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RESEARCH ARTICLE

# Lateral light transfer ensures efficient resource distribution in symbiont-bearing corals

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## ABSTRACT

Coral tissue optics has received very little attention in the past, although the interaction between tissue and light is central to our basic understanding of coral physiology. Here we used fibre-optic and electrochemical microsensors along with variable chlorophyll fluorescence imaging to directly measure lateral light propagation within living coral tissues. Our results show that corals can transfer light laterally within their tissues to a distance of ~2 cm. Such light transport stimulates $O_2$ evolution and photosystem II operating efficiency in areas >0.5–1 cm away from direct illumination. Light is scattered strongly in both coral tissue and skeleton, leading to photon trapping and lateral redistribution within the tissue. Lateral light transfer in coral tissue is a new mechanism by which light is redistributed over the coral colony and we argue that tissue optical properties are one of the key factors in explaining the high photosynthetic efficiency of corals.

**KEY WORDS: Coral reef, Tissue optics, Photobiology, Microenvironment, Microsensor, Photosynthesis**

## INTRODUCTION

The symbiotic interaction between dinoflagellate microalgae known as zooxanthellae and their cnidarian animal hosts is the foundation of one of the most diverse and productive ecosystems on Earth, the coral reef. The quantity and quality of light available for zooxanthellae photosynthesis *in hospite* (i.e. within the tissue) is a key environmental parameter regulating the successful interaction between symbionts and the coral host (Falkowski et al., 1984). Light drives symbiont photosynthesis, which provides carbohydrates and energy for the coral host and its calcification. In turn, the coral host provides a protected environment and metabolic waste products such as inorganic carbon and nutrients that enable efficient zooxanthellae photosynthesis (Muscatine et al., 1981). The interaction between light and corals has been intensively studied for decades, with a particular focus on the coral bleaching phenomenon, where a combination of excess light and temperature can lead to the breakdown of the symbiosis and the subsequent expulsion and/or degradation of zooxanthellae (Glynn, 1996). Coral bleaching is regarded as one of the major threats linked to ongoing climate change, potentially leading to the worldwide degradation of coral reefs, and much effort has been dedicated to understand bleaching episodes and patterns observed on reefs (Hughes et al., 2003; Hoegh-Guldberg et al., 2007). Although a central aim of such bleaching-related research has been to understand how solar radiation affects microalgal photophysiology, it is surprising that our knowledge of the actual light field of *Symbiodinium* within the tissue of corals is still very limited.

Microscale light habitats differ between coral species and are affected by absorption, scattering and fluorescence (Salih et al., 2000; Enriquez et al., 2005; Kaniewska et al., 2011; Wangpraseurt et al., 2012). Studies of coral optics have primarily dealt with effects of the pronounced light scattering in the coral skeleton (Enriquez et al., 2005; Reef et al., 2009; Terán et al., 2010; Kaniewska et al., 2011; Marcelino et al., 2013). The aragonite skeleton acts as a Lambertian-like diffuser, i.e. it scatters light isotropically, redirecting diffused photons back into the overlying tissue (Enriquez et al., 2005). Such scattering increases the path length of photons per vertical distance travelled, leading to an enhancement in tissue scalar irradiance [i.e. the integral quantum flux incident from all directions about a given point (Kühl and Jørgensen, 1992)] and thus enhanced absorption efficiency by symbiont photopigments (Enriquez et al., 2005; Stambler and Dubinsky, 2005; Kahng et al., 2012). The scalar irradiance at the coral tissue surface can be up to three times enhanced over the incident downwelling irradiance (Kühl et al., 1995), which has been thought to be the result of skeleton scattering, thus assuming a negligible role of the coral tissue (Enriquez et al., 2005). However, recent microsensor measurements within coral tissue revealed the presence of pronounced vertical light gradients, where lower tissue layers create optical microniches with low scalar irradiance inside coral tissues even under full solar irradiance levels at the tissue surface (Wangpraseurt et al., 2012). Such distinct light distribution characterised by enhanced scalar irradiance in upper tissue layers and light gradients towards lower layers suggests that scattering also occurs within coral tissues and that their optical properties can affect coral light fields. The presence of optical microniches within the coral tissue thus calls for a revision of our current view of coral–light interactions and a better understanding of coral tissue optics and scattering.

Tissue scattering involves a change in the angular light distribution, where vertically incident photons are redistributed laterally, causing an increasingly diffuse light field with tissue depth (Kühl and Jørgensen, 1994). Tissue scattering can be quantified through localized vertically incident illumination by a laser beam on the given tissue and by measuring the amount of laterally transported light, i.e. the spread of light around the beam. Light scattering is well studied in biological tissues such as human skin and plant tissue (e.g. Vogelman, 1993; Welch and van Gemert, 2011). For terrestrial plants, understanding of light transfer has resulted in detailed information on light habitats within leaves and optical controls of plant photobiology (Ramus, 1990; Vogelman et al., 1996; Johnson et al., 2005). For example, it is known that photon

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trapping occurs between tissue layers within leafs (Vogelman et al., 1996). Photon trapping describes the directional scattering of light along a boundary where light will not cross, but gets internally reflected (i.e. back into the same boundary). Directional scattering along distinct cell layers (e.g. cell walls, mesophyll) can cause an anisotropic light field (Gausman et al., 1974; Jacquemoud and Baret, 1990). Waveguiding, which is a special case of photon trapping where light is propagated continuously by total internal reflection, has been reported to occur in some tissues such as dark-grown plant tissues (Mandoli and Briggs, 1982). For aquatic plant and animal tissues, much less is known about tissue scattering and light transport (Lassen et al., 1994; Spilling et al., 2010; Kaniewska et al., 2011; Wangpraseurt et al., 2012). Lateral light guiding has been demonstrated in macroalgae (Ramus, 1978) and sponges (Brümmer et al., 2008), and light guiding in the coral skeleton has also been proposed (Highsmith, 1981). However, coral tissue optics and the role of lateral light transfer for coral photobiology have remained poorly understood, although light is arguably the most important environmental variable affecting the ecophysiology of photosynthesising corals and thus is a key parameter for the understanding of coral reef ecosystems.

In the present study, we used a combination of fibre-optic and electrochemical microsensors along with variable chlorophyll fluorescence imaging to investigate the following questions: (1) does lateral light transfer occur in corals, and is such transfer wavelength dependent; (2) what is the relative role of tissue and skeleton in light propagation; (3) does lateral light transfer affect coral photophysiology; and (4) can corals modify their light environment and light transfer via tissue adjustments? Three species of faviid corals were selected for this study: *Montastraea curta* (Dana 1846), *Goniastrea aspera* Verrill 1905 and *Favia speciosa* (Dana 1846). We provide the first direct evidence for lateral light transfer in living corals and discuss the ecological significance and implications of our finding for the basic understanding of coral photobiology.

