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Photobehavior of stony corals: responses to light spectra and intensity

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Summary

Tentacle expansion and contraction were investigated in four zooxanthellate coral species and one azooxanthellate coral (*Cladopsammia gracilis*). *Favia favus*, *Plerogyra sinuosa* and *Cladopsammia gracilis* expand their tentacles at night, while tentacles in *Goniopora lobata* and *Stylophora pistillata* are expanded continuously. Light at wavelengths in the range 400–520 nm was most effective in eliciting full tentacle contraction in *F. favus* and in *P. sinuosa*. Higher light intensities in the range 660–700 nm also caused tentacle contractions in *F. favus*. Tentacles in *C. gracilis* did not respond to light. Zooxanthellar densities in tentacles were significantly higher in *G. lobata*, which has continuously expanded tentacles, than in *F. favus* and *P. sinousa*, where tentacles are expanded at night. Photosynthetic efficiency in *F. favus* and *P. sinuosa* was lower in specimens with contracted tentacles. However, in the dark, no differences were found in the maximum quantum yield of photochemistry in PSII (Fv/Fm) of the expanded *versus* the contracted tentacles of any of the four species. This work suggests that species whose tentacles remain continuously expanded have either dense algal populations in their tentacles, as in *G. lobata*, or minute tentacles, like *S. pistillata*. Dense algal populations in tentacles allow harvesting of light while small tentacles do not scatter light or shade zooxanthellae in the underlying body of the polyp.

Key words: coral, tentacle contraction, fast repetition rate fluorometer (FRRF), chlorophyll fluorescence, diel expansion.

Introduction

Diel expansion and contraction patterns vary among anthozoan species, including reef-building corals (Kawaguti, 1954; Porter, 1974; Lasker, 1979), gorgonians (Wainwright, 1967) and sea anemones (Pearse, 1974; Sebens and Deriemer, 1977). Most reef corals expand their tentacles only at night (Lewis and Price, 1975; Porter, 1974). A few species expand their tentacles during daytime and several species have continuously expanded tentacles (Eguchi, 1936; Abe, 1939; Kawaguti, 1954; Porter, 1974; Lewis and Price, 1975). Corals that expand their tentacles at night remain open until dawn. However, a beam of light or mechanical stimulation can cause nocturnally expanded tentacles to contract immediately (Abe, 1939).

Reef-building corals, as well as several other reef organisms, harbour unicellular endosymbiotic algae (zooxanthellae) that supply much of their energy needs *via* daytime photosynthesis. Corals are carnivores and, since zooplankton is most abundant on coral reefs during the night (Sorokin, 1990), it has been suggested that most corals expand their tentacles at night to capture prey (Lewis and Price, 1975; Porter, 1974). Expansion behavior may be affected by water flow and availability of prey (Robbins and Shick, 1980); however, the extent to which any one of these factors controls tentacle behavior is not yet clear (Robbins and Shick, 1980).

In zooxanthellate sea anemones, a connection exists between photosynthesis and the expansion state. Organs with dense endosymbiotic algae (zooxanthellae) populations expand continuously, whereas tissues with few or without zooxanthellae contract during the day (Gladfelter, 1975; Sebens and Deriemer, 1977).

Lasker (1977) described the expansion behavior of the coral *Montastrea cavernosa*. In shallow water, large numbers of polyps remain partially expanded during the day; he named this ‘diurnal behavior’. ‘Nocturnal behavior’ or tentacle expansion during the night was observed in water deeper than 20 m, and at such depths polyp expansion during daytime was seldom, if ever, observed. This behavioral switch is probably based on zooxanthellae density (Lasker, 1977, 1979). It was proposed that diurnally active colonies have greater zooxanthellae densities than do nocturnal colonies (Lasker, 1977, 1979), but this study did not suggest any mechanism to explain this relationship.

Corals can flourish in nutrient-poor ‘blue desert’ waters due to their mutualistic symbiosis with zooxanthellae. Their carbon and energy requirements are met by different species-specific combinations of algal photosynthetic products and by predation on zooplankton, supplemented in some cases by minor contributions derived from dissolved organic carbon compounds and bacteria (Achituv and Dubinsky, 1990).

On the coral reef at Eilat, in the northern Red Sea, the

massive stony corals *Favia favus* and *Plerogyra sinuosa* expand their tentacles nocturnally and contract them at sunrise. *Goniopora lobata* and *Stylophora pistillata* are expanded continuously (O. Levy, personal observations). Tentacle morphology differs in the four coral species examined. In *P. sinuosa* and *F. favus* the tentacles are conical or cylindrical, and when expanded they are erect and well-separated. In *S. pistillata* tentacles are tiny (up to 2 mm) and extended during both day and night. The tentacles of *G. lobata* are cylindrical and project sideways from the top of the polyp to form a 'flower-like' crown of 24 tentacles. The polyps project several centimeters above the skeleton yet the entire polyp can retract into the coral skeleton.

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). Underwater light decreases exponentially with depth, roughly following the Beer–Lambert law. Underwater light is attenuated by the water itself, by dissolved and suspended matter and, most importantly, by phytoplankton. Light attenuation is not uniform over all wavelengths, and the water column behaves like a monochromator, narrowing the spectrum of the most penetrating light to a relatively narrow waveband (Falkowski et al., 1990). In the clear oligotrophic waters surrounding reefs, light extinction in the violet and blue parts of the spectrum is minimal, while its attenuation is higher at longer wavelengths. However, in such 'blue desert' shallow waters corals can also be exposed to considerable penetration of red wavelengths and non-visible (UV) wavelengths (Smith and Baker, 1979). Recently Gorbunov and Falkowski (2002) have shown that zooxanthellate corals even perceive blue moonlight, which consists of the most penetrating wavelengths in the area, typical of coral reef environments.

