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The in situ light microenvironment of corals

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Abstract

We used a novel diver-operated microsensor system to collect in situ spectrally resolved light fields on corals with a micrometer spatial resolution. The light microenvironment differed between polyp and coenosarc tissues with scalar irradiance (400–700 nm) over polyp tissue, attenuating between 5.1- and 7.8-fold from top to base of small hemispherical coral colonies, whereas attenuation was at most 1.5-fold for coenosarc tissue. Fluctuations in ambient solar irradiance induced changes in light and oxygen microenvironments, which were more pronounced and faster in coenosarc compared with polyp tissue. Backscattered light from the surrounding benthos contributed > 20% of total scalar irradiance at the coral tissue surface and enhanced symbiont photosynthesis and the local O_2 concentration, indicating an important role of benthos optics for coral ecophysiology. Light fields on corals are species and tissue specific and exhibit pronounced variation on scales from micrometers to decimeters. Consequently, the distribution, genetic diversity, and physiology of coral symbionts must be coupled with the measurements of their actual light microenvironment to achieve a more comprehensive understanding of coral ecophysiology.

The quantity and quality of light is one of the most important environmental factors affecting the ecology of reef-forming symbiont-bearing corals (Dubinsky et al. 1984; Falkowski et al. 1990; Iglesias-Prieto et al. 2004). Light drives photosynthesis of the endosymbiotic dinoflagellate microalgae of the genus *Symbiodinium* that are known as zooxanthellae and are harbored within the tissue of the cnidarian animal host. The coral host provides a protected environment for its symbionts with limited but constant nutrient availability in oligotrophic marine waters. Zooxanthellae photosynthesis generates O_2 and photosynthates that provide the coral host with organic carbon that can support > 95% of its respiratory demand (Muscatine et al. 1981). Although zooxanthellate corals are dependent on sufficient light for photosynthesis, high solar radiation during summertime in shallow waters can be stressful and cause the breakdown of symbiosis through symbiont expulsion or degradation, leading to visible paling of the colony (i.e., coral bleaching; Glynn 1996; Hoegh-Guldberg 1999). Various physiological aspects of light harvesting and light-related bleaching have been intensively studied over the past decades. However, a detailed understanding of the actual light field experienced by the photosymbionts in the coral tissue is limited, although such knowledge is a prerequisite for a better understanding of coral photobiology (Falkowski et al. 1990; Iglesias-Prieto and Trench 1994; Lesser and Farrell 2004) and ecophysiology (Rowan et al. 1997).

Solar radiation takes many detours until it reaches the tissue surface of a coral on a natural reef (Kirk 1994). The initial interaction of sunlight that has passed through the atmosphere is largely determined by the refractive index difference between air and seawater, causing refraction and reflection of incident radiation at the air–water interface. Light that has entered the water column undergoes scattering and absorption, which is caused by the inherent optical properties of the water and a major contribution of dissolved substances and solid particles (e.g., dissolved organic matter, plankton, suspended sediment, etc.; Kirk 1994). The quantity of downwelling irradiance reaching a coral reef at a certain depth could in principle be calculated by the spectral attenuation coefficient of the given overlying water mass, which would give a macroscale (i.e., meters to kilometers) approximation of irradiance over the area of interest (Kirk 1994).

However, for a given coral reef, irradiance is highly variable in both space and time. On a spatial scale, strong meso- (millimeter to meter) and microscale (micrometer to millimeter) light–matter interactions alter the light availability and quality for photosynthetic reef organisms (Anthony and Hoegh-Guldberg 2003). Over time, irradiance varies on scales ranging from yearly down to the smallest scales of milliseconds (Kirk 1994; Darecki et al. 2011). Optical phenomena such as wave focusing can be an important source of variability in the underwater light field causing light flashes of high amplitude and frequency (Stramski and Dera 1988). Especially in shallow-water environments, such as on coral reefs, wave focusing can induce light flashes at frequencies of > 100 times per

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minute with maximal amplitudes exceeding the mean irradiance by more than fivefold (Darecki et al. 2011).

Studies dealing with the mesoscale light distribution on coral reefs show that reef structures such as crevices and topographic elevations are important sources of variability in the diffuse light component present within the coral reef framework (Brakel 1979; Stimson 1985; Anthony and Hoegh-Guldberg 2003). Also, characteristic features of the colony morphology (e.g., colony shape, branch length, spacing, etc.) cause significant light attenuation and redistribution within a single coral colony (Helmuth et al. 1997; Anthony et al. 2005; Kaniewska et al. 2011). For instance, Kaniewska et al. (2011) showed that the incident downwelling irradiance measured above the coral tissue surface varies about one order of magnitude from the tip toward the base of a branch in the coral *Stylophora pistillata*. Although these mesoscale studies have given valuable insights, there are two major shortcomings with regard to their relevance for microalgal physiology.

Previous in situ studies have mainly quantified available light in terms of the incident downwelling irradiance (E_d). This parameter quantifies the downwelling quantum flux from the upper hemisphere through a horizontal surface area and does not take backscattered light into account. However, light from all directions can be used for microalgal photosynthesis; thus, E_d measurements generally underestimate the light available for symbiont photosynthesis in hospite (Kühl et al. 1995). A more appropriate parameter for quantifying light exposure relevant for microalgal photosynthesis is scalar irradiance, which is a measure of the total radiant flux from all directions around a point (Kühl et al. 1995).

All in situ light field studies on corals have used sensors that detect light variation only on a macro- or mesoscale. However, recent laboratory studies have revealed that tissue and skeleton optics strongly alter coral light fields on a microscale (Enriquez et al. 2005; Wangpraseurt et al. 2012*a*; Marcelino et al. 2013).