## RESULTS

### Light distribution

Fibre-optic microprobe measurements showed that scalar irradiance of both red (636 nm) and near-infrared (785 nm) light was enhanced in the coral tissue as far as 14–20 mm away from the tissue area directly illuminated by the incident laser beam (Figs 1, 2). The lateral attenuation of near-infrared radiation (NIR) scalar irradiance occurred homogeneously within the tissue of an intact coral and was almost identical to the lateral attenuation observed on the bare skeleton (compare Fig. 1A and 1B and see ratio of 785 nm light in 1E). However, for 636 nm light there were clear differences in the lateral scalar irradiance distribution around the incident laser beam between the intact coral and the bare skeleton (Fig. 1C–E). Lateral

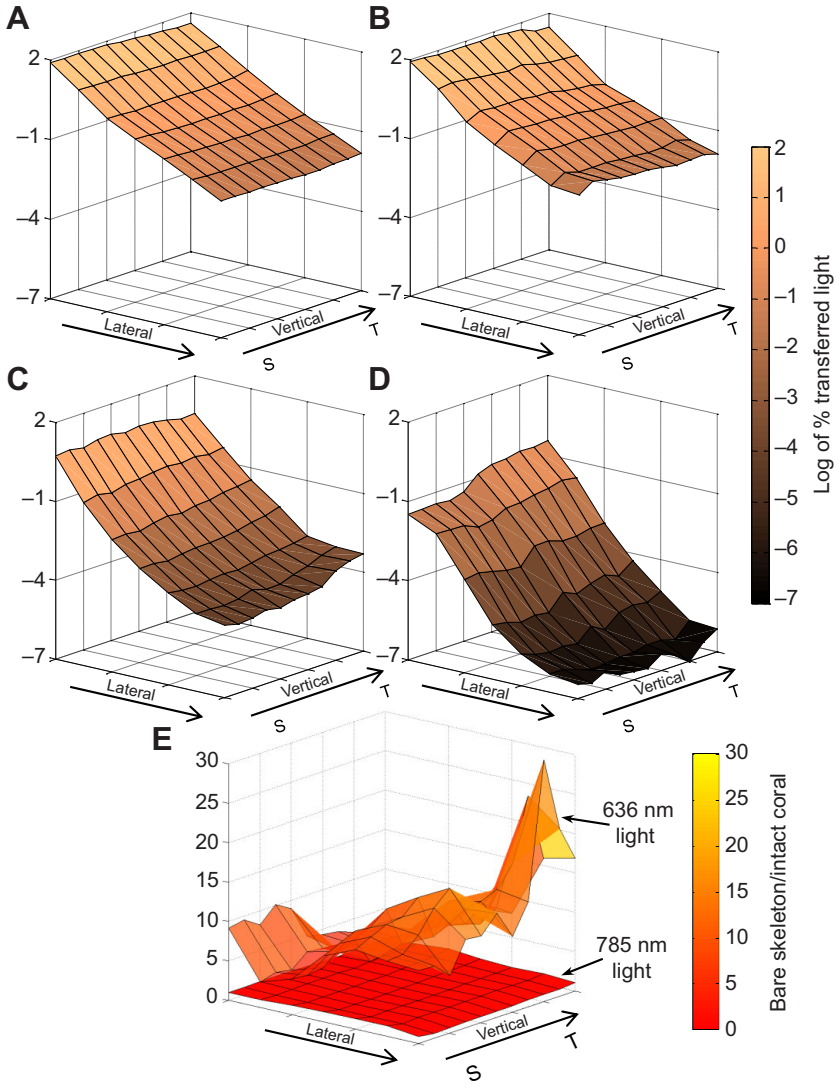


**Fig. 1. Lateral light distribution in *Favia speciosa*.** Plots were constructed based on vertical and lateral scalar irradiance microsensor profiles with incident (A,B) near-infrared radiation (NIR; 785 nm) and (C,D) red (636 nm) laser light. Each interval on the lateral axis represents a step of 2 mm, with the first interval starting 2 mm away from the incident light source. On the vertical axis, each interval represents 200 µm, with the first interval starting at the skeleton surface, profiling upwards into the tissue surface/water column. (A,C) Measurements performed on the bare skeleton; (B,D) measurements performed on an intact coral. (E) The ratio of measurements obtained on the bare skeleton to measurements on the intact coral.

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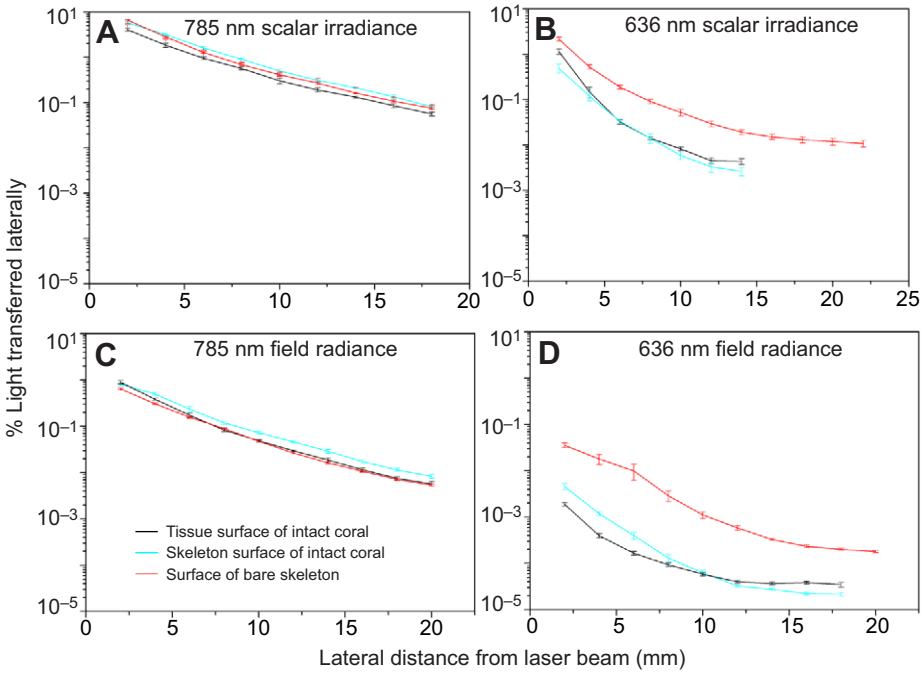


**Fig. 2. Microprofiles of lateral light transfer in *Favia speciosa*.** Lateral light measurements (means ± s.e.m.; *N*=6–7 corallite-level replicates) were taken across coenosarc tissue in steps of 2 mm away from the incident laser beam. Measurements were taken from the skeleton surface of an intact coral (cyan), the tissue surface of an intact coral (black) and the skeleton surface of the bare skeleton (red) (corresponding to supplementary material Fig. S3 measurement positions 1–3). (A,B) Scalar irradiance for 785 and 636 nm, respectively; (C,D) field radiance at a zenith angle of 180 deg for a laser beam of 785 and 636 nm, respectively.

attenuation of 636 nm scalar irradiance was more rapid on an intact coral compared with the bare skeleton (see ratio in Fig. 1E). Additionally, we found that on a vertical scale there was a clear tendency for an increase in 636 nm scalar irradiance from the skeleton surface towards the tissue surface for an intact coral but not in measurements above the bare skeleton. For instance, at ~2 mm away from the laser beam, measurements on the tissue surface of the intact coral were approximately twice as high as at the underlying skeleton surface (1.15±0.15 versus 0.49±0.11% of laterally transferred light, means ± s.e.m.), while values on the surface of the bare skeleton were similar to the values in the ambient water above it (2.16±0.22 versus 1.93±0.06% of laterally transferred light; Fig. 2, supplementary material Fig. S1). Such a relative increase in 636 nm scalar irradiance for vertical microprofiles from the skeleton towards the tissue surface as opposed to microprofiles from skeleton through ambient water indicates the occurrence of scattering and photon trapping within the tissue (compare Fig. 1C and 1D).