The aim of this study was to find out if the expansion and contraction behavior of zooxanthellate corals occurs as a direct response to light, or as an indirect response to it mediated by photosynthetic activity of their symbiotic algae. We examined the possibility that the expansion/contraction behavior of tentacles optimizes photosynthesis. We examined expansion and contraction responses to different light intensities and wavelengths over different times, including in the azooxanthellate coral *Cladopsammia gracilis*. We studied the absorption and the action spectra for photosynthesis and the distribution of zooxanthellae within the corals. We also studied the photosynthetic characteristics of the four species using the SCUBA-based, fast repetition rate fluorometer (FRRF; Kolber et al., 1998).

Materials and methods

Coral collection and maintenance

Colonies of four species of zooxanthellate scleractinian corals, *Favia favus* Forskal, *Goniopora lobata* Milne Edwards and Haime, *Stylophora pistillata* Espar and *Plerogyra sinuosa* Dana and the azooxanthellate coral *Cladopsammia gracilis* Milne Edwards and Haime were collected from depths of 5–7 m from reef adjacent to the Interuniversity Institute for Marine Science at Eilat (Gulf of Eilat, Red Sea). The colonies, each less than 6 cm in diameter, were then transferred to the laboratory and placed in a shallow tank with running seawater at 24°C for 10 h of acclimation before sampling their tentacles. After acclimation the corals exhibited the same expansion/contraction behavior in the laboratory as their undisturbed counterparts on the reef.

Measurement of the light spectrum

The visible light spectrum was measured at a depth of 5 m at the coral collection site. Spectral scans between 350 and 750 nm were conducted on several cloudless days in February 2001 using a Li-Cor LI1800 scanning spectroradiometer (Lincoln, NE, USA). Scans were made every 30 min at 2 nm wavelength intervals from 6:00 h to 18:00 h.

Effect of light on tentacle contraction

Colonies were tested at low light intensities, up to 1.5% of the sea surface light level, which is the lower light intensity of euphotic zone and the limit of hermatypic coral distribution. *F. favus*, *G. lobata*, *S. pistillata* and *C. gracilis* were illuminated at 10 and 30 μmol quanta m^{-2} s^{-1} (N=5 corals for each irradiance level). Colonies of *P. sinuosa* were illuminated at 30 μmol quanta m^{-2} s^{-1} (N=3). A Xenon lamp of 450 W (Kratos–Schoeffel Instruments, Doisberg, Germany) acted as a light source and included a LH-151/2 lamp housing and LPS-255 h power supply. The beam from the lamp housing was passed through a monochromator (Bausch & Lomb Instruments, New York, USA) to provide light at wavelengths of 400–700 nm.

Tentacle contraction experiments were conducted in a 25 l recirculating flow tank (modified from Vogel and Labarbera, 1978). The tank was 100 cm long × 10 cm wide × 25 cm high. Water was circulated by a propeller connected to a 12 V d.c. motor and flow speed was computer-controlled at 5 cm s^{-1}. Flow speed was calibrated using a video camera with a close-up lens (Sony CCD 2000E, Hi8 PAL system; Tokyo, Japan) to follow the movement of brightly illuminated particles along a ruler placed in the tank (Trager et al., 1990).

All experiments were conducted at night in a darkroom. Two colonies, an experimental colony and a control colony, were placed in the flow tank well-separated from each other to ensure that there would be no interference to the flow received by each. A recirculating bath at 24±0.1°C, which is equal to the sea temperature, controlled the water temperature. Water was replaced every 2 h. *F. favus*, *G. lobata*, *S. pistillata* and *C. gracilis* colonies were illuminated at two irradiance levels, 10 and 30 μmol quanta m^{-2} s^{-1}, and at 16 different wavelengths between 400 and 700 nm at intervals of 20 nm, while colonies of *P. sinuosa* were exposed only to 30 μmol quanta m^{-2} s^{-1}. Circulation in the tank was stopped when the corals were fully expanded. After 15 min, the experimental coral was illuminated with all 16 wavelengths in a random order, to prevent a habituation effect. Tentacle contraction behavior of the coral was scored on a scale of 0–4, where 0 was no

expansion (i.e. full contraction) and 4 was 100% expansion. Final analyses were performed only on the 0% and 100% expansion scores. The scores referred to polyps of the entire colony (see Lasker, 1979) (Fig. 1). The behavior of the corals was documented every minute for a total of 30 min for each wavelength. In each experiment a second, non-illuminated coral was used as a control. We also conducted these experiments with the corals exposed to the photosynthetic inhibitor DCMU (3-(3,4-dichlorophenyl)-1,1-dimetheyl urea), at a final concentration of 10 μmol l^{-1} (see Rahav et al., 1989). DCMU blocks photosystem II and prevents production of photosynthates. The experiments were also conducted with the azooxanthellate coral *Cladopsammia gracilis*, which expands mostly at night. In addition to the 10 and 30 μmol quanta m^{-2} s^{-1}, *C. gracilis* was exposed to light intensities between 250 and 400 μmol quanta m^{-2} s^{-1}.

