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Photoreceptors in the cnidarian hosts allow symbiotic corals to sense blue moonlight

Abstract—In many species of symbiotic corals, spawning occurs synchronously several nights after the full moon. This process is correlated with the level of lunar irradiance, but the mechanism by which these cnidarian/zooxanthellate symbioses can detect such low levels of light remains unknown. Here we report the first biophysical evidence that the host animal exhibits extraordinarily sensitive photoreception in the blue region of the spectrum. Using a high-resolution laser-induced signal to detect tentacle scattering, we measured the effect of low irradiance on the contraction of polyps in the corals that normally have their tentacles extended in darkness. Similar to most deep-sea invertebrates, the action spectra of coral photoreception reveal a maximum sensitivity in the blue, at 480 nm, with a spectral band width (at full-width half-maximum) of ca. 110 nm. The spectra closely overlap the maximal transparency of oligotrophic tropical waters, thus optimizing the perception of low light at depth. The detected threshold of photoreception sensitivity is $\sim 1.2 \times 10^{15}$ quanta m^{-2} s^{-1} in the blue region. This makes corals capable of sensing the blue portion of lunar irradiance, as evidenced from the recorded slight contractions of polyp tentacles under variations in moonlight intensity.

For more than six decades, marine scientists have been puzzled by the phenomenon of mass coral spawning that occurs over the majority of coral reefs. In many species, the spawning occurs synchronously several nights after the full moon, thus exhibiting lunar periodicity (Marshall and Stephenson 1933; Harrison et al. 1984; Babcock et al. 1986). Although several environmental factors such as temperature, tidal periodicity, and day length have been suggested to influence larvae release in corals (Harrison et al. 1984; Babcock et al. 1986, 1994), this process appears to be triggered by the level of lunar irradiance (Harrison et al. 1984; Jokiel et al. 1985; Babcock et al. 1994). How do these organisms perceive moonlight?

There are several hypotheses for the mechanism of low-light perception by corals. First, extremely low rates of photosynthetic electron transport in zooxanthellae under moonlight may trigger a pH gradient across thylakoid membranes (Falkowski et al. 1984), thereby influencing the photosynthetic metabolism in the coral and, thus, potentially, the reproductive cycle (Jokiel et al. 1985). Second, the invertebrate host may have cellular linked photoreceptors that have not yet been discovered (Jokiel et al. 1985). Finally, zooxanthellae themselves may have photoreceptors independent of the photosynthetic apparatus. Which component of this invertebrate/algal symbiosis provides perception of low light: the cnidarian host or the endosymbiotic zooxanthellae? In an attempt to answer this question, we measured the action spectrum and the threshold of photoreception sensitivity in a number of Caribbean zooxanthellate corals and identified the location of photosensitive cells, the action spectrum of the response, and the response sensitivity to photon flux density. Here we demonstrate that a blue photoreceptor in corals is located in the invertebrate host cells and is responsible for sensing lunar photon fluxes.

Methods and materials—Field studies were conducted at Lee Stocking Island (23°46′N, 76°05′W), Bahamas, during the coastal benthic optical properties field experiments in January 1999, May 1999, and May 2000. Samples (~20–50 cm^2) of the flower coral *Eusmilia fastigiata,* the boulder coral *Montastraea cavernosa,* the rose coral *Manicina areolata,* and the brain coral *Diploria labyrinthiformis* were collected at North Perry Reef (16 m) and North Norman's Reef (2 m). We studied the so-called "nocturnal" morph of *M. cavernosa,* in which polyps exhibit nocturnal expansion and diurnal contraction (Lehman and Porter 1973; Lasker 1979). Samples were placed in laboratory aquaria with running seawater. The flow rate was fixed at ~3 cm s^{-1}. Following 24 h of adaptation on the ambient photoperiod, measurements were made at night (2200 h to 0500 h local time). The influence of circadian rhythm on polyp expansion/retraction (Sweeney 1976) was alleviated due to night measurements.

