Δa (Fig. 4B) is obtained simply by replacing ΔA_s by $2\pi a \Delta a$ in Eq. 3. Recognizing that $a = s \tan \theta$ and $\Delta a = s$

$\sec^2 \theta \Delta \theta$, the incremental power can be expressed solely as a function of θ , and the integral over the plane of the scattering surface can be readily evaluated, yielding

$$\Phi_{\text{abs}}^{(s)} = 2\pi L_0 C_{\text{abs}} \quad (4)$$

This expression represents the flux absorbed by the particle from the light backscattered by the surface.

It is now necessary to evaluate the constant L_0 , representing the radiance of the surface along the surface normal. For this purpose, we consider again the light scattered by the element ΔA_s . Assuming that the particle is small (a few microns, for example), its presence produces a negligible modification of the incident beam. Thus, the irradiance reaching the scattering surface is constant and equal to E_{inc} , and the flux incident on the surface element ΔA_s is $\Delta \Phi_{\text{inc}} = E_{\text{inc}} \Delta A_s$. The total flux radiated by the surface element into the hemisphere can be written as

$$\Delta \Phi_{\text{sca}} = \int I_s(\theta) d\Omega = \int \Delta A_s L_0 \cos \theta d\Omega \quad (5)$$

where the integration is over the whole of the hemisphere. Since $d\Omega = \sin \theta d\theta d\phi$, where ϕ is the azimuthal angle, and the scattering pattern is isotropic (i.e., independent of ϕ), we find that $\Delta \Phi_{\text{sca}} = \pi L_0 \Delta A_s$. Writing the flux scattered by this surface element as $\Delta \Phi_{\text{sca}} = R \Delta \Phi_{\text{inc}}$, where R is the reflectance of the surface ($0 \leq R \leq 1$), and equating these two expressions, we find that

$$L_0 = \frac{R}{\pi} E_{\text{inc}} \quad (6)$$

Thus, the total flux absorbed by the particle can finally be written as

$$\Phi_{\text{abs}} = \Phi_{\text{abs}}^{(i)} + \Phi_{\text{abs}}^{(s)} = (1 + 2R) \Phi_{\text{abs}}^{(i)} \quad (7)$$

This shows that a flat scattering surface can enhance the absorption of the particle by a factor of up to three ($R = 1$ for a nonabsorbing surface). Inspection of Fig. 2A, which contains the reflectance spectra of a clean skeleton, reveals that at $\lambda = 675$ nm, $R \approx 0.96$, which leads to an enhancement factor of 2.92. This factor can be larger if multiple scattering between the diffusing surface and the particle is significant or if the surface is concave, as a coralite. The simple analysis presented above can be repeated with a dilute layer of randomly positioned particles with a size distribution, leading to, essentially, the same conclusions. The problem, however, becomes intractable by analytical means when multiple scattering between the particles is important and/or when more realistic skeleton geometries are considered. Although the geometry employed in our calculation is highly idealized, the results show that an enhancement in the absorption due to the presence of the skeleton is to be expected on theoretical grounds and that the measured enhancement factors are quite reasonable. Furthermore, direct determinations of the light enhancement properties of skeletons from more than 50 species of Indo-Pacific corals indicate this enhancement is greater than that based on our theoretical predictions using flat surfaces (Enrquez et al. unpubl. data).

The biological and ecological implications of the optical

properties of the intact coral structure revealed by this study are diverse. Estimations of the minimum quantum requirements of photosynthesis or its inverse, the maximum quantum yield, provide useful information regarding the efficiency of light capture and use (Dubinsky et al. 1984, 1990; Wyman et al. 1987; Lesser et al. 2000). Comparative analyses of the efficiencies of light absorption and use are particularly important for the study of the photoacclimatory capacities of different coral species (Wyman et al. 1987; Lesser et al. 2000; Iglesias-Prieto et al. 2004). Minimum quantum requirements are calculated from the initial slope of the photosynthesis versus irradiance curve and the absorption efficiency of the photosynthetic pigments (Dubinsky et al. 1984; Falkowski et al. 1990). The data presented here indicate that determinations of the absorption cross section of chlorophyll, based on measurements with freshly isolated symbionts, underestimate the absorption efficiency of the same symbionts in the intact coral structure. These results can explain why most of the maximum quantum yields reported in the literature are much larger than the theoretical minimum of eight photons absorbed per molecule of oxygen evolved (Dubinsky et al. 1984, 1990; Wyman et al. 1987; Lesser et al. 2000). Further comparative analyses of the photoacclimation capabilities of different coral species should incorporate the role of the skeleton in modulating its light-absorption properties. Maximizing light-absorption efficiency at low pigment investment costs may be critical for the survival of symbiotic corals in oligotrophic environments. In habitats with high levels of solar radiation, the presence of pigments such as green fluorescent proteins or pocilloporins (Salih et al. 2000; Dove 2004), functioning as “optical dampers,” can modulate the internal light fields, reducing the enhancement effect of the skeleton. Although the photoprotective role of the pocilloporins and related proteins has been recently challenged (Mazel et al. 2003), our results suggest that the specific absorption coefficient of any pigment, including pocilloporins and mycosporine-like amino acids, would be augmented as a result of the interaction between solar radiation and the coral skeleton. Photosynthetic pigment density is highly variable among coral species (Drew 1972; Dubinsky et al. 1984, 1990) and dependent on the prevailing environmental conditions (Falkowski and Dubinsky 1981). During photoacclimation to low-light environments, pigment densities may increase four times without a change in symbiont density (Falkowski and Dubinsky 1981). Under those conditions the loss of absorption efficiency due to the self-shading of photosynthetic pigments (Dubinsky et al. 1984, 1990; Lesser et al. 2000) may be counterbalanced by the intensification of the local irradiance by the skeleton, allowing corals to colonize habitats with very low light availability.

The high efficiency with which corals collect solar radiation may have negative effects when these organisms are exposed to some stressful conditions. For example, coral bleaching is initiated when the photosynthetic function of the symbionts is impaired after exposures to elevated temperatures (Iglesias-Prieto et al. 1992; Brown 1997; Hoegh-Guldberg 1999). Reductions in photosynthetic capacity of symbiotic algae exacerbate the photoinhibitory effects of excessive solar radiation (Jones et al. 1998; Warner et al.

1999). A reduction in Chl *a* density resulting from either losses in symbiont density or reductions in cellular Chl *a* content would result in significant increases in the available irradiance and therefore further photodamage of the remaining algae. Under those conditions, the photoprotective mechanisms responsible for thermal dissipation of excess energy may be overwhelmed. The nonlinear increase in local irradiances due to a reduction in pigment density can explain how the partial impairment of the photosynthetic function of symbiotic dinoflagellates can be magnified, resulting in coral bleaching and mortality.

The results presented here indicate that symbiotic corals are one of the most efficient solar energy collectors in nature. These organisms are capable of harvesting the same amount of incident radiation as the leaf of a terrestrial plant with six times less pigment density (Björkman and Demming 1987). Dinoflagellates in symbiosis with scleractinian corals exhibit higher absorption efficiencies than free-living microalgae (Geider and Osborne 1992). Coral skeletons play a key role in modulating the light environment in which their symbiotic algae function. This role, hitherto neglected, appears to be as significant as its role as a protective substrate for the coelenterate tissue. Coral skeletons exhibit a broad array of morphological traits (i.e., polyp size, number and size of septa, distance between septa, etc.) with potentially important consequences for the regulation of the optical properties of the individual coral species. Consequently, light harvesting may be one of the fundamental driving forces in the evolution of scleractinian skeletons.

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