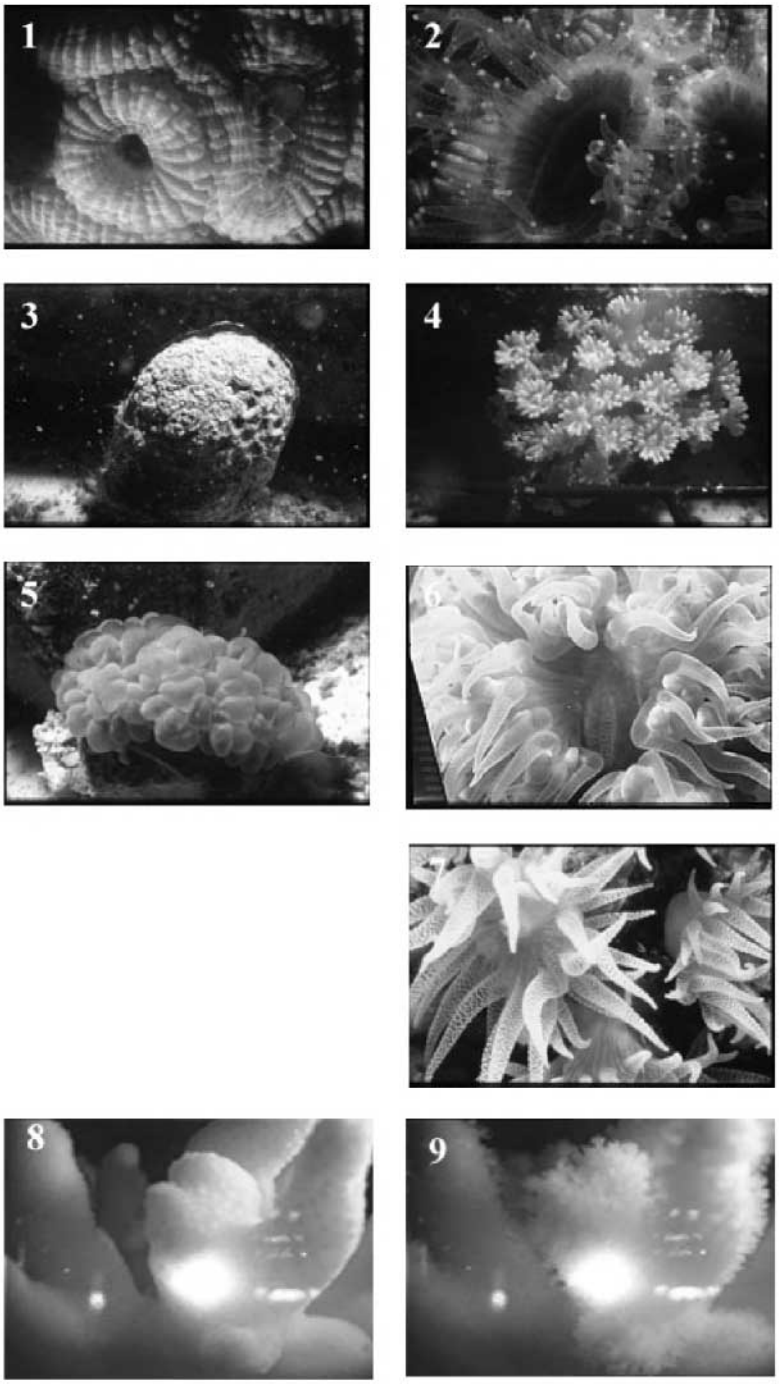

Fig. 1. Two stages of tentacle expansion, 0% (1,3,5,8) and 100% (2,4,6,7,9), in the five coral species. (1,2) *Favia favus*; (3,4) *Goniopora lobata*; (5,6) *Plerogyra sinuosa*; (7) *Cladopsammia gracilis*; (8,9) *Stylophora pistillata*.

Zooxanthellar density

Zooxanthellar densities were measured in *F. favus* (*N*=5), *P. sinuosa* (*N*=4), *S. pistillata* (*N*=4) and *G. lobata* (*N*=4). Except for *G. lobata*, colonies were placed in an anaesthetizing solution of 7.5% $MgCl_2$ in (1:1 v:v) distilled water and seawater at room temperature (Sebens and Miles, 1988) for approximately 3 h. Tentacles (*N*=30) were removed from different polyps using tweezers and small scissors. Manipulations were carried out during the day and anaesthetization was necessary because these colonies are normally contracted during the day. Tentacles (*N*=30) were removed from *G. lobata* in running seawater and without anesthetization as this species is normally expanded during the day. Severed tentacles were photographed using a Nikonos V camera with close-up tubes, and their surface area was calculated assuming their shape to be a cylinder, according to the formula:

$$SA = 2\pi rh + 2\pi r^2 , \quad (1)$$

where *SA* is tentacle surface area, *r* is the tentacle radius and *h* is tentacle length. Zooxanthellae in the tissue were removed from the tentacles using a small glass homogenizer, and their number was determined under the microscope (×400) using a Neubauer haemocytometer. Zooxanthellae densities were converted to number of algae per unit surface area of each tentacle. Measurements of the surface area of coral colonies with their tentacles expanded were performed on four *G. lobata* colonies. Before measurement, photographs of the colonies with expanded tentacles were taken, and the polyps of each coral counted. The estimated surface area of one tentacle was multiplied by 24 (the number of tentacles on each polyp). The surface area of a single polyp was then multiplied by the total number of the polyps on the coral, and added to the surface area of the coral skeleton. The surface area of the whole-expanded coral was thus calculated according to the formula:

$$So_T = Sc_T + N_p \times Nt_P \times [2\pi r_t^2 + (2\pi r_t \times h_t)] , \quad (2)$$

where r_t is tentacle radius, h_t is tentacle length, N_p is number

of polyps, Nt_P is number of tentacles per polyp, Sc_T is surface area of the coral colony with polyps contracted, and So_T is surface area of the coral when expanded.