Averaged lateral scalar irradiance attenuation profiles within the tissue and across the skeleton surface of an intact coral as well as measurements at the surface of the bare skeleton showed in all cases that NIR was more efficiently transferred than red light (Fig. 2A,B, Table 1). For NIR, the lateral light attenuation was well described by a first-order exponential attenuation ($y=y_o+Ae^{-Kx}$) for all measurements, as there were no differences between the $R^2$ values for the tissue surface and the skeleton surface of the intact coral or the surface of the bare skeleton ($0.92<R^2<1.00$; Fig. 2A, Table 1). For 636 nm light, however, the lateral attenuation of scalar irradiance was not always well described by a first-order exponential decay (Fig. 2B, Table 1). The most obvious result was the low $R^2$ of 0.71 found on the skeleton surface of the intact coral, which considerably improved to a high $R^2$ of 0.92 on the bare skeleton, thus indicating the presence of heterogeneous light transfer within the tissue.

When comparing lateral attenuation profiles of scalar irradiance with the directly upwelling field radiance (i.e. the radiant flux incident at a given point from the 0 deg zenith angle), we found that lateral attenuation profiles for 785 nm light were similar for all measurement locations (compare Fig. 1A and 1C). In contrast, scalar irradiance of 636 nm attenuated faster than the respective field radiance, showing that red light distribution was not completely isotropic (compare Fig. 1B and 1D, and see *K*-values in Table 1).

First measurements on the effects of coral tissue re-arrangement showed that tissue contraction and expansion affected the distribution of 636 nm scalar irradiance around the area directly illuminated by the incident laser beam (Fig. 3). The scalar irradiance at lateral distances of 2–6 mm from the incident laser beam was

**Table 1. Lateral attenuation coefficients (*K*) and $r^2$ of laterally transferred light**

| | $K$ (mm$^{-1}$) | | $r^2$ | |
|---|---|---|---|---|
| | Scalar irradiance | Field radiance | Scalar irradiance | Field radiance |
| 636 nm | | | | |
| Tissue surface of intact coral | 1.04 | 0.75 | 0.87 | 0.90 |
| Skeleton surface of intact coral | 0.71 | 0.66 | 0.71 | 0.83 |
| Surface of bare skeleton | 0.70 | 0.34 | 0.92 | 0.84 |
| 785 nm | | | | |
| Tissue surface of intact coral | 0.38 | 0.42 | 0.92 | 0.96 |
| Skeleton surface of intact coral | 0.31 | 0.29 | 0.96 | 0.95 |
| Surface of bare skeleton | 0.43 | 0.36 | 1.00 | 0.96 |

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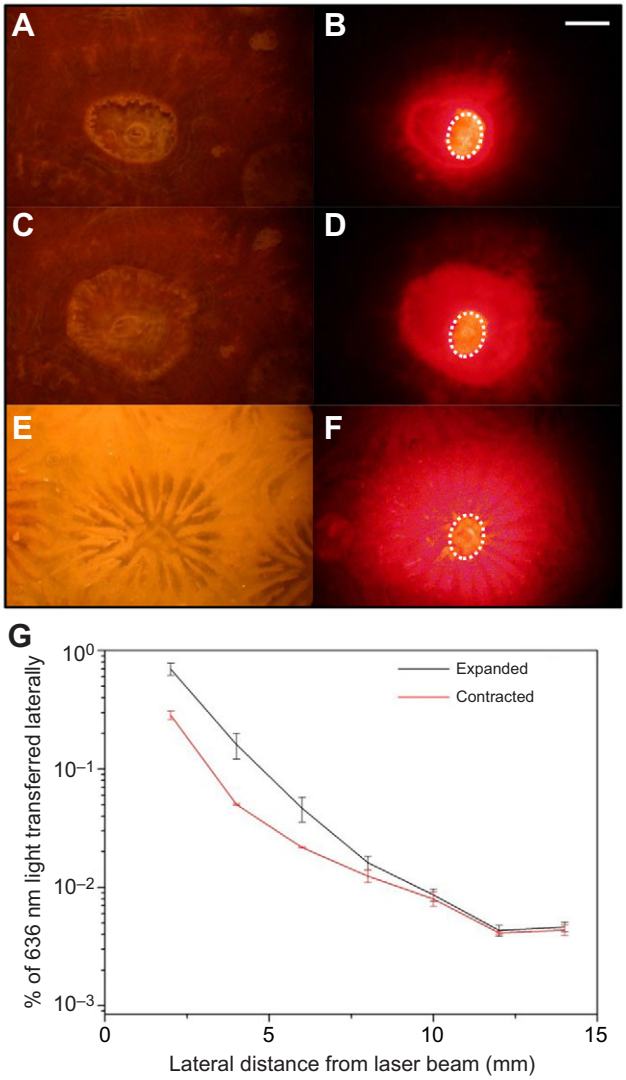


**Fig. 3. Effects of tissue behaviour on lateral light transfer in the coral *Favia speciosa*.** (A,C,E) Structure of coral surface when tissue was (A) contracted, (C) expanded and (E) removed. (B,D,F) Respective broadening of a 636 nm laser beam that was employed vertically incident on the coral surface. The camera aperture and exposure time were kept constant and digital images were taken at the same focal distance. Dotted white circles indicate the direct incident area of the laser beam. Scale bar, 2 mm. (G) Average tissue surface scalar irradiance along a horizontal transect away from an incident 636 nm laser beam (*N*=3 corallite-level replicates).

approximately three times higher when tissue was expanded compared with when it was contracted. With increasing horizontal distance, the difference in scalar irradiance between contracted and expanded tissue decreased and was no longer detectable at distances >10 mm from the beam (Fig. 3).

### Lateral light transfer effects on $O_2$ microenvironment

By repeatedly switching on and off the 636 nm laser light incident on a ~2 mm wide coral surface area, we observed a rapid increase and decrease in surface concentrations of $O_2$ in areas laterally distant from the laser beam (Fig. 4A); such shifts between $O_2$ production and consumption were repeatable over several on/off cycles of the laser module. We quantified the contribution of $O_2$ evolution induced by the laser beam as the decrease in tissue-surface $O_2$ concentration when laser light was on relative to that when laser

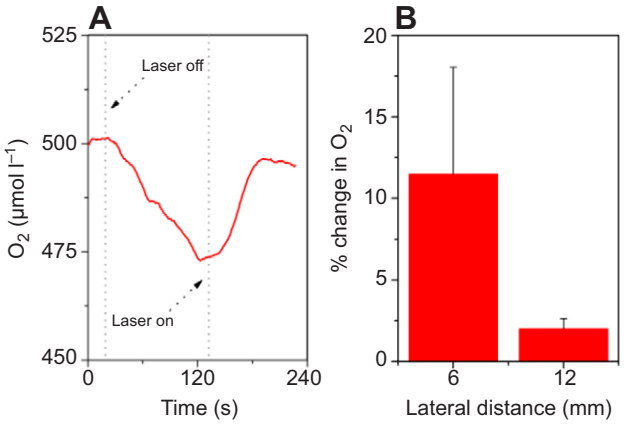


**Fig. 4. Light transfer effects on the $O_2$ microenvironment.** (A) Example of temporal $O_2$ concentration (µmol $l^{-1}$) dynamics measured in the upper tissue layer 6 mm away from an incident red laser beam (636 nm) on the coral *Favia speciosa*. Arrows show time points when laser was switched on or off. (B) Mean change in $O_2$ concentration (±s.e.m.) at measuring positions 6 and 12 mm away from the incident laser beam (*N*=3 corallite-level replicates).

light was subsequently switched off. Our results show that at a horizontal distance of 6 mm from the illuminated area, the laterally redistributed light accounted for ~11.5±6.5% of the surface $O_2$ concentration. At a distance of 12 mm, the contribution was smaller but still detectable (2.0±0.64%; Fig. 4B).