Light is strongly scattered at the water–tissue interface and within the coral tissue, where photon trapping and redistribution leads to significant enhancement in the local scalar irradiance compared with the incident downwelling irradiance (Kühl et al. 1995; Wangpraseurt et al. 2012*a*). Light that has entered the tissue can be transferred laterally, most likely through anisotropic scattering (Wangpraseurt et al. 2014). Additionally, reflective, fluorescent, or both host pigments are synthesized by many corals, which further alters the intensity and spectral quality of light due to, for example, intense scattering and red-shifted emission (Salih et al. 2000). Finally, photons that pass through the tissue are backscattered by the aragonite skeleton, further enhancing tissue scalar irradiance and thus photon availability for zooxanthellae photosynthesis (Enriquez et al. 2005; Marcelino et al. 2013). On a microscale, light is thus strongly affected by the inherent optical properties of corals, which can vary between coral species depending on their skeletal microstructure, tissue types, and degree of polyp contraction and expansion (Wangpraseurt et al. 2012*a*; Marcelino et al. 2013; Yost et al. 2013). Microscale light–tissue interactions can thus not be neglected if one aims at a detailed understanding of coral photobiology (Wangpraseurt et al. 2014).

The assessment of microscale optics in corals in their natural habitats has until now been limited by the lack of suitable technology, making it impossible to examine the relationships between the macro-, meso- and microscale light distributions in coral reefs. To bridge this gap, we developed here a submersible, fiber-optic–based spectrometer module that can be connected to a diver-operated microsensor system (Weber et al. 2007) to measure the first spectrally resolved in situ microscale light measurements in corals. We used this instrument to study in situ spectral scalar irradiance at the coral tissue surface of various massive faviid corals and one branching acroporid. We compared the attenuation of light in a coral colony from top to base, focusing on differences between coenosarc and polyp tissues. Additionally, we quantified the contribution of the benthos surrounding the coral to the local scalar irradiance at the coral surface and assessed its role in coral photosynthesis. We discuss our results in the context of microenvironmental controls of coral function and *Symbiodinium* ecophysiology.

Methods

Study site and coral species—In situ microsensor measurements were taken in November 2012 on the shallow reef flat next to the Heron Island Research station (152°06′E, 20°29′S), Southern Great Barrier Reef, Australia. Measurements were performed between 09:00 h and 17:00 h at water depths ranging from 0.5 to 2.5 m (as measured from the benthos to the water surface). Low and high tide measurements were taken by snorkeling and SCUBA diving, respectively.

Massive corals of the family Faviidae (*Goniastrea aspera, Platygyra lamellina, Favites pentagona*) were chosen because of their microscale tissue optical properties, as previously measured with microsensors under laboratory conditions (Wangpraseurt et al. 2012*a*). The branching *Acropora millepora* specimens were additionally selected to compare light attenuation over massive corals with the more pronounced light attenuation known to occur in branching growth forms (Kaniewska et al. 2011).

Underwater microsensor system—Ambient scalar irradiance of photosynthetically active radiation (PAR, 400–700 nm) was measured with a miniature scalar irradiance sensor (3 mm diameter; Walz GmbH) connected to an underwater microsensor meter (UnderWater Meter system, Unisense A/S). Spectrally resolved scalar irradiance was measured with a fiber-optic scalar irradiance microsensor prepared as previously described (Lassen et al. 1992). The microsensor had a spherical light-collecting tip with a diameter of $\sim$ 80 μm and an isotropic angular response. Both sensors were linearly calibrated against a calibrated spherical quantum sensor (US-SQS/L, Heinz Walz GmbH) connected to a PAR light meter (Li-250A, Li-COR); equipment calibration took place at midday in a white seawater-filled container. The sensors were aligned next to each other (2–3 cm distance) and submersed in the

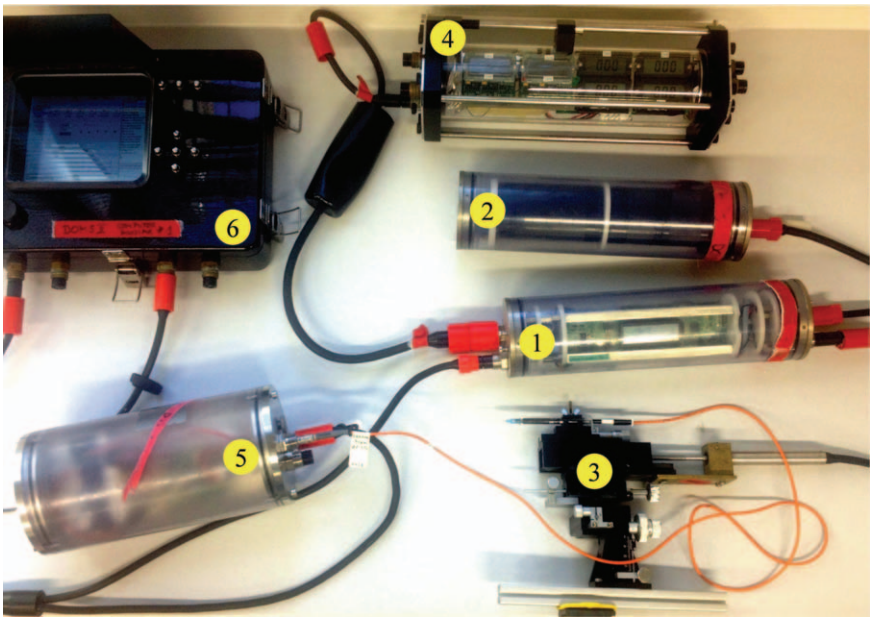

Fig. 1. Diver-operated microsensor system (DOMS) with (1) the measurement control and data storage module, (2) the battery, (3) the motorized micromanipulator equipped with the spectral scalar irradiance microsensor (orange fiber), (4) the commercial underwater PAR meter, (5) the underwater module containing the Ocean Optics spectrometer, and (6) the underwater personal computer module. Modules (1–3) were part of the original design developed by Weber et al. (2007); modules (5 and 6) were designed and developed during this study.

container (depth of ~ 15 cm) such that the angle between the sun and the sensor axis was 45°. Subsequently, the sensor readings were taken at 50% and 100% solar radiation (blue sky), the former achieved by a neutral density filter with 50% transmittance.