Pigment and chlorophyll analysis

Small pieces were collected from *F. favus* and *P. sinuosa* colonies, chlorophyll was extracted in 90% acetone, the absorbance spectrum at 400–700 nm was measured using a Cary spectrophotometer (Varian, Palo Alto, CA, USA) and the concentration calculated using the equations of Jeffrey and Humphrey (1975). A tissue homogenate was prepared from these species for estimates of zooxanthellar pigments. The homogenate was obtained by removing all tissue with an airbrush (modification of the Water–Pik method of Johannes and Wiebe, 1970). The homogenate was centrifuged twice in seawater, at 1500 ***g*** for 15 min in order to separate the algae from the host tissue. The zooxanthellae pellet was taken for pigment identification by high-performance liquid chromatography (HPLC), using the reverse-phase HPLC system after Yacobi et al. (1996). Pigments were identified using ChromaScope (BarSpec, Israel), a spectral peak analyzer. The pigments were identified by the spectral data of the peaks separated by HPLC and their retention times, using the data of Rowan (1989) and Jeffrey et al. (1997). Quantification of compounds represented by the peaks was obtained by injection of known concentrations of pigment into the HPLC system. All pigment concentrations presented here are the means of duplicate measurements. Individual measurements did not differ by more than 10% between the duplicates.

Fluorometer measurements

A fast repetition rate fluorometer (FRRF) was positioned on a tripod adjacent to the flow tank. FRRF measurements were taken by aiming the instrument at a coral in the tank and triggering the instrument. Measurements were made in the dark on corals with expanded and contracted tentacles. The action spectrum for photosynthesis was obtained by FRRF taken with corals illuminated by wavelengths of 400–700 nm. An illumination intensity of 10 μmol quanta m^{-2} s^{-1} was obtained using the Xenon lamp and monochromator. FRRF measurements involve a series of subsaturating 'flashlets' that cumulatively saturate PSII within ~100 μs (Falkowski and Kolber, 1995; Kolber et al., 1998). The FRRF technique enables non-invasive and rapid measurement of maximum quantum yield of photochemistry in PSII (Fv/Fm, where Fv is variable fluorescence and Fm is maximum fluorescence) and the photosynthetic parameter Sigma, which is the cross section of PSII (σ_{PSII}) (Kolber et al., 1998).

Results

Peak illumination at 5 m on a cloudless day occurred around noon, 12:00–13:00 h (Fig. 2). There was a small attenuation (~20%) of the wavelengths >600 nm. There was nevertheless a considerable penetration of all wavelengths between 400 and 700 nm at 5 m depth. The distribution of underwater light varies due to changes in the angle of the sun and the peak of penetration at all wavelengths is during the midday hours.

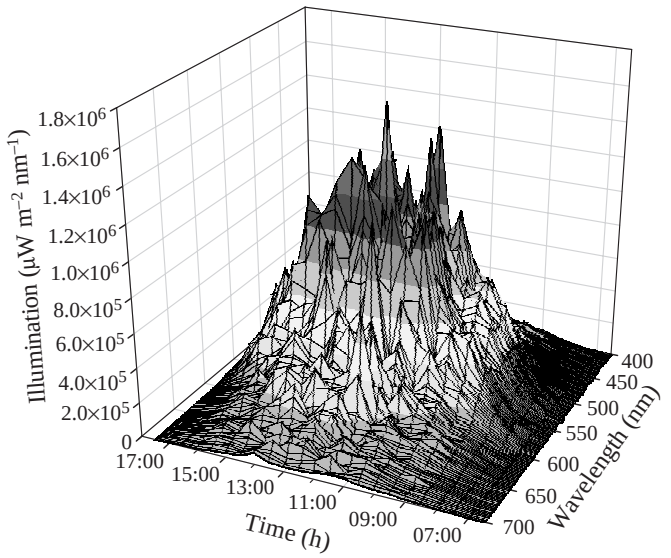

Fig. 2. A 3-dimensional structure of the daily illumination (μW m^{-2} nm^{-1}) in the visible light spectrum (400–700 nm) measured at 5 m depth in Gulf of Eilat, Red Sea, in front of the Interuniversity Institute for Marine Science. Measurements were conducted on a cloudless day on February 14, 2001. The spectrum was scanned between 5:00 h and 18:30 h, with readings taken every 30 min at 2 nm intervals.

Tentacles of *Favia favus* fully contracted within 5–6 min when exposed to low light intensities (10 and 30 μmol quanta m^{-2} s^{-1}) at wavelengths of 400–520 nm (Fig. 3A,B). At 10 μmol quanta m^{-2} s^{-1} (N=5) a significant difference was found between the response time at 400–520 nm and at 540–700 nm to elicit full tentacle contraction (Fig. 3B; one-way analysis of variance, ANOVA, followed by the Student's t-test; P<0.0005). Differences related to response time of tentacle contraction were also significant in *F. favus* colonies (N=5) at 30 μmol quanta m^{-2} s^{-1} between wavelengths of 400–500 nm and >660 nm and the rest of the visible spectrum (540–560 nm) (Fig. 3A; one-way ANOVA followed by the Student's t-test, P=0.0016). Contraction occurred at wavelengths of 660–700 nm when colonies were illuminated at 30 μmol quanta m^{-2} s^{-1}. Tentacle contraction at 540–640 nm was very slow regardless of illumination intensity. Tentacles did not contract even after 30 min of illumination in some corals. Control colonies, which were not illuminated, remained fully expanded during all the experiments (N=5, for each set of experiments). *Goniopora lobata*, *Stylophora pistillata* and *Cladopsammia gracilis* did not respond to light at any wavelength.