### Variable chlorophyll fluorescence imaging

Lateral light transfer occurred in all examined corals and for all investigated wavelengths (405, 532 and 636 nm), as indicated by our observation of laser-induced chlorophyll fluorescence detectable beyond areas of the directly incident beam (Fig. 5A–E). The observed impact distance, i.e. the zone beyond the directly incident light beam that showed stimulation of chlorophyll fluorescence, ranged between ~2 and 6 mm. For 405 nm light, we found both tissue- and species-related differences. The impact distance was ~10–15% higher on coenosarc tissue than on polyp tissue for all investigated coral species (ANOVA, $F$=4.9, $P$<0.05; Fig. 5C). For 532 nm light, lateral light transfer was not affected by tissue type but differed between coral species, with the lowest values found for *G. aspera* (Fig. 5D). Similar patterns were observed for 636 nm light, where the impact distance was approximately two times smaller for *G. aspera* than for *F. speciosa* and *M. curta* (Tukey's HSD *post hoc* test, $P$<0.05), with the latter two species showing similar values (Fig. 5A). Tissue type (i.e. coenosarc versus polyp) had no effect on the impact distance for red light (ANOVA, $F$=0.69, $P$>0.05).

We found an effect of 636 nm laser light on photosystem II (PSII) operating efficiency at remote tissue areas for all coral species. The distance over which PSII operating efficiency was affected ranged between ~1 and 4 mm and differed between coral species. The highest values were measured on coenosarc tissue of *M. curta* (4.2±0.57 mm), which was approximately 2.6 times higher than the lowest values measured on coenosarc tissue of *G. aspera* (1.6±0.23 mm; Fig. 5F).

## DISCUSSION

In the present study, we demonstrate the presence of lateral light transfer, which is a newly identified mechanism of light propagation in corals. We also give the first evidence that lateral light transfer affects coral photosynthesis in tissue areas distant to the direct beam and thus is a mechanism for distributing solar radiation over the

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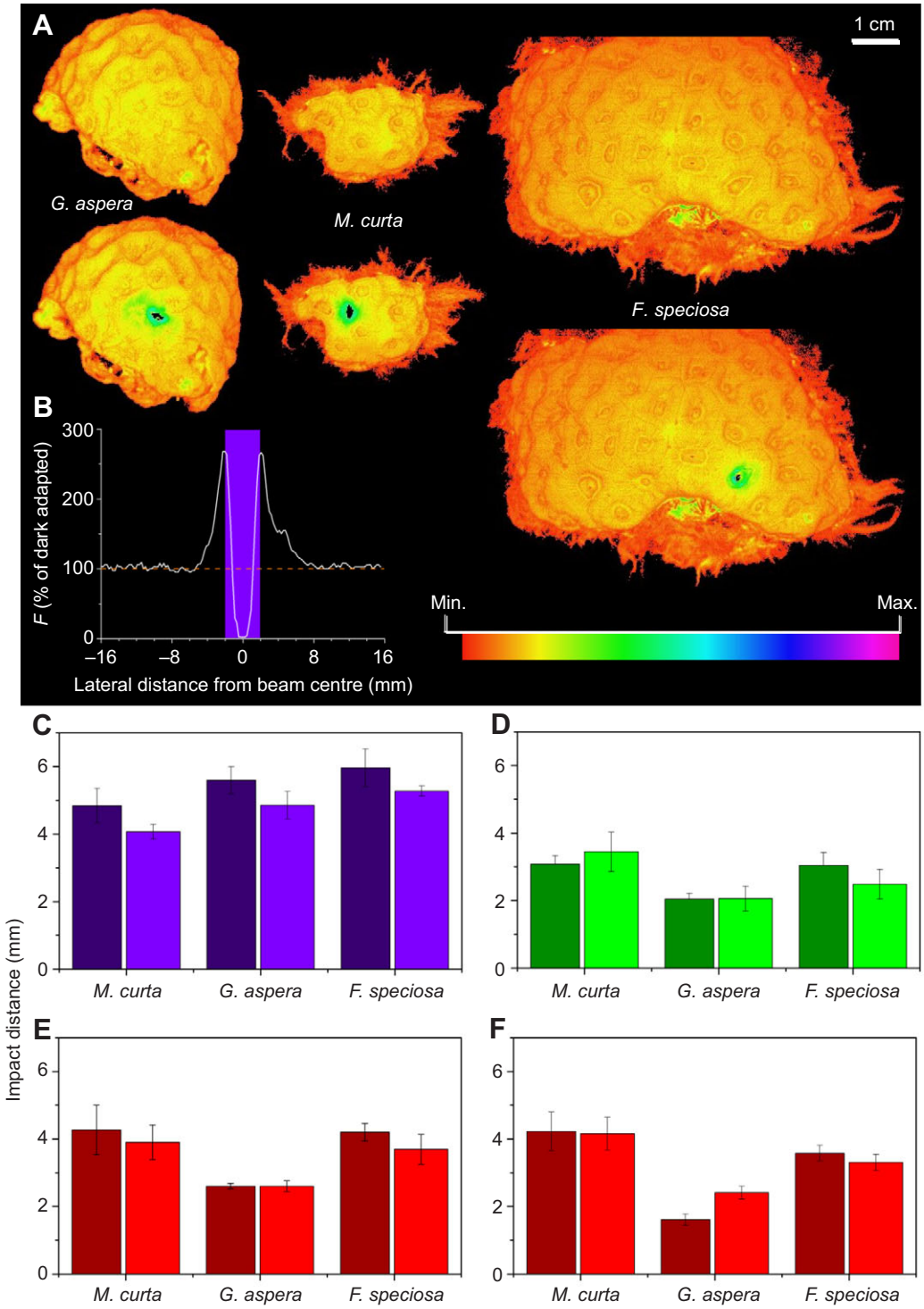


**Fig. 5. Light transfer effects on coral photobiology.** (A) Pulse-amplitude modulation images of fluorescent yield before illumination (upper row of images) and after illumination (lower row of images) with a violet laser (405 nm). Images are colour-coded to the same scale. (B) Lateral line transect through impacted area (laser on) normalised to fluorescent yield levels (*F*) in the dark-adapted state (laser off). Violet zone indicates the width of the incident laser beam and dotted red line indicates the background fluorescence in the dark-adapted state. (C–E) Lateral impact distance (means ± s.e.m.) on steady-state chlorophyll fluorescence yield for different coral species and tissue types. Columns with dark colour tone represent coenosarc tissue and columns with light colour tone represent polyp tissue (*N*=3 corallite-level replicates). Corals were illuminated with laser light of wavelengths (C) 405 nm (violet), (D) 532 nm (green) and (E) 636 nm (red). (F) Light transfer effects on photosystem II operating efficiency ($\Phi_{PSII}$). Lateral impact distance (means ± s.e.m.) of red laser light (636 nm) on $\Phi_{PSII}$ for coenosarc (dark colour tone) and polyp (light colour tone) tissues of faviid corals (*N*=3 corallite-level replicates).

complex coral topography that enables efficient use of light in photosynthesis.