We measured the photoreceptive responses by monitoring the effect of low irradiance on the contraction of polyps in coral species that normally have extended tentacles in darkness. The contraction response was stimulated by actinic light (i.e., light that elicits a response) and detected by following changes in the back-scattered signal induced by a measuring (nonactinic) light beam (Fig. 1). The actinic light was provided by either a 100 W halogen lamp with a set of

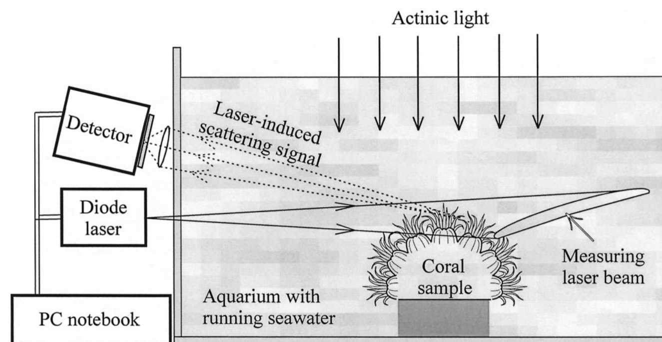

Fig. 1. Diagram of the experimental setup developed for measuring photoreceptive responses in corals. Expanded polyp tentacles are illuminated by an elliptical laser beam with divergence of 3° × 30°. A laser-induced scattering signal is recorded off axis by a computer-coupled photodiode detector.

interference filters (10-nm bandwidth each, Corion) or by natural moonlight. Preliminary experiments showed that red light (>600 nm) had no effect on polyp expansion or contraction, hence we selected a red low-power laser diode (660 nm, peak power 3 mW, modulation frequency 100 kHz) as a source of the measuring beam. The laser-induced scattering signal was proportional to the amount of polyp biomass in the sounding volume. The laser beam illuminated only tentacle tips (Fig. 1), making the scattering signal very sensitive to minute changes in tentacle retraction. The signal was isolated by an interference filter (660 nm with a bandwidth 10 nm), detected by a photodiode with a high frequency electronic filter, and recorded by an analog-to-digital converter interfaced to a notebook computer. The photon flux density (PFD) of monochromatic actinic light was calculated from the optical power, measured by a wavelength adjusted power meter (1815-C, Newport), and the known emission wavelength. The PFD was varied from 1.2×10^{15} to 5×10^{18} quanta m^{-2} s^{-1}, using a set of calibrated neutral density filters. The wavelength dependent attenuation coefficients for each filter were determined using a spectrophotometer. The PFD of moonlight was measured by a custom-built light sensor calibrated against a LiCOR 2π quantum meter under full moonlight. Since the LiCOR meter measures photosynthetically available radiation in the visible spectral region (400 to 700 nm), the values given below (e.g., Fig. 4) represent the visible fraction of moonlight.

The action spectra were deduced by monitoring the effect of actinic monochromatic light as a function of wavelength. At a given wavelength, λ, the action of light is defined by a product of PFD and the photoreception absorption cross section, σ, at this wavelength. We define the action spectrum as the wavelength dependence of the absorption cross section, i.e., $\sigma(\lambda)$. For each λ, we determined the level of PFD(λ) at which the steady-state level of polyp retraction was the same (ca. 30% decrease in the scattering signal, level C in Fig. 2). This control level of polyp contraction was chosen for the maximum achievable precision of the measurements. After reaching the steady state at each PFD level, the scattering signal was averaged over 10 to 15 min (Fig. 2). Assuming $\mathrm{PFD}(\lambda) \times \sigma(\lambda) = constant$ in the process, the

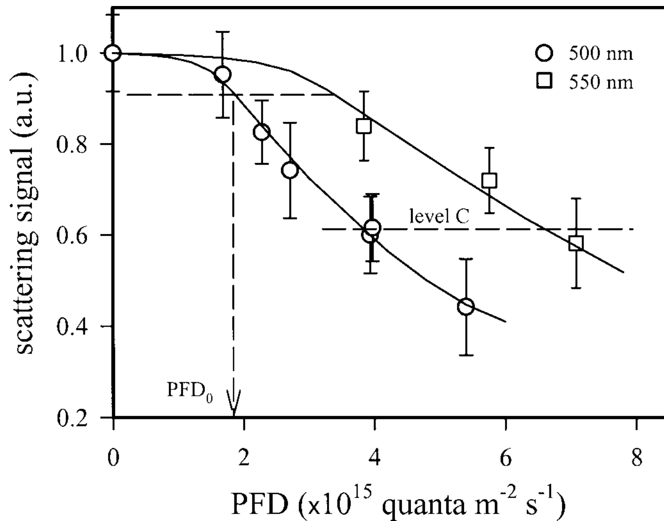

Fig. 2. The effect of monochromatic actinic light (wavelength 500 nm and 550 nm) on the steady-state level of polyp retraction in the coral *E. fastigiata.* As the photon flux density (PFD) of actinic light increases, the laser-induced scatter signal decreases, indicating that polyps become more retracted. When the wavelength of actinic light changes from 500 nm to 550 nm, a higher PFD is required for the same level (e.g., "level C") of polyp retraction to be achieved, suggesting a proportional lower absorption cross section of photoreception. At a given wavelength, the threshold of photoreception is defined as the level of photon flux density (PFD_0), at which the measured scatter signal deviates from the dark level by the value of its standard deviation.