Colonies of *Plerogyra sinuosa*, exposed to 30 μmol quanta m^{-2} s^{-1}, contracted their tentacles at wavelengths of 400–540 nm. A mean period of 1–2 min elapsed after exposure to light until the full response was reached. This coral also responded to light of 660 nm

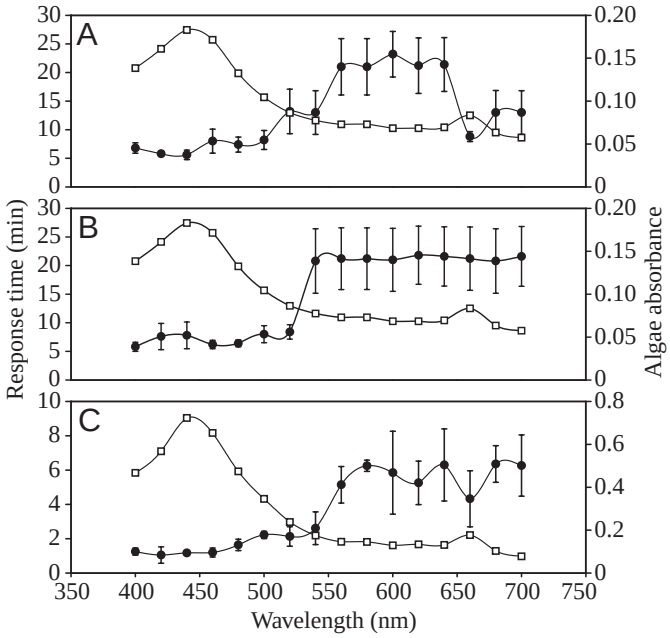

Fig. 3. Action spectra of tentacle contraction in *Favia favus* and *Plerogyra sinuosa* (filled circles). Values are means ± S.D., N=5. (A) Comparison of the action spectrum of *F. favus* tentacle contraction to the light spectrum absorbed by the zooxanthellae at an irradiance level of 30 µmol quanta m^{-2} s^{-1} (open squares) (Pearson's correlation, r=–0.7557, P<0.0007). (B) Comparison of the action spectrum of *F. favus* tentacle contraction to the light spectrum absorbed by the zooxanthellae at an irradiance level of 10 µmol quanta m^{-2} s^{-1} (open squares) (Pearson's correlation, r=–0.8543, P<0.0001). (C) Comparison of the action spectrum (*in vitro*) of *P. sinuosa* tentacle contraction to the light spectrum absorbed by the zooxanthellae at an irradiance level of 30 µmol quanta m^{-2} s^{-1} (open squares) (Pearson's correlation r=–0.8667, P<0.0001, N=3).

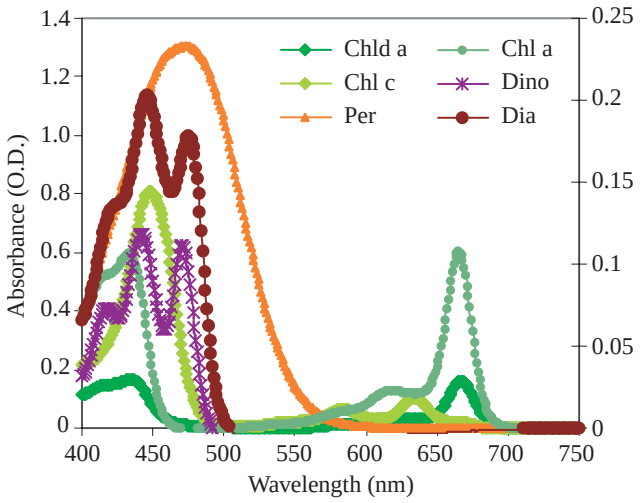

Fig. 4. Absorption characteristics of the major pigments extracted from *F. favus* zooxanthellae. Pigments are: Chl, chlorophyll; Chld, chlorophyllidae; Per, perdinin; Dia, diatoxanthin; Dino, diadinoxanthin.

(Fig. 3C). Wavelengths of 400–540 nm had a significantly different effect from wavelengths of 560–700 nm (one-way ANOVA followed by the Student's t-test; P<0.0001).

In the coral species that did respond to the light stimuli the wavelengths that were most efficient in triggering the polyp contraction were correlated with the *in vitro* absorption spectra of their symbiotic algae (Pearson's correlation, r=–0.8543, P<0.0001, N=5 and r=–0.7557, P<0.0007, N=5 for irradiance levels of 10 µmol quanta m^{-2} s^{-1} and 30 µmol quanta m^{-2} s^{-1}, respectively) (Fig. 3A,B). In *P. sinuosa*, the correlation between the spectral absorbancy of the zooxanthellae and the action spectrum of tentacle contraction was significant (Pearson's correlation, r=–0.8667, P<0.0001, N=3).