We found that lateral light transfer differed for different spectral regions, where NIR was more efficiently transferred than red light. Lateral transfer of NIR was similar between the coral tissue surface and the bare skeleton, which means that the role of tissue optics for lateral NIR propagation is negligible and mainly a function of skeleton scattering. Coral skeleton scattering theory implies that NIR is isotropically scattered by the skeleton (Enriquez et al., 2005), which was here confirmed by a perfectly described exponential decay, typical for systems where isotropic scattering dominates (Smith, 1966) (Figs 1, 2, Table 1). In contrast, the lateral attenuation profile of red light differed within the tissue of the intact coral and over the bare skeleton, suggesting that tissue optics influences lateral transfer of red light in a more complex interplay of tissue scattering and absorption than algal absorption alone (Fig. 1E, Table 1). Together, these findings demonstrate that NIR fields in corals are largely determined by skeleton optics, while wavelengths in the visible range that interact with host and zooxanthellae pigments and cell walls are strongly controlled by coral tissue optics, with some additional contribution of backscattered light from the skeleton.

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Light transfer in biological tissues often has an anisotropic character (e.g. Vogelman, 1993; Tuchin, 1997). Anisotropic light transfer results from light travelling between discrete tissue layers (i.e. optical boundaries) of different refractive indices, where photons crossing these boundaries are redirected because of Fresnel reflection (Kienle et al., 2004). If photons are travelling at very low angles relative to the boundaries, they can be total internally reflected in cases where tissue layers differ in their refractive index. This then makes the tissue act as a directional waveguide. Such highly anisotropic light transfer can occur in human dentin as well as in sponge and plant tissues (Mandoli and Briggs, 1982; Kienle and Hibst, 2006; Brümmer et al., 2008). Our results show that light propagation through coral tissue is also anisotropic.

The lateral attenuation profile of red light differed when measured with scalar irradiance and field radiance microsensors (compare Fig. 1B and 1D, Table 1). A light field surrounding a given point is isotropic when scalar irradiance equals the integral of field radiance with identical magnitude irrespective of the directional origin, i.e. photons around that point are equally distributed (Kühl and Jørgensen, 1994); under such asymptotic light field conditions, the attenuation coefficients of field radiance and scalar irradiance become identical. Thus, the difference in the attenuation of upwelling field radiance and scalar irradiance indicates anisotropy. Anisotropic lateral light propagation was also indicated by vertical differences in the light field distribution within the coral tissue. At close lateral distances (~2 mm) from a red laser, scalar irradiance was more than two times higher at the tissue surface than on the skeleton surface of an intact coral, whilst this effect was quickly cancelled out with increasing lateral distance from the incident light. Such heterogeneities in lateral light propagation between tissue layers indicate that some inherent optical properties (i.e. refractive index, scattering coefficient and/or absorption coefficient) must vary between layers.

Different coral tissue layers vary in their composition: coral mucus contains sugars, proteins and bacteria (Meikle et al., 1988), the gastroderm is rich in zooxanthellae, and the mesoglea has a high concentration of lipids (Stimson, 1987). Protein, sugar and lipid concentration affect the refractive index of biological tissues (Bolin et al., 1989; Van Gemert et al., 1989; Kohl et al., 1994) and refractive index differences in tissues control light propagation (Welch and van Gemert, 2011). Additionally, fluorescent host pigments affect light scattering and spectral conversion, and their location can vary within the coral tissue (Salih et al., 2000). Therefore, differences in the composition of tissue layers could lead to refractive index heterogeneities that modulate light distribution in corals. Based on the discussion of our results, we have summarized the main optical events that we consider likely to be involved in lateral light transfer (Fig. 6). This scheme provides the basis for a characterisation of the inherent optical properties of coral tissue, information that is a prerequisite for understanding and modelling light propagation in corals.

We found that lateral light transfer affects coral physiology, as there was an enhancement in $O_2$ evolution and PSII operating efficiency beyond the directly laser-illuminated area (Fig. 4, Fig. 5F). Such effects on coral photobiology might at first be surprising as only ~1–10% of the incident light is laterally transferred. However, these values describe an enhancement of irradiance measured within the tissue, and thus describe photons directly available for algal photosynthesis. The irradiance reaching algal symbionts within gastrodermal tissue differs from the ambient irradiance, especially for symbionts in deeper tissue layers, where scalar irradiance can be <10% of the tissue surface values (Wangpraseurt et al., 2012). Therefore, small enhancements in within-tissue irradiance due to

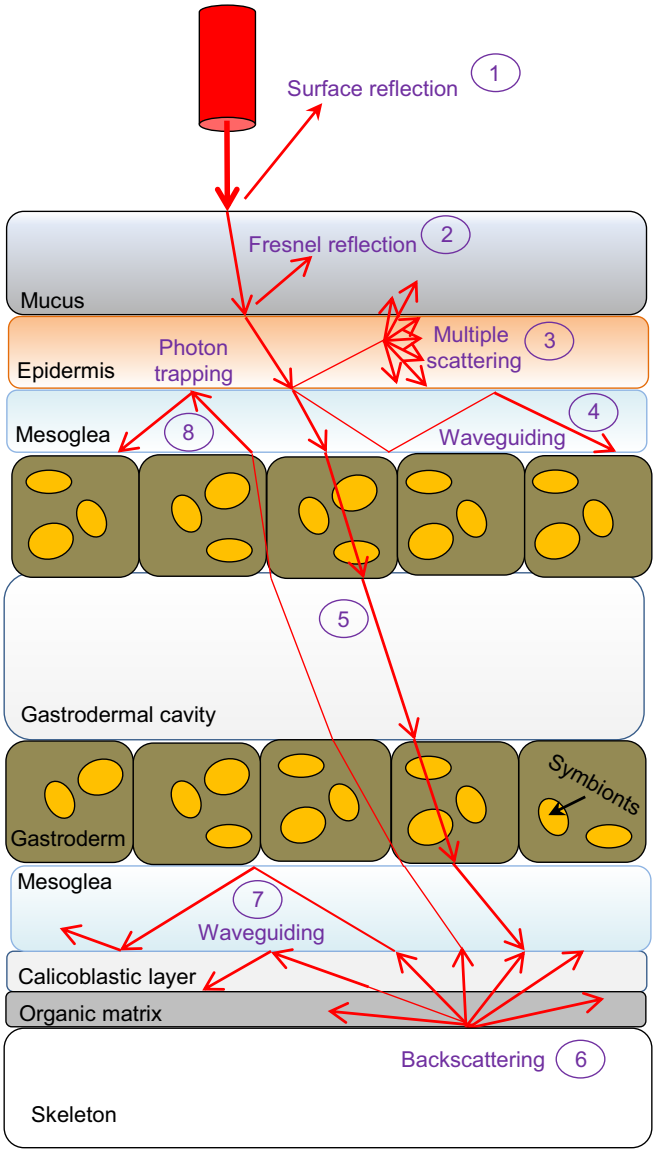


**Fig. 6. Light propagation in corals.** Schematic of potential light transfer mechanisms within coral tissue and skeleton. (1) An incident collimated laser beam of red light interacts with the surface of the tissue. Part of this light is reflected at the surface and does not enter the tissue. Such surface reflection is the result of a mismatch in the refractive index between the water and the upper tissue layer (or here mucus). (2) Transmitted light has changed its direction and may then undergo Fresnel reflection when crossing tissue boundaries. Here, part of the light is trapped within a given tissue layer. (3) Trapped light may be scattered again within the tissue structure because of microscopic fluctuations of the refractive index. Such multiple scattering events within the matrix cause a localised enhancement in scalar irradiance, especially pronounced at wavelengths experiencing low absorption by photopigments. (4) Light that has passed through several tissue layers will become highly diffuse as it has undergone several scattering events. This enhances photons travelling at oblique angles, some of them reaching a critical angle where all of the photons are totally internally reflected and the tissue structure could act as a waveguide. Such lateral light transfer will be highly anisotropic. (5) Some part of the light will reach the skeleton, where it undergoes multiple scattering in the skeleton matrix. (6) Such isotropic backscattering induces a greater proportion of photons travelling at oblique angles, (7) further stimulating photon trapping and waveguiding along tissue boundaries. Waveguiding could occur between any boundaries with sufficient refractive index mismatch. (8) Photons that are backscattered into the tissue matrix can become trapped within upper tissue layers, thereby further enhancing localised scalar irradiance.