Oxygen measurements were made with a Clark-type O_2 microsensor (Revsbech 1989). The sensor had a tip diameter of ~ 50 μm, response time of < 2 s, and stirring sensitivity of < 1.5% and was adapted for underwater use as previously described (Wangpraseurt et al. 2012*b*). Linear calibrations before and after each dive were done using readings in air-saturated and anoxic seawater, the latter achieved by flushing with N_2 gas.

In situ microsensor measurements were performed using a diver-operated motorized microsensor (DOMS) profiler operated as previously described (Weber et al. 2007). The O_2 microsensor and the PAR minisensor meter were connected to the analog inputs of the DOMS, whereas the fiber-optic–based scalar irradiance microsensor was connected to a separate water-proof module. This module contained a spectrometer (USB 4000, Ocean Optics) and a custom-made board that allowed acquisition and storage of spectra at time intervals of 1 s or more, as triggered by a digital signal provided externally by the DOMS (Fig. 1). The integration time intervals of the spectral acquisition were adjusted interactively during the measurements to optimize the dynamic range of the sensor. The spectral signal output was followed during the measurements via a custom-made underwater PC module (Fig. 1). At the end of each deployment, the raw spectral data were read out via a custom-built circuit connected to a computer and processed as described below.

In situ measurements of the scalar irradiance distribution—To identify differences between coral species and different tissue types with respect to their light microenvironment, spectral scalar irradiance was first measured on the upper light-exposed surface of the corals and compared with the incident downwelling spectral irradiance (Fig. 2a). This was done for coenosarc and polyp tissue of each of the three massive faviid corals (*P. lamellina*, *F. pentagona*, and *G. aspera*). For each measurement, the microsensor was carefully positioned at the corresponding tissue surface with the aid of a magnifying glass. The angle between the sensor and the coral–sun line was 45° to avoid self-shading. Scalar irradiance spectra were recorded in 5 s intervals over a period of 0.5–1 min and averaged. The incident downwelling spectral irradiance (E_d) was determined by measuring the signal above a black nonreflective surface next to the coral at approximately the same height as the coral measurement spots; this was done for each coral after the microscale scalar irradiance mapping (every 20 min).

To quantify the distribution of light at the coral surface over a larger scale, spectral scalar irradiance was additionally mapped from top to bottom of the coral colonies at three or four positions over the coral colony (Fig. 2b) and for each position over one coenosarc and one polyp tissue area. During all measurements, the ambient PAR photon scalar irradiance next to the coral was monitored using the miniature spherical PAR sensor, arranged in the same direction and at about the same height as the scalar irradiance microsensor. These data were used to account for small variations (generally < 10%) in the ambient light field by multiplying the values measured with the light

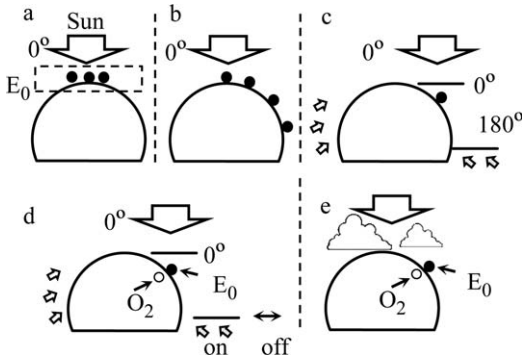

Fig. 2. Schematic representation of measurement geometry for (a) upper surface mapping of different faviid coral species, where E_0 was measured exclusively at the upper light-exposed surfaces for coenosarc and polyp tissue ($n = 3$). (b) Colony surface mapping, where E_0 was mapped from top to base around the colony; one coenosarc and polyp tissue area were mapped each. (c) Contribution of direct (0° zenith angle) and indirect light (180° zenith angle) to E_0 measured at ~ 45° from hemispherical colony center (around 5 cm from the benthos). We used a black cloth to block out light from the different zenith angles. (d) Microscale O_2 and E_0 measurements following repeated darkening of the sediment benthos. (e) Temporal O_2 and E_0 dynamics on polyp and coenosarc tissue measured on a cloudy day. The hemisphere represents the idealized structure of the massive faviid corals. The thick arrow represents the incident solar radiation (at 0° zenith angle, or varying angles over time if not specified), and the small white arrows represent indirect, diffuse light. Black and white dots show relative measurement positions of tissue scalar irradiance E_0 and O_2 concentration, respectively.

microsensor on the coral with the factor by which the ambient light field had changed.

Effect of backscattered light on coral light and O_2 microenvironments—The relevance of diffuse light for scalar irradiance and O_2 levels at the coral tissue surface was studied for *G. aspera*. The scalar irradiance and oxygen microsensors were positioned on the tissue surface close to each other, both oriented at an angle of 45° relative to the coral–sun line. The measured locations were on a coral surface oriented at about 45° relative to the benthos surface and about 5 cm away from the benthos. Subsequently, a thick black cloth (0.5 × 0.5 m) was placed above the coral or above the benthos next to the coral to block, respectively, the direct sunlight or backscattered light from the benthos (Fig. 2c,d) while measuring the scalar irradiance and oxygen concentrations. Measurements were done at solar noon on both coenosarc and polyp tissues. During all measurements, the ambient PAR was recorded to ensure comparable ambient irradiance regimes.

In situ dynamics of microscale scalar irradiance and O_2—Using the same arrangement of microsensors as above, spectral scalar irradiance and O_2 concentrations in coenosarc and polyp tissues of *F. pentagona* were monitored continuously during early afternoon on a partially cloudy day. Ambient scalar irradiance was recorded during all measurements.