The addition of DCMU did not affect the tentacle contraction response at any of the different wavelengths, however, it did block oxygen production. Tentacle contraction in the azooxanthellate coral *Cladopsammia gracilis* did not occur in response to illumination at any wavelength, even with light intensities as high as 400 µmol quanta m^{-2} s^{-1}, regardless of wavelength. The spectral data of the separated peaks revealed that most of the major pigments have considerable absorbance between 400–540 nm, with major peaks between 440–480 nm. The widest absorbancy spectral profiles belong to the accessory carotenoid pigments, such as perdinin, diatoxanthin and diadinoxanthin, which display blue/blue–green absorption bands that partially overlap the chlorophyll absorption bands in that domain (Fig. 4).

Highest zooxanthellar densities were found in the tentacles of *Goniopora lobata* (1.78±0.58×10^6 cells cm^{-2}). Lower densities were found in the tentacles of *Plerogyra sinuosa*. No zooxanthellae were found in the tentacles of *Favia favus* or *Stylophora pistillata* (Table 1), although occasional

Table 1. *Zooxanthellae densities in tentacle tissues and in total tissue for four coral species*

Coral species	Number of colonies	Cells in total coral tissue (cells×10^6 cm^{-2})	Cells in the tentacles (cells×10^6 cm^{-2})	Cells in tentacle/ total cells	Duncan grouping*
S. pistillata	4	0.93±0.07	0	0	B
F. favus	5	0.34±0.19	0	0	B
P. sinuosa	4	1.96±1.11	0.47±0.05	0.238	C
G. lobata	4	3.25±0.93	1.78±0.58	0.547	A

Values are means ± S.D. (ANOVA, $F_{(2,19)}$=54.59; Duncan grouping, P<0.0001).
*Duncan groupings with the same letter are not significantly different.

zooxanthellae were seen when tentacles were examine under the microscope. The ratio of zooxanthellar density in the tentacles to the density in the whole coral was highest in *G. lobata* (Table 1). Tentacles were nearly devoid of algae in the other zooxanthellate species.

The surface area of *G. lobata* was found to be 7.5±0.86 (mean ± S.D.) times higher when the polyps were expanded than when they were contracted. Calculations of *G. lobata* surface area did not take into account the trunk (which was not fully extended all the time) of the polyps, only their tentacle crown. Measurements of the fluorescence parameters of corals with expanded and contracted tentacles using the FRRF instrument in the dark clearly demonstrated that minimum fluorescence (Fo), variable fluorescence (Fv) and maximum fluorescence (Fm) all increase when the tentacles are contracted in the two nocturnal corals *F. favus* and *P. sinuosa*. In *S. pistillata* and *G. lobata* no significant change in these parameters was observed when the corals were manually touched in order to induce tentacle contraction. Of the photosynthetic parameters, Fv/Fm did not change significantly when the polyps became contracted in any of the four zooxanthellate species (Fig. 5A). In *F. favus* and *P. sinuosa* the functional absorption cross section of PSII (σ_{PSII}) was significantly lower in the expanded than the contracted tentacles (*t*-test, $P<0.05$, d.f.=146), whereas in *G. lobata* and in *S. pistillata* these changes were not significant (Fig. 5B). Measurements of the action spectrum of photosynthesis showed that maximum chlorophyll fluorescence differences [related to the dark measurements (ΔF′/Fm′–Fv/Fm)/Fv/Fm, where ΔF′/Fm′ is the quantum yield] were highest in the blue zone. In all four species the lowest values were recorded when corals were illuminated with wavelengths of 540–620 nm (Fig. 6).

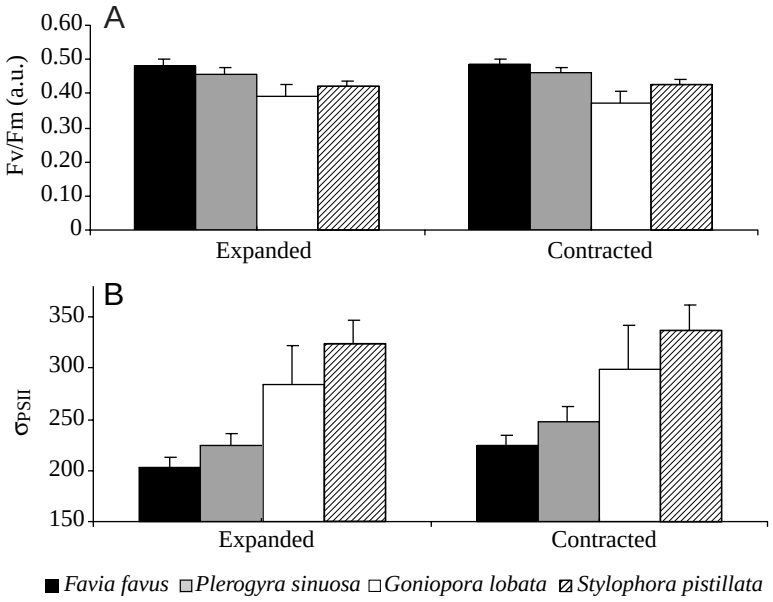

Fig. 5. Photosynthetic characteristics of corals with expanded and contracted tentacles (N=4 for each coral species). (A) The quantum yield of photochemistry in PSII (Fv/Fm). (B) The functional absorption cross section for PSII (σ_{PSII}). a.u., arbitrary units.