lateral light transfer will likely make a pronounced difference to the symbiont light budget *in hospite*. On a colony scale, structural complexity leads to the presence of low light niches in branching corals (Kaniewska et al., 2011), and similar heterogeneities exist along the colony structure of massive corals, where the light exposure at the colony sides can be approximately one order of magnitude lower above polyp tissue than above adjacent coenosarc tissue (D.W., unpublished). Under such light-limiting conditions, lateral light transfer is likely an important contribution of light available for symbiont photosynthesis operating in low light niches, and may thus contribute to efficient colony-scale light energy distribution.

Enhancement of light capture by modulating tissue and skeleton optical properties could be an evolutionary strategy that readily becomes disadvantageous when corals are under supra-optimal irradiance regimes, such as during low tide and mid-day sun (Marcelino et al., 2013). Under such conditions, an enhancement in local light fields by lateral light transfer appears counterproductive and would suggest that corals have evolved regulatory mechanisms to control light exposure. Our results also show that corals have the ability to regulate the amount of light exposure and lateral light transfer by re-arranging their tissues. We thus observed that in an expanded tissue state, much more light (approximately three times in close vicinity) is transferred to the surrounding tissue and skeleton than in a coral with contracted tissue (Fig. 3).

It is known that coral behaviour is affected by the ambient irradiance regime. In many faviid corals, for instance, high irradiance leads to tissue contraction, while dim light or darkness leads to tissue expansion (Levy et al., 2003). It has been suggested that tissue contraction has a photoprotective role, while tissue expansion enhances photosynthesis (Fabricius and Klumpp, 1995; Brown et al., 2002). Here, we show that light transfer is indeed limited when tissue is contracted and enhanced when tissue is expanded. This points to an important photoacclimatory role of tissue movement and arrangement in corals. Under very high irradiance, shifts in lateral light distribution, e.g. because of tissue contraction and host pigment exposure, may alleviate local light stress and photoinhibition by reducing photosymbiont exposure and regulating the amount of light travelling in tissue versus skeleton. Coral tissue optics and the spatial arrangement of skeleton and tissue may thus also be important in optimizing light harvesting and exposure under shifting ambient irradiance regimes.

We found that the magnitude of lateral light transfer differed between species even within one coral family (Fig. 5). Together with the finding that local scalar irradiance fields (Wangpraseurt et al., 2012) and skeleton scattering characteristics (Marcelino et al., 2013) differ between coral species, these results underscore the complexity of coral light fields surrounding their photosymbionts. For our understanding of coral stress physiology and bleaching patterns, it is thus important to consider that corals have unique microenvironmental optical controls that create dynamic light habitats for resident zooxanthellae. It has been shown that species-specific differences in skeleton scattering coefficients partly correlate with observed bleaching patterns (Marcelino et al., 2013). We argue that including tissue optics into skeleton light-scattering models will benefit our understanding of the light regime surrounding zooxanthellae, which will also strengthen predictive models for light-related stress responses of corals.

In the present study, we have investigated in detail the microscale light propagation of red light and NIR, of which red light is relevant for the photosynthetic action spectrum of shallow-water corals (Halldal, 1968; Dustan, 1982; Dubinsky and Falkowski, 2011). However, with increasing water depths, longer wavelengths rapidly attenuate (Kirk, 1994) and corals located in deeper waters rely more heavily on light of shorter wavelengths, such as blue and green light (Dustan, 1982; Mass et al., 2010). Our imaging pulse-amplitude modulation (PAM) results also showed that lateral light transfer occurs for violet (405 nm) and green (532 nm) light, thus suggesting that lateral light transfer is effective over a wide part of the visible light spectrum (Fig. 5). Lateral light transfer thus makes an important contribution to photosynthesis of shallow-water corals and may even play a role for corals in deeper water. Certainly, a detailed quantification of the magnitude of lateral light propagation for shorter wavelengths within photosynthetically active radiation (PAR) is promising and will likely improve our understanding of this new optical mechanism for corals under *in situ* conditions.

In conclusion, we provide the first experimental evidence that corals are capable of efficient lateral light transfer. Lateral light transfer was strongly affected by tissue optics in the visible spectrum, while NIR transfer was mainly affected by skeleton scattering. The visible light field within coral tissue is anisotropic, likely a result of anisotropic scattering along different tissue layers. Lateral light transfer stimulated zooxanthellae photosynthesis up to ~1 cm away from the incident laser beam. All investigated corals exhibited lateral light transfer, albeit the magnitude of transferred light differed between species. As skeleton and tissue optics vary considerably between corals, a more detailed understanding of the optical mechanisms underlying lateral light transfer should be a core component of future coral photobiology research. Lateral light transfer in corals strongly affects light harvesting and overall light exposure, and could be instrumental in ensuring a high photosynthetic efficiency of their photosymbionts.

## MATERIALS AND METHODS

### Corals

Small colonies of faviid corals were sampled on the shallow-water reef flat of the Heron Island lagoon, Great Barrier Reef, Australia (152°06′E, 20°29′S). We sampled one small colony of each *Montastraea curta*, *Goniastrea aspera* and *Favia speciosa*. Samples were kept in aquaria supplied with continuously flowing lagoon water at Heron Island Research Station before transportation to the coral holding facility at the University of Technology, Sydney. Corals were maintained under continuous flow, a water temperature of 25°C, a salinity of 33 and a photon irradiance of ~150 µmol photons $m^{-2}$ $s^{-1}$ (400–700 nm; 12 h:12 h light:dark cycle).

### Microsensors and laser modules

Scalar irradiance microsensors (tip diameter ~80 µm) had an isotropic angular response (s.d.=5%) (Lassen et al., 1992). Field radiance microsensors (tip diameter ~35 µm) had a narrow acceptance half angle of ~30 deg (Kühl and Jørgensen, 1992). $O_2$ microsensors had a tip size of ~50 µm, a response time of <2 s and a stirring sensitivity of <1.5% (Unisense A/S Aarhus, Denmark) (Revsbech, 1989). Oxygen sensors were linearly calibrated from signal readings in air-saturated seawater and anoxic seawater.