Data analysis—Data were analyzed with routines written in Matlab (MathWorks, version 2012a). Spectral data were either normalized to the incident downwelling irradiance or converted to photon spectral scalar irradiance (μmol photons m^{-2} s^{-1} nm^{-1}). The latter conversion involved two steps. The raw USB4000 spectrometer data was corrected for spectral sensitivity (μmol photons $count^{-1}$), based on sensitivity data acquired previously (Finke et al. 2013) using a calibrated spectrometer (Jazz, Ocean Optics). The spectra acquired during the calibration experiment (*see* above) were then integrated over wavelengths in the PAR region and plotted against the corresponding output of the PAR sensor. This resulted in a calibration line whose slope was subsequently used to convert all spectral sensitivity–corrected spectra to micromole photons per square meter per second per nanometer (μmol photons m^{-2} s^{-1} nm^{-1}). When relevant, spectra were also integrated over the 400–700 nm wavelength range to quantify the total photon scalar irradiance of PAR.

Results

In situ spectral scalar irradiance at the upper surface of faviid corals—Spectral scalar irradiance at the upper surfaces of faviid corals (E_0) differed markedly from the incident downwelling irradiance (E_d; Fig. 3). Depending on the wavelength in the PAR region, the $E_0 : E_d$ ratio varied between 0.8 and 2.4, with the most pronounced enhancement at wavelengths 500–640 nm and > 680 nm (Fig. 3a–c). Coenosarc and polyp tissues had characteristic spectral signatures, which differed between the studied coral species (Fig. 3a–c). Contributions of fluorescent host pigments could be clearly seen in the scalar irradiance spectra of the polyp tissue in *P. lamellina* and *F. pentagona* (arrows in Figs. 3a, 1c). Light in the far-red region (685–700 nm) was enhanced by about 40% and 80% in the polyp tissue compared with coenosarc tissue in *F. pentagona* and *P. lamellina*, respectively, whereas such enhancement was not present in *G. aspera*.

The relative enhancement of integrated PAR (400–700 nm) differed at the tissue surface between coral species and tissue types (Fig. 3d). For instance, for *P. lamellina*, PAR was enhanced by about 36% in polyp tissue compared with 15% in coenosarc tissue, whereas this trend was reversed for *G. aspera* (42% in coenosarc vs. 6% in polyp).

Light distribution along colony architecture—Variation of scalar irradiance across massive corals differed strongly between polyp and coenosarc tissues (Fig. 4). While the decrease in scalar irradiance from top to base of the coral colonies was strong at the surface of polyp tissues (up to a sevenfold decrease), for coenosarc tissues the scalar irradiance was fairly homogeneously distributed for *F. pentagona*, decreased up to 1.5-fold for *P. lamellina*, or even increased by about 10% toward the base for *G. aspera*. For the branching species *A. millepora*, scalar irradiance at the tissue surface decreased by about one order of magnitude from the apical tip toward the base of the branch (Fig. 4m–o). For all studied coral species, these trends were similar for all wavelengths in the PAR region.

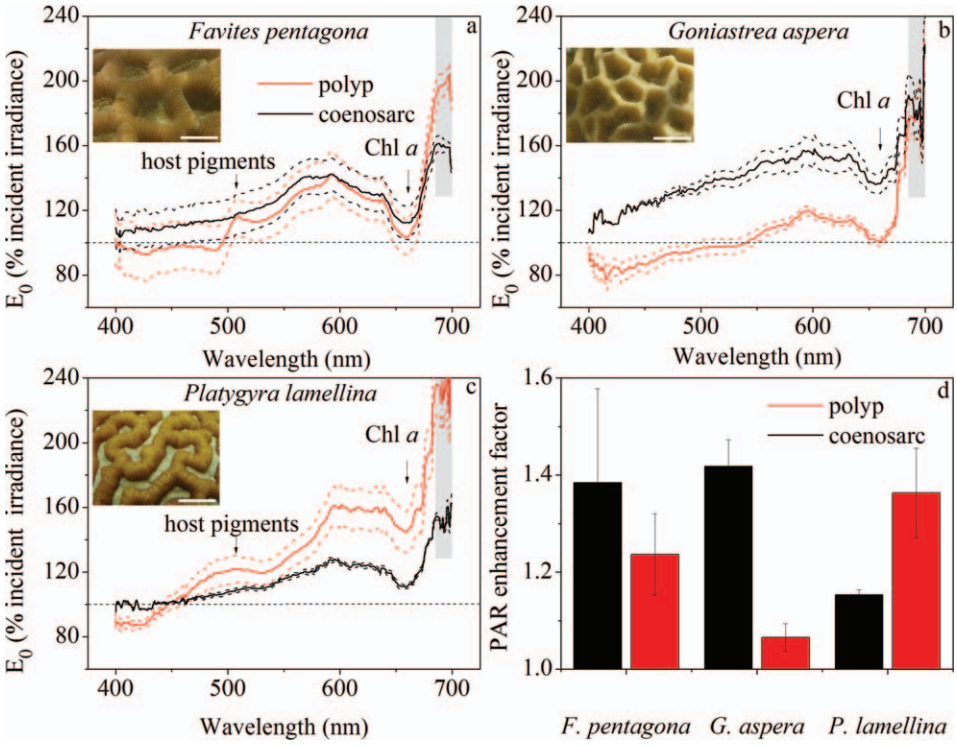

Fig. 3. Microscale spectral scalar irradiance (E_0) measured in situ on the surface of polyp and coenosarc tissues located on the colony top of (a) *F. pentagona,* (b) *G. aspera,* and (c) *P. lamellina*. Measurements were normalized to the downwelling spectral irradiance E_d to allow easier comparison between coral species and tissue types. Solid lines show means (E_0 in percentage of E_d), dashed lines represent mean ± standard error (SE; $n = 3$). Measurements were done around noon when the sun was close to zenith. Insets illustrate the structure of the corals and different coenosarc (black circles) and polyp tissues (red circles; scale bar = 1 cm). Grey areas represent spectral regions where in vivo chlorophyll *a* absorption is insignificant, and thus the scalar irradiance is affected mainly by light scattering on coral skeleton. (d) Photon scalar irradiance integrated over the PAR region (400–700 nm) normalized to the PAR-integrated incident downwelling irradiance ($n = 3$).