Discussion

The response of *Favia favus* and *Plerogyra sinuosa* to illumination at different wavelengths is correlated to the absorption spectrum of their symbiotic zooxanthellae. There is ample evidence that the action spectra of photosynthetic pigments are close to those of their absorption spectra (Kinzie et al., 1984). The decrease in the quantum yield (ΔF′/Fm′) in different photosynthesis action spectra, as measured in the present study using FRRF, was also associated with the tentacle contraction behavior. This correlation may indicate that the tentacle contraction response of these corals is mediated, at least indirectly, by the photosynthesis of its symbionts. This correlation corresponds to the findings of Lasker (1979) who showed that the diurnal morph colonies of *Montastrea cavernosa* failed to expand when their zooxanthellae were bleached or lost. Likewise Sawyer et al. (1994), have shown that in sea anemones the neural response to light in zooxanthellate individuals is more intense than in apozooxanthellate conspecifics and in azooxanthellate species, as explained by higher extra-sensory information received from the endosymbiotic algae. The term extra-sensory information in the sense used by these authors is interpreted by us as changes in photosynthetically induced chemical changes in the coral's cells. Exposure of the corals to DCMU (24 h) in the present study may have been too brief to cause any change

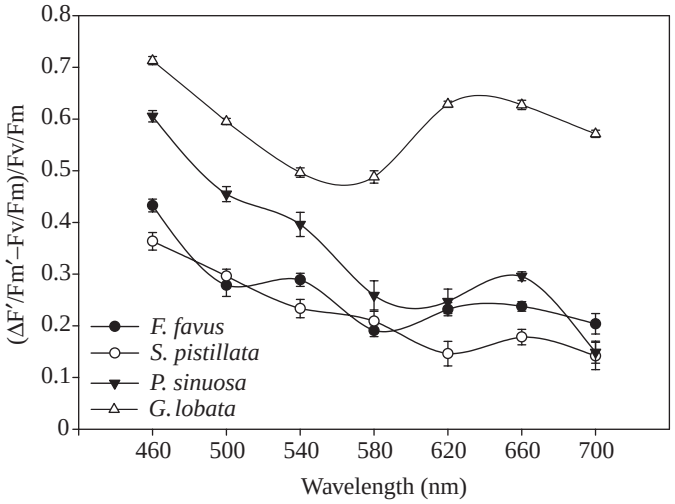

Fig. 6. Effect of the light spectrum (460–700 nm at intervals of 40 nm) at an irradiance level of 10 μmol quanta m^{-2} s^{-1} on the quantum yield of photochemistry in PSII (ΔF′/Fm′) related to dark measurements (Fv/Fm) in four coral species: *Favia favus* (filled circles; N=3); *Stylophora pistillata* (open circles; N=3); *Plerogyra sinuosa* (filled triangles; N=3); *Goniopora lobata* (open triangles; N=3).

in the behavior of tentacle contraction. Furthermore, the polyps may express an entrained circadian daytime expansion initiated in response to resident zooxanthellae, but capable for persisting for a few diel cycles after zoxanthellar cues were interrupted by DCMU, as suggested by Pearse (1974). Alternatively, since DCMU does not block PSI (photosystem I), but does block oxygen production by PSII, it is possible that the host animal responds to some of the effects of the residual PSI activity, such as energy charge or pH gradients. It is also possible that there is a low rate of photosynthetic electron transport in zooxanthellae even under moonlight, which can trigger a pH gradient across thylakoid membranes (Falkowski et al., 1984). In the tentacles of *Favia favus* and *Stylophora pistillata*, only sparse algae were observed by light microscopy, and due to their low numbers, attempts to quantify the density of these zooxanthellae using a haemocytometer failed (Table 1). We thus conclude that the number of zooxanthellae in *F. favus* and *S. pistillata* tentacles is negligible. Therefore, the tentacular status in these corals hardly affects their photosynthetic rates, as was also confirmed by our FRRF measurements (Fig. 5). By contrast, the far larger number of zooxanthellae in the tentacles of *P. sinuosa* was easily quantified by direct haemocytometer counting (Table 1). The density of algal cells in the tentacle compared to the total average density in the coral tissue was much higher in *G. lobata* than in the other three species of corals examined. The two species with low zooxanthellae densities in their tentacles (*F. favus* and *P. sinuosa*) remained contracted during daylight, while the corals with high zooxanthellae densities in their tentacles (*G. lobata*) expanded their polyps diurnally (O. Levy, personal observation). The different polyp architecture of *P. sinuosa* and *F. favus* as opposed to *G. lobata* implies that their tentacles have different roles. The finger-shaped tentacles of the two former species function mainly for prey capture. They probably have little or no role in controlling the light available for photosynthesis of the zooxanthellae and are expanded only at night. By contrast, the flower-shaped tentacles of *G. lobata* extend during the day to absorb light, which is also reflected by the zooxanthellae density in the tentacular tissue. When *G. lobata* tentacles are open, the colony tissue surface area increases approximately 7.5 times. This value was obtained without including the height of the polyp stalk, which would further increase the colony surface area. Such a large increase in surface area during expansion supports the hypothesis that corals with a high zooxanthellae density in their tentacles will tend to stay expanded during the daytime for efficient light absorption, resulting in more energy being transferred to the coral. *P. sinuosa* colonies consist of feeding tentacles and bulb-shaped vesicles. The vesicles contain a large number of zooxanthellae ($5–15\times10^6$ cells cm^{-2}), but do not contain nematocysts. The bulb-shaped vesicles expand during daytime, whereas the tentacles that contain nematocysts expand during the night, and the vesicles increase in volume with depth, thus compensating for the decrease in light availability (Vareschi and Fricke, 1986). The absence of nematocysts in the vesicles with high zooxanthellae densities, and the finding that tentacles which contain nematocysts have only small numbers of zooxanthellae, indicate that the role of the vesicles is to harvest light, similar to the tentacles of *G. lobata*, whereas the tentacles of *P. sinuosa* function only for predation.