The light sources were all continuous wave solid-state laser-diode modules. We chose a red laser (636 nm, 4.5 mW, beam Ø=2.05 mm; Edmunds Optics, Barrington, NJ, USA) as the primary wavelength to investigate in detail lateral light propagation in coral tissues. Red lasers are one of the most common, reliable and cost-effective laser sources. Additionally, red light is an important contribution of the underwater spectral light field that corals receive on shallow-water coral reefs (Dustan, 1982), such as on the reef flat of the Heron Island lagoon (for a typical underwater spectrum, see supplementary material Fig. S2). The intensity of the incident downwelling irradiance in the red spectrum was comparable to the intensity in the blue and green spectrum of visible light (~1.5–2 µmol photons $m^{-2}$ $s^{-1}$ $nm^{-1}$) that was measured at our study site at ~1 m water depth during mid-day sun on a cloudless day (supplementary

material Fig. S2). The 636 nm laser module is also within the peak of the chlorophyll (chl) *c* $Q_y$ absorption band and is close to the $Q_y$ band of chl *a* and can thus be used to investigate light propagation effects on algal photosynthesis (e.g. Halldal, 1968). In contrast, wavelengths beyond 700 nm are out of the range of photopigment absorption, and earlier studies have shown that coral tissue is fairly transparent to such NIR (Magnusson et al., 2007; Wangpraseurt et al., 2012). Therefore, to differentiate light propagation due to tissue and skeleton optics, we additionally measured in detail the propagation of laser light with 785 nm emission (3.0 mW, beam Ø 2.01 mm; Edmunds Optics, Barrington, NJ, USA). To further investigate whether lateral light transfer occurs over a range of wavelengths within PAR, we also chose an intermediate green laser module of 532 nm (5 mW, beam Ø=2.03 mm; World Star Tech, Toronto, ON, Canada), which is within the absorption range of the peridinin–chlorophyll–protein complex, as well as a violet laser module of 405 nm (5 mW, beam Ø=3.98 mm; LaserMan, London, UK), which excites a range of fluorescent host pigments within the faviid corals (Salih et al., 2000).

### Light distribution

We illuminated defined tissue areas of the coral *F. speciosa* with red light (636 nm) and NIR (785 nm) and measured the beam spread along vertical and horizontal dimensions with fibre-optic sensors for scalar irradiance and field radiance (supplementary material Fig. S3). Microsensor measurements were conducted with the coral placed in a heated (25°C) flow-through chamber system supplying artificial seawater at a flow rate of ~3 cm $s^{-1}$ (Wangpraseurt et al., 2012). During these measurements, coral tissue was in an intermediate state of retraction, i.e. neither fully expanded nor contracted. For light microsensor measurements, the fibre-optic microprobes and laser diode were each mounted on a different micromanipulator (Pyro-Science, Aachen, Germany, and Märtzhäuser, Wetzlar, Germany) and aligned parallel to each other perpendicularly to the coral surface. The setup allowed for a minimum horizontal distance of 2 mm between the sensor tip and the laser beam. For each vertical profile, the microsensor was carefully inserted into the coenosarc tissue (in between skeleton ridges) by micro-incision until the sensor touched the coral skeleton (Wangpraseurt et al., 2012). Measurements were conducted on the coenosarc, which has a more even topography and less contractile tissue as compared with polyp tissue, thus allowing repeated measurements and more accurate estimates of horizontal light transfer. Vertical microprofiles were measured using the automatic profiling function of the motorized micromanipulator in steps of 200 µm from the skeleton surface (defined as 0 µm) upwards into the tissue until the tissue surface was reached. Between each vertical profile, the laser diode was moved horizontally away from the fibre in steps of 2 mm by manually using the micromanipulator. After measurements on the intact coral, the tissue was removed with an airgun and measurements were repeated on the bare skeleton under the same underwater conditions; measurement spots were chosen to be similar to coenosarc areas on the live coral (i.e. in between skeleton ridges). Residual air trapped between skeleton ridges was released by carefully tapping the skeleton and brushing its surface underwater with a paintbrush.

Vertical profiles on bare skeletons were measured from the water–skeleton surface until 2000 µm above the skeleton, as this was approximately the thickness of tissue covering the live coral (supplementary material Fig. S3). We performed six to seven corallite-level replicate profiles for each treatment, i.e. on the live coral and bare skeleton, with 636 and 785 nm laser modules for both scalar irradiance and field radiance microsensors on the *F. speciosa* specimen, yielding a total of 51 microsensor profiles. We chose here corallite-level rather than colony-level replication (i.e. biological variation) because we were interested in the mechanistic processes underlying light propagation. Additional scalar irradiance measurements were taken to investigate whether tissue behaviour affected lateral light transfer. Measurements were performed as described above, but only on the tissue surface (i.e. not with depth within the tissue). An expanded tissue state was achieved by dark-adapting the coral for ~1 h. Tissue contraction was induced by gently touching the centre of the oral disc of the polyp with a small needle. For each treatment, three corallite-level replicates were performed on *F. speciosa*.

Scalar irradiance and field radiance spectra were recorded with microsensors interfaced to a PC-controlled fibre-optic spectrometer (USB2000+ and Spectrasuite, Ocean Optics, Dunedin, FL, USA). The measured raw spectra (counts versus wavelength) were normalised to the measured incident intensity of the laser beam (i.e. 100% signal). For scalar irradiance measurements, the 100% signal was achieved by positioning the microsensor at an angle of 45 deg to the centre of the laser beam under the same measurement conditions and setup as with the measurements on the coral (i.e. the same vertical distance from the beam). For field radiance measurements, the microsensor was aligned so that the tip pointed directly into the centre of the beam. This was performed *in situ* underwater in a beaker at the same distance between the laser and the sensor, as for the measurements on the coral. To avoid signal saturation of microsensors, a neutral density filter (Optics Balzers, Balzers, Liechtenstein) was mounted perpendicularly in the laser diode beam and the 100% intensity was back-calculated according to the filter's known transmittance values.

The lateral attenuation of light at the skeleton surface and tissue surface of an intact coral as well as the bare skeleton surface (supplementary material Fig. S3) was fitted to an exponential decay equation: $y=y_o+Ae^{-Kx}$, where $A$ is the amplitude/light intensity, $K$ is the attenuation coefficient and $y_o$ is the $y$ offset/noise, with $y_o \leq 0.01A$. Lateral attenuation coefficients ($mm^{-1}$) were then expressed as $\mu=1/K$. Fitting was done using Origin Pro 8.0 (OriginLab, Northampton, MA, USA).

### Light transfer effects on $O_2$ evolution

To investigate whether lateral light transfer had an effect on $O_2$ evolution, we used $O_2$ microsensors. Measurements were performed as with the fibre-optic microprobes (see above), but with additional illumination of the coral with a background downwelling photon irradiance (~250 µmol photons $m^{-2}$ $s^{-1}$) as provided by a fibre-optic tungsten-halogen lamp (KL-2500, Schott, Mainz, Germany). This was done to avoid tissue movement, which would interfere with the $O_2$ measurements. The microsensor was positioned at 6 mm (minimum lateral distance possible) and 12 mm away from the incident red laser beam (636 nm), and the $O_2$ signal was recorded over time with and without laser illumination. The effect of laser illumination was then calculated as the percentage change between steady-state $O_2$ with/without laser illumination at each spot.