action spectrum $\sigma(\lambda)$, in arbitrary units, was calculated as the reciprocal of PFD(λ). To avoid influence on polyp expansion by experimental artifacts, reference measurements at the wavelength of 500 nm were used to bracket the measurement at any other wavelength. When the two reference measurements did not coincide (presumably because of the impact of a circadian rhythm), the data were not included in the analysis. Following each light stimulus, samples were dark-adapted until the polyps were fully extended (~20–30 min). Each sample was tested at all wavelengths at least once; the wavelengths were chosen in random order.

Results—Under our experimental conditions (fixed flow rate and apparently constant particle abundance in the flow), expansion/retraction of polyps was primarily driven by the level of ambient light. During the photophase, polyps were retracted, but they rapidly became extended in a darkened aquarium. At night, polyps were normally extended, but illumination induced retraction. After the dark–light shift, the polyp retraction followed a 2 to 3 min time lag and reached a plateau within ca. 10 min in *E. fastigiata* and ca. 40 min in *M. cavernosa* (Fig. 3). The reciprocal polyp expansion in darkness exhibited similar kinetic parameters (Fig. 3); however, after exposure to bright light (>ca. 2×10^{19} quanta m^{-2} s^{-1}), it usually took more than an hour of darkness for the polyps to become fully extended (not shown), presumably because of saturation of the photoreceptor cycle.

Threshold of photoreception sensitivity—The behavioral response occurred under extremely low levels of irradiance, suggesting a very low threshold of photoreception sensitivity. In all studied corals, the characteristic change in the laser-induced signal was detectable under actinic blue-green light with PFD of 1.2×10^{15} quanta m^{-2} s^{-1} to 2.5×10^{15} quanta m^{-2} s^{-1}, which is comparable to the photon flux density levels of moonlight.

The low threshold of photoreception sensitivity prompted us to investigate whether natural moonlight is capable of influencing the state of polyps in corals. We chose the coral *E. fastigiata* for most experiments under natural moonlight because it exhibited the fastest response. These experiments were conducted in an outside aquarium exposed to natural moonlight. We discovered that full moonlight also stimulated minute polyp contractions, as evidenced from the light-induced decrease in the scattering signal (Fig. 4). Although invisible with the naked eye, this response was readily detectable using a sensitive laser-induced signal (Fig. 4). The change in the signal observed under the shift from moonlight to darkness and vice versa was statistically significant (*t*-test, $P < 10^{-5}$) and consistently observed in three samples of *E. fastigiata* during several nights under the full moon. In other corals, such as *M. cavernosa* and *M. areolata,* the moonlight also stimulated a change in the laser-induced signal. However, the slow kinetics of polyp expansion and retraction did not allow us to accumulate plausible statistics for these species. The observed behavioral response under variations in moonlight clearly indicates that the threshold of photoreception sensitivity is low enough for the corals to sense natural moonlight.

Action spectra—The action spectra of photoreception sensitivity are presented in Fig. 5. Within the precision of the measurements, the experimental points are well fitted with Dartnall nomograms (Dartnall 1953). The analysis revealed that the spectra have a maximum sensitivity at a wavelength of ca. 480 nm with a half-width of ca. 110 nm (Fig. 5). In other corals, *M. areolata* and *Diploria,* polyp retraction was also induced only by light <600 nm (not shown). Within the precision of the measurements, the spectra obtained for *E. fastigiata* and *M. cavernosa* are not significantly different (Fig. 5) and are remarkably similar to the absorption spectra of rhodopsins isolated from a number of marine invertebrates (Brown and Brown 1958; Hubbard and St. George 1958; Hara and Hara 1965; Cronin and Forward 1988). Invertebrate rhodopsins have been isolated from complex eyes capable of imaging; such organs are absent in Anthozoa.