Expansion of tentacles with low zooxanthellae densities might lead to net energy loss, since expansion requires energy (Pearse, 1974; Robbins and Shick, 1980; Lasker, 1981). In addition daytime expansion of tentacles with low numbers of zooxanthellae may lead to an overall decrease in the photosynthetic rate, due to light scattering. Some zooxanthellate sea anemones contain two types of specialized organs: pseudotentacles, with a high concentration of zooxanthellae, and true tentacles with few or no algae. The pseudotentacles expand during daylight and are photosynthesis active. The true tentacles expand during the night and are used for zooplankton capture (Lewis, 1984; Sebens and Deriemer, 1977; Pearse, 1974; Gladfelter, 1975). The coral *Montastrea cavernosa*, which has two morphotypes, exhibits a similar type of behavior; colonies containing a dense zooxanthellae population tend to remain open during the daytime, while morphotypes with sparse zooxanthellae expand only during the night (Lasker, 1977, 1979).

We suggest that differences in algae density and their distribution within the tissue may lead to differences in the relative contribution of their energy sources. The relative importance of autotrophy *versus* heterotrophy in a given species can be reflected in the diel behavioral patterns of tentacle expansion and contraction. Levy et al. (2001) showed that polyps of *Favia favus* could be induced to expand under high flow velocity and low–medium light (below the compensation point), regardless of the presence of prey. Thus in corals with a low density of zooxanthellae in their tentacles there is a hierarchy of responses, with light level and flow speed overruling the presence of prey. These results probably do not apply to corals that contain high algal densities in their tentacles (such as *G. lobata*), which would benefit from expansion whenever light levels are high. Crossland and Barnes (1977) claimed that polyp retraction in *Acropora acuminata* can be a way of avoiding light by self-shading. They showed that the light saturation level and the compensation point were 25% higher when polyps were contracted than when they were partially expanded. Similarly, when contracted, Xeniids completely stopped their oxygen evolution (Svoboda, 1978).

FRRF measurements demonstrate that extended tentacles in nocturnal species scatter some of the radiation. Thus, less excitation energy reaches the zooxanthellae. As a consequence, the efficiency of chlorophyll excitation decreases and fluorescence is reduced (Fo, Fm). σ_{PSII}, the functional absorption cross section of PSII, also decreases. The retraction of tentacles stimulated by specific wavelengths corresponding to the algal radiation absorbance profile therefore enhances light harvesting, and thus increases photosynthetic performance. The increase in photosynthetic efficiency appears to proceed without any change in the efficiency at which the absorbed quanta are used, as indicated by the constancy of Fv/Fm, in

agreement with general photosynthetic theory; regardless of their wavelength-dependent probability of absorption, once absorbed, all quanta are utilized with the same efficiency. However, corals that expand their tentacles during daylight (*G. lobata* and *S. pistillata*) did not exhibit changes in σ_{PSII} and in the Fv/Fm parameter when the tentacles were contracted or expanded. This may be related to the higher zooxanthellae density in the tentacles, at least in *G. lobata*, compared to the nocturnal corals. Nevertheless, in *S. pistillata* the tentacles are so small (1–2 mm) that the scattering effect is minimal and it may be assumed that this is the reason why *S. pistillata* colonies are fully expanded during daytime. Salih et al. (1995) suggested an alternative explanation. Coral expansion and contraction changes the density of the fluorescence pigment in the chromatophores; at high light levels, polyp contraction leads to denser concentrations of tissue fluorescent pigments (FPs), forming a thicker and a quasi-continuous FP layer, which acts as an effective sunscreen.

Our results on the effect of light spectrum on tentacle contraction behavior in *F. favus* and *P. sinuosa*, and the absence of this effect in azooxanthellate corals, support the notion that this behavior is related to the photosynthetic activity of the zooxanthellae. FRRF measurements indicated that the two species that contract diurnally have a significantly lower photosynthetic performance when their tentacles are expanded than when they are contracted. In *G. lobata* and *S. pistillata* there is no such significant change in photosynthetic performance, regardless of their tentacle state. We assume that the expansion/contraction behavior of the tentacles acts as a shutter, optimizing the photosynthesis of the coral colony. Maximum photobehavior response is in the blue/green zone, which matches the maximum transparency of oligotrophic tropical waters (Jerlov, 1968). Although clear sense organs such as photoreceptors are not known in corals, Gorbunov and Falkowski (2002) have recently suggested that corals exhibit the absorption spectra of rhodopsins isolated from a number of marine invertebrates. It is usually accepted that these pigments indicate sensitivity to light, which is not mediated by any known receptor in Anthozoa (Martin, 2002), but is presumably associated with neurons concentrated just beneath the translucent surface of the epidermal cells. Our results seems to point to a causative relationship between the photosynthesis of the zooxanthellae (or the products thereof) and tentacle behavior in corals, but cannot totally exclude the possibility that such cells are sensitive to the same wavelengths as the photosynthesis, and may also play a role in coral behavior.

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