Environmental effects of benthos optics on coral light and O_2 levels—For coenosarc tissue located about 5 cm from the benthos and oriented at about 45° relative to the benthos surface, blocking of direct sunlight led to a decrease in the scalar irradiance at the tissue surface by 80–90%, whereas the reduction was 15–20% when the light backscattered from the sediment surrounding the coral was blocked (Fig. 5a). Thus, about 10–20% of the light exposure was perceived as indirect light at the given spot. Simultaneous microscale measurements of spectral scalar irradiance and O_2 revealed that O_2 concentrations at the tissue surface changed immediately on blocking of the light backscattered from the sediment surrounding the coral (Fig. 5b,c), implying that indirect light plays a significant role in coral photosynthesis. For coenosarc tissue, light blocking led to a decrease in local scalar irradiance by 250–500 μmol photons m^{-2} s^{-1} (20–30% of total irradiance) and a corresponding reduction in O_2 concentration by $>$ 25 μmol L^{-1} (i.e., $>$ 12% air saturation; Fig. 5b). The effect was stronger for polyp tissue, where the same blocking decreased the local scalar irradiance by about 50% and led to a decrease in O_2 concentration by $>$ 50 μmol L^{-1} (Fig. 5c). When the sensor was placed toward the top of the coral, those effects were no longer visible (data not shown).

In situ dynamics of light and O_2 on coral surfaces—Simultaneous in situ measurements of O_2 and spectral scalar irradiance at the tissue surface of *G. aspera* revealed highly dynamic microenvironmental conditions (Fig. 6). For coenosarc tissue, O_2 concentrations reached up to 450 μmol L^{-1} (about 200% air saturation) when the tissue surface scalar irradiance was around its peak value of 980 μmol photons m^{-2} s^{-1}. With cloud cover, the tissue surface scalar irradiance dropped within seconds from 950 to 150 μmol photons m^{-2} s^{-1}, resulting in a gradual decrease in O_2 concentrations by about 60 μmol L^{-1} (Fig. 6a).

Maximal O_2 concentrations at the surface of polyp tissue were ~ 25% lower than on coenosarc tissue (350 vs. 450 μmol L^{-1} O_2), consistent with the observed trend for the tissue surface scalar irradiance (compare Fig. 6a and 6b). The O_2 dynamics at the surface of polyp tissue did not closely follow changes in the tissue surface scalar irradiance (Fig. 6a). Interestingly, changes in the scalar irradiance at the surface of polyp tissue appeared somewhat "buffered"