Since polyp retraction in corals and sea anemones may be mediated, at least indirectly, by the production of photosynthetic products by zooxanthellae (Sebens and DeRiemer 1977; Shick and Brown 1977; Lasker 1979), we examined whether there is a correlation between the observed polyp retraction and photosynthesis. Specifically, we measured in detail the effect of red light with a wavelength of 660–670 nm (the maximum of the chlorophyll Q_y absorption band) on the state of polyps. Within the range of applied PFD (1.2×10^{15} to 5×10^{18} quanta m^{-2} s^{-1}), we did not detect any polyp contraction under the exposure to the red light. A calculation of effective cross sections (σ) revealed that it is at least three orders of magnitude lower at 670 nm than at 480 nm.

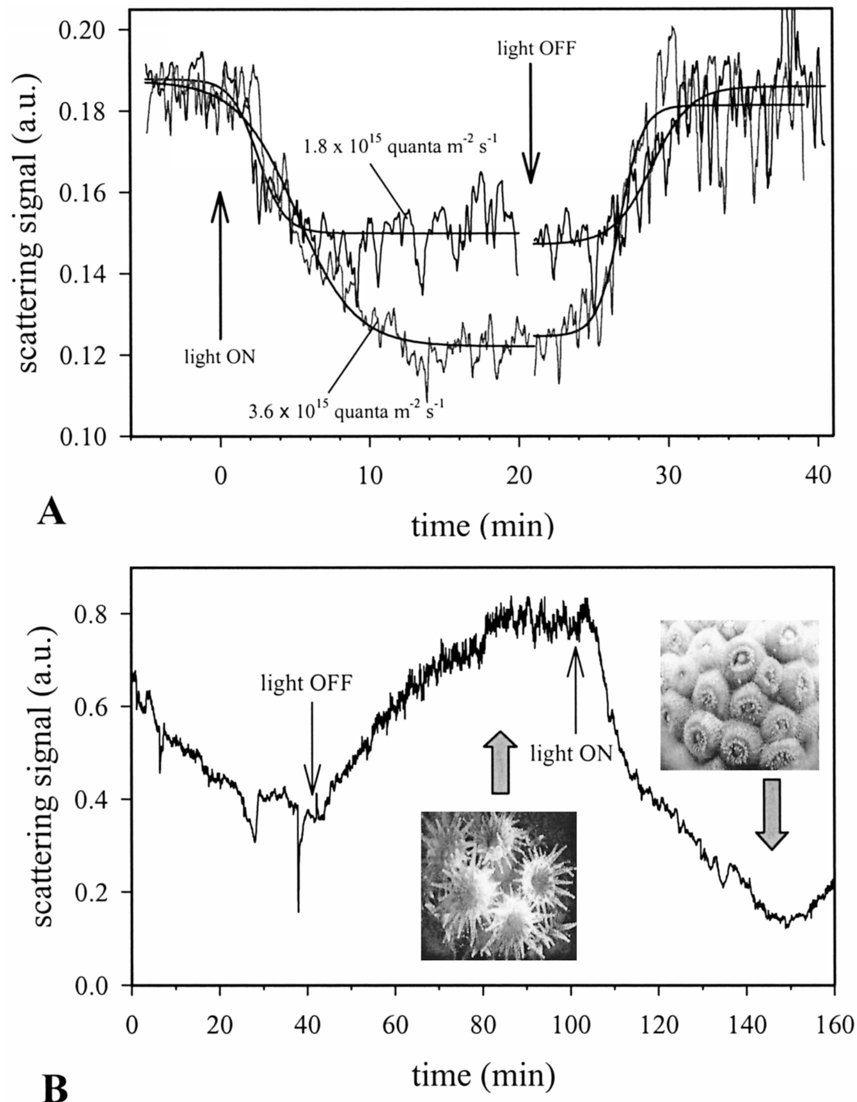

Fig. 3. Kinetics of the laser-induced scattering signal that characterizes polyp retraction/expansion under turned on/off actinic light (wavelength 480 ± 20 nm). The profiles were recorded in the corals (A) *E. fastigiata* and (B) *M. cavernosa.* Rapid random variations in the signal are due to the inherent movement of extended tentacles, whereas a long-term decrease in the signal is a consequence of tentacle retraction. The images of the coral, *M. cavernosa,* were recorded by a compact video camera interfaced to a frame grabber as described by Gorbunov et al. (2000).