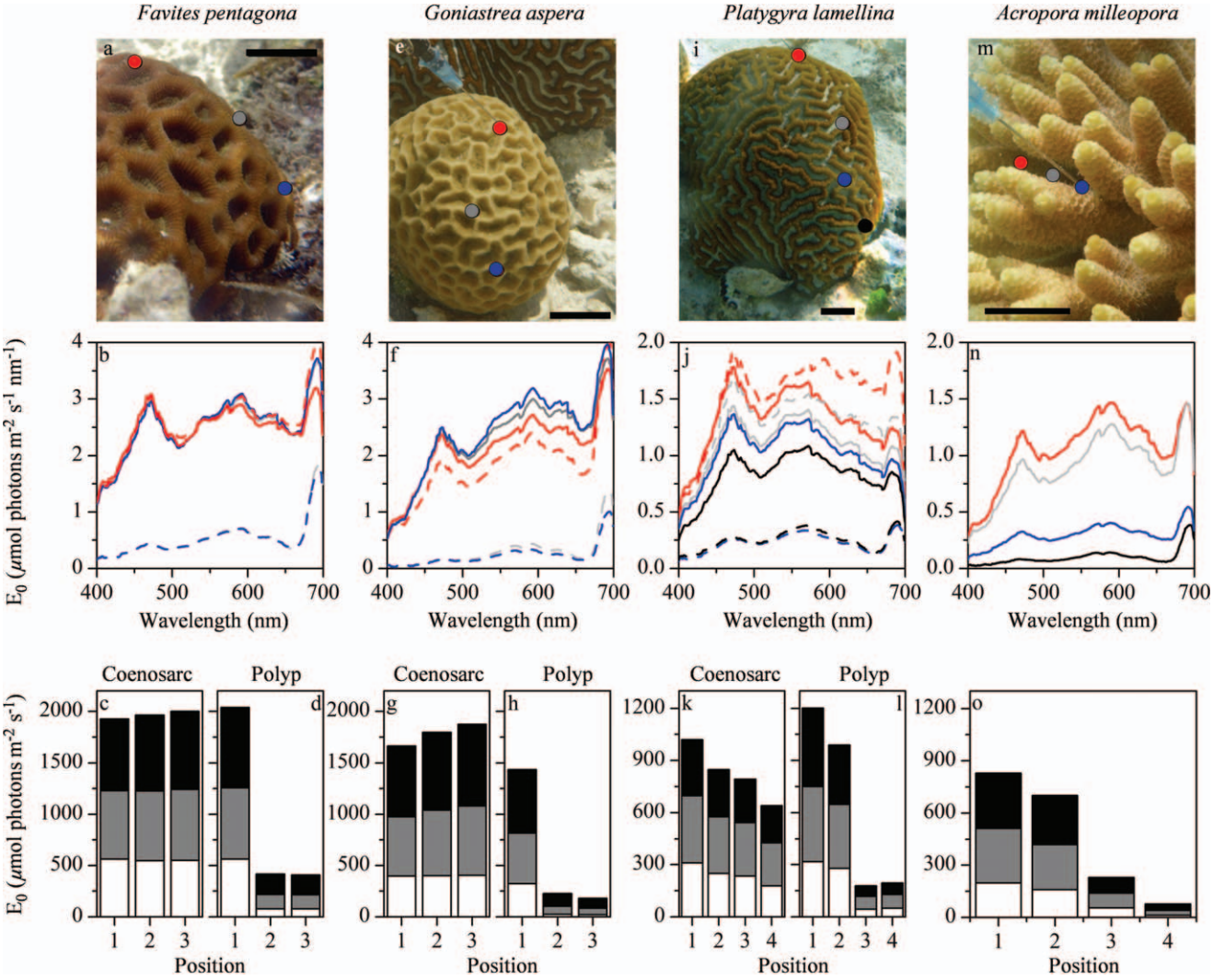

Fig. 4. Macroscale in situ distributions of spectral scalar irradiance over coral colonies and branches measured separately on the surface of polyp (dashed lines) and coenosarc (solid lines) tissues in locations marked by circles in the coral images. For *A. millepora*, polyp and coenosarc were not differentiated because of small polyp size. Also, because position 4 was deeper along the branch of this coral, it is not marked in the image. Bar graphs on the right show scalar irradiance integrated over three wavelength bands in the PAR region (*see* legend in panel O). Note the different *y*-axis scales. During the measurements, the PAR photon scalar irradiance above the sediment next to the coral was 2500 (*F. pentagona*), 2400 (*G. aspera*), 1700 (*P. lamellina*), and 1300 μmol photons m^{-2} s^{-1} (*A. millepora*). Scale bar = 2 cm.

compared with the dynamic changes in the ambient scalar irradiance. For instance, a 4.4-fold decrease in ambient scalar irradiance (from 1750 to 400 μmol photons m^{-2} s^{-1}) led to only a 2.4-fold decrease in scalar irradiance at the polyp tissue (from 126 to 53 μmol photons m^{-2} s^{-1}; Fig. 6b). In contrast, the relative changes in microscale and ambient scalar irradiance were equal for coenosarc tissue.

Discussion

We used a novel diver-operated microsensor system for the first in situ characterization of coral spectral light fields with micrometer spatial resolution. Our study provides evidence for the occurrence of different optical niches in different spatial compartments of corals under natural reef conditions and highlights the importance of microscale optics in controlling coral light exposure.

Photon scalar irradiance of PAR was enhanced over the incident PAR, and the magnitude of light enhancement differed between the investigated coral colonies and their tissue types (Fig. 3). Such modulation of microscale irradiance with respect to incident irradiance is attributable to skeleton- and tissue-type–specific scattering and absorption properties (Wangpraseurt et al. 2012*a*, 2014; Marcelino et al. 2013). For instance, spectral signatures of host pigments in polyp tissue of *P. lamellina* (Fig. 3a,c) likely explained the ~ 20% enhancement of PAR in polyp compared with coenosarc tissue, because fluorescent host pigments around the polyp mouth can scatter light and lead to longer wavelength emission (Salih et al. 2000). Corals

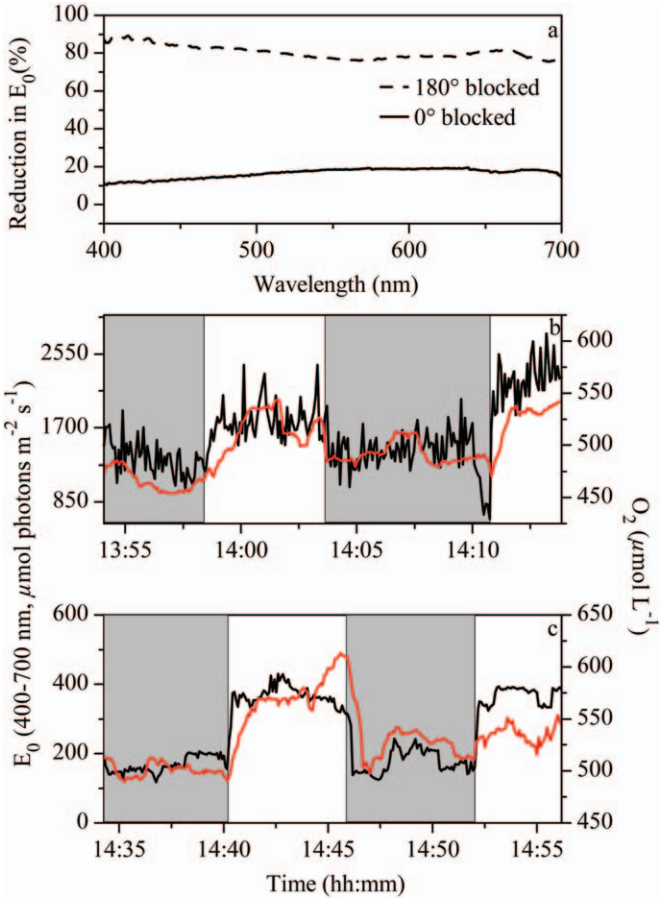

Fig. 5. (a) Spectral scalar irradiance (E_0) was measured when direct light (0° zenith angle) and indirect diffuse light backscattered from the benthos (180° zenith angle) was blocked and is expressed in percentage of the scalar irradiance measured without blocking. Measurements were performed on coenosarc tissue of *Favites pentagona* (*see* Fig. 2 for details of the measurement approach). (b, c) Variation of the local PAR photon scalar irradiance and O_2 concentration induced by artificial blocking of the diffuse backscattered light (indicated by gray areas), as measured at coenosarc (b) and polyp (c) tissue of *G. aspera*. For both measurements, the microsensor tips were about 5 cm from the sediment. The ambient downwelling irradiance remained stable during blocking, as checked by simultaneous light measurements next to the coral.

show a plastic response to the ambient light field by altering pigment content (Dubinsky et al. 1984), tissue structure (Winters et al. 2009), and growth morphology (Muko et al. 2000), all of which will likely affect the optical environment for corals. Therefore, and because our measurements are from a limited number of corals, the absolute values of light enhancement cannot be considered unique to a certain species. However, the observed in situ differences in the coral microscale light field (Fig. 3) suggest that despite identical regimes of incident irradiance, a given symbiont population is exposed to different in vivo light fields as a result of light modulation by the optical properties of the animal host environment and surrounding benthos.

The in situ light distribution around the faviid corals points to a central role of corallite architecture in controlling irradiance levels. Studies on colony-level light redistribution have focused on branching and foliose corals (Helmuth et al. 1997; Hoogenboom et al. 2008) and only recently, a light capture model was developed for a massive coral, but without any support from direct light measurements at the corallite level (Ow and Todd 2010). We show that PAR at the surface of polyp tissue was reduced more than sevenfold from colony top to base during midday, whereas no substantial attenuation occurred over coenosarc tissue (Fig. 4). Light is thus redistributed by the skeleton and efficiently absorbed by adjacent coenosarc tissue, thereby inducing optical micro niches in polyp tissue, even on small hemispherical colonies ($<$ 30 cm) under high solar radiation during midday. The magnitude of light attenuation found on massive corals is similar to the attenuation observed from branch shading in *A. millepora* (Fig. 4) and other branching corals (Kaniewska et al. 2011), supporting the role of tissue optics and corallite architecture in regulating colony-level light capture of massive corals.

We found that diffuse backscattered light from the sediment contributed considerably to the microscale light field of corals (Fig. 5). Light reflection from the reef benthos has previously been proposed to control coral photophysiology (Brakel 1979; Colvard and Edmunds 2012; Fine et al. 2013), but hitherto no quantification of backscattered light effects on local O_2 evolution have been reported. Diffuse backscattering from the reef sediment was found to contribute as much as 10–50% of the total scalar irradiance at the tissue surface, and such diffuse light can stimulate photosynthesis and enhance local O_2 concentrations by $>$ 50 μmol L^{-1} ($\sim$ 25% air saturation; Fig. 5). This identifies a central role of indirect diffuse light on coral reefs. The contribution of indirect light to local irradiance and photosynthesis will depend on the distance and orientation of the coral surface relative to the benthos. Also, backscattering of light from the benthos will differ between benthos types such as sediment (Kühl and Jørgensen 1994), macroalgae (Colvard and Edmunds 2012), and coral types (Marcelino et al. 2013) and will thus likely influence estimates of coral productivity on ecosystem scales.

Coral reef light fields are not static but are modulated by temporal fluctuations in solar radiation that operate on temporal scales ranging from annual (Kirk 1994) to millisecond fluctuations (Darecki et al. 2011). Cloud formation was found to induce fluctuations in light exposure of coenosarc tissue up to sixfold within a minute (Fig. 6a), whereas light fields of polyp tissue were less fluctuating and exhibited an apparent dampening of light fluctuations in relation to shifts in the ambient irradiance (Fig. 6b). Such differences might be related to an enhanced contribution of diffuse over direct radiation induced by cloud cover (Kirk 1994). For terrestrial forests, it is known that diffuse light penetrates deeper into understory canopies than direct light does (Urban et al. 2007). We speculate that diffuse light likewise penetrates deeper into the corallite microtopography (*see* structure in Fig. 3) and reaches the polyp tissue surface compared with direct light, which gets more easily attenuated by the corallite structure