Distribution of photoreception cells—To identify location and distribution of photosensitive cells in corals, we used a collimated (1 to 5 mm diameter) beam of light, emitted by a blue light-emitting diode (Nichia Chemical Industries, NLPB500, maximum emission at 460 nm, 30 nm bandwidth) with an incorporated iris and a collimating lens. The peak PFD, provided by the beam on the target, was $\sim 5 \times 10^{17}$ quanta m^{-2} s^{-1}. This light source allowed for an individual polyp tentacle or its small part to be illuminated. In the corals *M. cavernosa, E. fastigiata,* and *M. areolata,* selective illumination of any individual polyp tentacle led to its retraction, thereby leaving all other tentacles unaffected. Furthermore, illumination of a small portion of a long tentacle caused this part to retract until it was outside of the beam. On the other hand, illumination of the mouth or the base of polyps had no visible impact on polyp tissue expansion. By illuminating different parts of tentacles with a collimated light beam, we deduced that the photoreceptive cells are distributed uniformly in polyp tentacles.

Discussion—The spectral sensitivities of light receptors in marine invertebrates have classically been determined by three principal methods: (a) measurement of the action spectra for photoresponses, (b) measurement of an electrical response in individual cells, and (c) measurement of the absorption spectra of isolated photoreceptors or intact photosensitive cells (for a review, *see* Cronin 1986). The first permits elucidation of a receptor via a behavioral response without a priori knowledge of where the photosensitive cells are localized. Using this approach, we made, to our knowl-

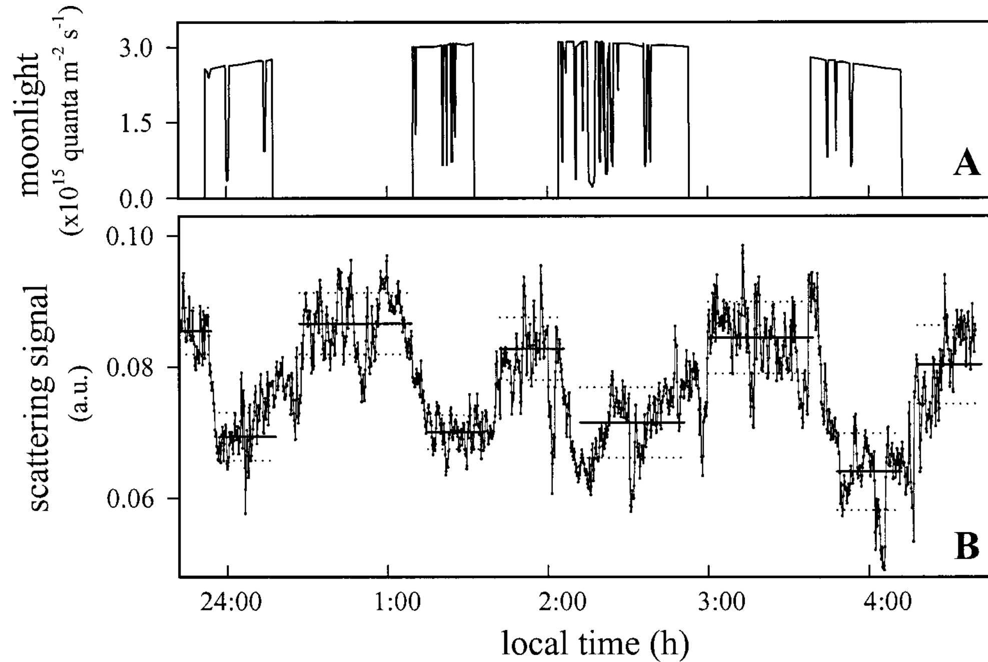

Fig. 4. The effect of variations in natural moonlight on the state of polyps in the coral *E. fastigiata.* The measurements were made under full moon. (A) Variations in the PFD of moonlight during the experiment. The short-term variations in PFD were caused by clouds passing across the sky. Long (~h) periods of darkness were simulated by screening the aquarium. The PFD of the background sky was ~3 orders of magnitude lower than that of the full moon. (B) In the dark, the laser-induced scattering signal was maximal, indicating that polyps were fully extended. The moonlight stimulated minute retraction of polyps, leading to a decrease in the scattering signal. Rapid drops in the signal are due to contractions of individual polyps when they capture particles from the flow. Means ± standard deviations are plotted for each dark/light period.