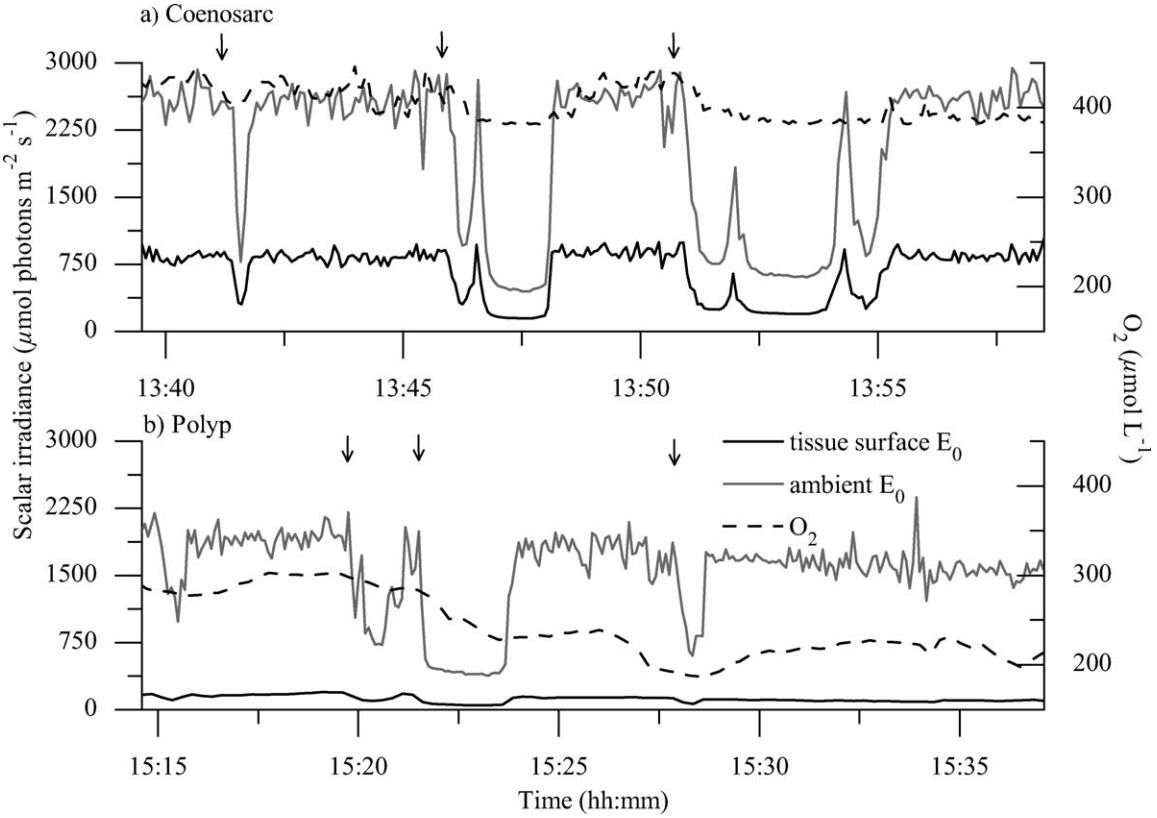

Fig. 6. In situ dynamics of scalar irradiance (PAR) and O_2 concentration at the surface of (a) coenosarc and (b) polyp tissue of the upper colony surface of *P. lamellina* during a sunny day with many intermittent clouds (onsets marked by arrows). Ambient scalar irradiance was measured next to the coral above strongly reflecting sediment.

(e.g., polyp walls; Figs. 3, 4). Thus, enhanced penetration of diffuse light into the corallite matrix may counterbalance a decrease in the intensity of light during cloud cover and could thus explain the observed dampening of temporal fluctuations in light capture present over polyp tissue. The dynamics reported are limited by the temporal resolution of our underwater meter, which operates on the scale of seconds. High-amplitude, millisecond pulses of light from wave focusing (Darecki et al. 2011) could thus not be captured. Future in situ studies combining light microsensors with systems capable of capturing high-frequency irradiance fluctuations are thus needed to resolve the importance of high-frequency light pulses in coral photophysiology.

Additionally, we found that the O_2 microenvironment was highly dynamic in coenosarc tissue and fluctuated closely with changes in the ambient irradiance, whereas the O_2 microenvironment of polyp tissue was less dynamic and did not fluctuate simultaneously with changes to the ambient irradiance (Fig. 6b). Such decoupling of O_2 vs. irradiance fluctuations in polyp tissue is likely related to the intricate polyp topography and associated flow patterns forming complex patterns of O_2 exchange with the environment (Wangpraseurt et al. 2012*b*). These observations highlight that different spatial compartments within a single coral colony also exhibit different temporal fluctuations of the local physicochemical microenvironment, adding further complexity to the landscape of ecological microniches in corals.

Our results shed new light onto the control of *Symbiodinium* ecophysiology. The distribution of *Symbiodinium* geno- and phenotypes can be controlled by irradiance across water depth gradients (Rowan and Knowlton 1995) and within a single colony (Rowan et al. 1997). However, often such spatial distribution patterns of *Symbiodinium* in relation to irradiance are ambiguous (Warner et al. 2006; Ulstrup et al. 2007) and thus the role of light compared with, for example, host specificity (Lajeunesse et al. 2004) in regulating *Symbiodinium* distribution within corals has remained disputed. If it is true that irradiance controls *Symbiodinium* distribution (Rowan et al. 1997; Iglesias-Prieto et al. 2004), then any detailed patterns will be masked by the spatial and temporal complexity of the light microenvironment reported here. Our results thus call for a reassessment of *Symbiodinium* distribution in relation to its actual light microenvironment. As a first step, it will be useful to compare differences between coenosarc and polyp tissue because they differ in total light exposure and spectral quality (Figs. 3, 4; Wangpraseurt et al. 2012*a*) and can exhibit different patterns of photoacclimation (Ralph et al. 2002).

The presence of different optical microniches in different spatial compartments within corals supports the suggestion that such niches can serve as refugia during light-related

bleaching conditions (Hoegh-Guldberg 1999; Loya et al. 2001). For instance, polyp tissue at the sides of massive corals will be effectively sheltered (Fig. 4), thereby alleviating local light stress during bleaching conditions. It is thus possible that minor symbiont populations are harbored within those niches and can play an important role for the repopulation and redistribution of symbionts after a bleaching event.

It has long been reported that an organism's capacity to adapt to environmental change depends on its previous exposure to a given environmental parameter (e.g., temperature or irradiance; Brown et al. 2002). Whereas initially only the role of the organism's exposure to the average of that parameter has been considered, more recently, it has been proposed that adaptive capacity is determined by the degree of environmental variability (i.e., differences in the magnitude of fluctuation) the organism has been exposed to (Deutsch et al. 2008). The differences in fluctuation of the physicochemical microenvironment (i.e., light and O_2) reported here thus suggest that symbionts harbored within different spatial compartments (e.g., coenosarc vs. polyp; Fig. 6) have a different exposure history of environmental variability. Such different exposure history could translate to and explain differential patterns of adaptation, acclimation capacity, or both characteristics observed in corals (Loya et al. 2001). Although the detailed ecological implications remain to be investigated, we show here that corals harbor complex light microenvironments that can now be characterized at micrometer resolution under in situ conditions. Such optical microniches show pronounced spatiotemporal variation and differ strongly from the incident underwater irradiance regime, in terms of both intensity and spectral quality. The optical properties of the surrounding benthos also affect local light fields and photosynthesis in corals, and such interaction needs further attention in coral photobiology studies. A detailed understanding of the in situ microenvironmental ecology of healthy corals will thus be a key to better interpret the spatiotemporal complexity of stress-related patterns observed on reefs.

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