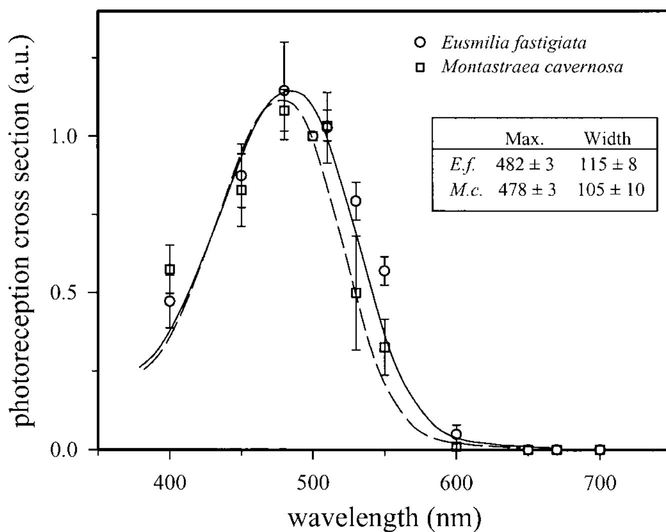

Fig. 5. Action spectra of photoreception, measured in the corals *E. fastigiata* and *M. cavernosa.* Data points and vertical lines are means ± standard deviations ($n = 3$ to 5 at each wavelength). Lines are fitted Dartnall nomograms. The calculated peaks of the spectral sensitivity and the spectral half band widths (both in nanometers) for the two corals are shown in the insert.

edge, the first determination of the action spectra and sensitivity threshold of low-light reception in symbiotic corals.

Our results clearly suggest that the low-light reception in corals is not related to the photosynthetic activity of zooxanthellae. First, if the photoreception would be mediated, at least in part, by photosynthesis, its spectral response should include the regions of absorption by photosynthetic pigments. This is clearly ruled out by the absence of the response at the long-wavelength maximum (670 nm) of chlorophyll *a* absorption (Fig. 5). Second, the threshold of photoreception is two orders of magnitude lower than photon fluxes needed to maintain photosynthetic electron flow. In oxygenic photosynthesis, electrons and protons are extracted from water by a four-electron/four-quanta coupled oxidation reaction (reviewed by Ananyev et al. 2001). The linear electron flow and the formation of a pH gradient across the thylakoid membrane require that the rate of quanta absorbed by photosystem II (PSII) exceeds the rate of back reactions in the water-oxidizing complex. The rate of quanta absorbed and subsequently used in PSII is estimated from measured photosynthetic parameters as follows (adapted from Kolber and Falkowski 1993):

$$P_e = F\sigma_{PSII}F_v/F_m$$

where σ_{PSII} is the functional absorption cross section of PSII and F_v/F_m is the quantum yield of primary charge separation. Given a typical value of σ_{PSII} and F_v/F_m for zooxanthellate

corals (≈400 Å^2 and ≈0.4, respectively, Gorbunov et al. 2000), a photon flux with the density of 1.2×10^{15} quanta m^{-2} s^{-1} produces $P_e \approx 2 \times 10^{-3}$ s^{-1}, i.e., one electron per 500 s. This interval between absorbed photons is more than an order of magnitude longer than that of the longest lived intermediate redox state of the water-oxidizing complex (Falkowski and Raven 1997). While we do not have direct measurements of the effective absorption cross sections of photosystem I, chlorophyll/P700 ratios in zooxanthellae (Falkowski and Dubinsky 1981) predict that these are similar to the cross sections of PSII. As a consequence, in zooxanthellate corals the ΔpH-induced changes in fluorescent and photosynthetic yields are only detectable at photon flux densities $\gtrsim 10^{17}$ quanta m^{-2} s^{-1} (Gorbunov et al. 2001), which are two orders of magnitude higher than the photon flux densities of moonlight. Finally, in the corals *M. cavernosa* and *E. fastigiata,* the photoresponse is observed under illumination of tentacles lacking zooxanthellae and is absent under direct excitation of zooxanthellae-rich parts (polyp mouth and base) of the corals. The distribution of photosensitive cells in areas lacking zooxanthellae clearly suggests that photoreception is provided through a sensor in invertebrate host cells.

The spectral sensitivity of coral photoreception resembles that of deep-sea marine invertebrates (Denys and Brown 1982; Frank and Widder 1999; Partridge 1999), including various zooplankton (Forward 1988) and crabs (Cronin and Forward 1988). The maximum photoreception matches the maximum transparency of oligotrophic tropical waters (Jerlov 1968), thus optimizing the perception of low light at depth. This is formally referred to as the sensitivity hypothesis, which states that the spectral position of photosensitivity is matched to the spectral distribution of light in an animal's environment (Munz 1958).

Photosensitivity in the phylum Cnidaria is characterized by two types of sensors: extraocular photoreceptors and ocelli (Burr 1984; Taddei-Ferretti and Musio 2000). Both types are found in several medusae and jellyfish (for a review, *see* Burr 1984), but extraocular photoreceptors appear to be the only type of photosensors in Anthozoa. Medusa photosensitivity is maximal at 480–550 nm and has a half band width of ca. 200 nm (Weber 1982; Arkett 1985), which is nearly twice as wide as that of coral action spectra. The spectral shift to the green may reflect the medusa photoreception accommodating to the green light that dominates the eutrophic coastal waters, while the wide spectrum may be indicative of several spectrally distinct visual pigments. The position of the rhodopsin absorption peak varies significantly (e.g., *see* Stawenga and Schwemer 1984). It covers virtually the whole visible and near-UV region and provides the basis for color discrimination, but the spectral half band width of individual receptors is highly conserved, averaging 100 to 115 nm. Although the biochemical identity of the photoreceptors in corals remains unknown, the striking similarity of the action spectra of coral photoreception (Fig. 5) to the absorption spectrum of rhodopsins isolated from marine invertebrates raises the possibility that corals may have rhodopsin-like photoreceptors. Although the presence of several spectrally distinct photoreceptors cannot be ruled out, the narrow action spectrum implies that low-light photoreception may be mediated by a single spectral pigment, which provides maximum sensitivity, but with a reduction in color discrimination. Thus, coral photoreceptors may represent an early stage in the ciliary line of photoreception evolution, from scattered photosensitive cells toward organized photosensitive organs.

A large number of reef creatures are only active at night. Light-driven expansion/retraction rhythms are typical for many of these organisms, including corals (Abe 1938; Kawaguti 1954; Lewis and Price 1975; Lasker 1979), gorgonians (Wainwright 1967), and sea anemones (Gladfelter 1975; Sebens and DeRiemer 1977); however, the pattern of this behavior varies between species. Diurnal expansion is observed in corals and anemones that exhibit high densities of zooxanthellae in the tentacles (Kawaguti 1954; Gladfelter 1975; Sebens and DeRiemer 1977). This stimulates photosynthetic production by enhancing the gas exchange and increasing the availability of light to zooxanthellae (reviewed by Falkowski et al. 1990). In contrast, nocturnal expansion is generally observed in species having tentacles that contain no or few zooxanthellae (Kawaguti 1954; Sebens and DeRiemer 1977). In these organisms, the diurnal retraction of tentacles may reduce the self-shading effect, thus increasing photosynthetic light absorption and use. The nocturnal expansion of corals and sea anemones has traditionally been related to the increased availability of prey at night, while their diurnal retraction has been related to the increased grazing by reef fish during the day. The presence of sensitive photoreceptors in polyp tentacles implies that the light-stimulated retraction may also protect them against photodamage as it protects zooxanthellae in intertidal corals against photoinhibition (Brown et al. 1994). Additionally, the nocturnal expansion of photoreceptor-rich tentacles minimizes shading of photoreceptive cells, thus increasing the efficiency of low-light reception.

Our results are the first evidence showing that moonlight has a direct impact on the morphological state of corals via blue-sensitive photoreceptors in the invertebrate host. These findings have implications for the long-term puzzle on how lunar cycles trigger coral spawning. The majority of coral species spawn in darkness between sunset and moonrise (Babcock et al. 1986), thereby with artificially extended light periods spawning is delayed (Harrison et al. 1984). The spawning appears to be induced after a specific period of darkness, ranging from a few minutes to several hours after sunset (Harrison et al. 1984; Babcock et al. 1986). This period is likely needed for the expansion of polyps to be completed, while the appearance of moonlight prevents the polyp tissue from fully expanding. The sensing system we described must be coupled to a photon counter in order to create a lunar synchronized clock (Jokiel et al. 1985). Such a clock appears to be widely distributed in Metazoans, but its evolutionary origin and biochemical and biophysical mechanisms remain to be elucidated.

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