### Chlorophyll fluorescence imaging

We used a variable chlorophyll fluorescence imaging system (Maxi I-PAM, Walz, Effeltrich, Germany) (Ralph et al., 2005; Kühl and Polerecky, 2008) to investigate the lateral effect of laser-based illumination on the quantum yield of chl *a* fluorescence ($F$) and the maximum quantum yield of PSII. We mounted the imaging system vertically on a heavy-duty stand and illuminated samples with laser diodes almost vertically (<15 deg) from above. We used laser diodes for violet (405 nm), green (532 nm) and red (636 nm) light illumination of the corals within a narrow ~2 mm wide zone. Corals were dark-adapted (~30 min) and placed in a chamber with thermostated (25°C) and aerated seawater. The minimum fluorescence yield in the dark-adapted state ($F_o$) was determined using weak measuring light. A saturating light pulse (2500–3000 µmol photons $m^{-2}$ $s^{-1}$ for 0.8 s) was given in the dark to determine the maximum fluorescence yield ($F_m$). Maximal quantum efficiency of PSII in the dark-adapted state was calculated as $F_v/F_m$, where $F_v$ denotes the variable fluorescence, $F_v=F_m-F_o$. After 1 min, the sample was illuminated with a laser diode, upon which the transient fluorescence yield ($F_t$) changed in tissue areas beyond the one illuminated by the laser. Three corallite-level replicate measurements were performed on one colony for each of the three coral species (*F. speciosa*, *M. curta* and *G. aspera*) with each of three laser modules (405, 532 and 636 nm) and for both tissue types (coenosarc and polyp), yielding a total of 54 measurements. During fluorescence imaging, the tissue was neither fully expanded nor contracted.

Another saturating pulse yielded a measurement of $F'_m$, i.e. the maximum fluorescence yield in the presence of laser-based actinic light. The effective quantum yield of PSII was calculated as $\Phi_{PSII}=(F'_m-F)/F'_m$, and was used as 'PSII operating efficiency' to describe an estimate of the quantum yield of linear electron flux through PSII (Baker, 2008) as a function of impact distance of the laser-based actinic light. This calculation was performed only

for red laser light, which was chosen as the most relevant of the used laser modules in terms of the chlorophyll absorption spectrum for corals in shallow water. To calculate the horizontal distance over which the fluorescence yield changed, we used the transect function of Imaging Win (v2.21; Walz). The $F$ (laser on) transect was normalised to the $F_o$ (laser off) transect over the same tissue parts to reveal areas of laser beam impact (i.e. fluorescence ≠ 100%). The total impact width was then subtracted by the width of the respective laser beam and divided by 2 in order to obtain the average impact distance on one side of the laser beam (see Fig. 5B for an example). We also calculated transects of $\Phi_{PSII}$ relative to transects of the initial dark-adapted $F_v/F_m$ to investigate the impacts of lateral light transfer on coral photosynthetic potential. The distance over which laser light affected $F_v/F_m$ was calculated in the same manner as with $F$.

## Statistical analyses

Differences in fluorescent yield values ($F$) for each incident wavelength were analysed in a two-way factorial ANOVA between coral species and tissue type using Statistica version 10 (Statsoft, Tulsa, OK, USA). No differences were tested between wavelengths as differences in the laser output power affect the lateral impact distance. Assumptions for homogeneity of variance and normality were tested using Cochran's $C$-test and the Shapiro–Wilk test, respectively.

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### Competing interests

The authors declare no competing financial interests.

### Author contributions

D.W., M.K. and J.F. designed the research; D.W. and M.S. performed the research; M.K. and P.J.R. contributed new reagents/analytic tools; D.W., M.K., A.W.D.L., J.F. and M.S. analysed the data; and D.W. and M.K. wrote the paper with the help of all co-authors.

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### Supplementary material

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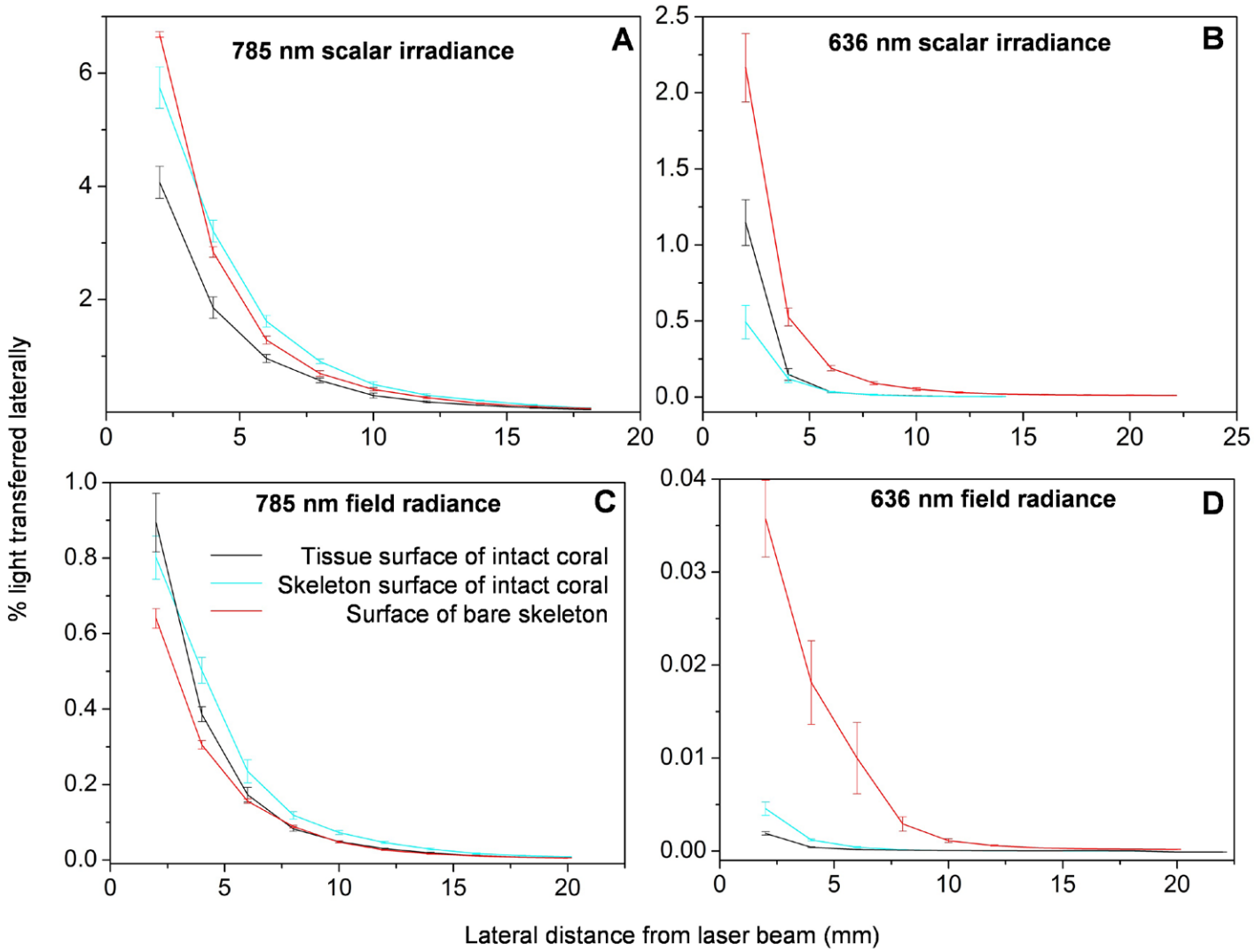


**Fig. S1.** Microprofiles of lateral light transfer in *Favia speciosa* plotted on a linear scale. Lateral light measurements (means ± s.e.m.; *N*=6–7 corallite-level replicates) were performed across coenosarc tissue in steps of 2 mm away from the incident laser beam. Measurements were performed on the skeleton surface of an intact coral (cyan), the tissue surface of an intact coral (black) and the skeleton surface of the bare skeleton (red) (corresponding to supplementary material Fig. S3 measurement positions 1–3). (A,B) Scalar irradiance for 785 and 636 nm, respectively; (C,D) field radiance at a zenith angle of 180 deg for a laser beam of 785 and 636 nm, respectively.

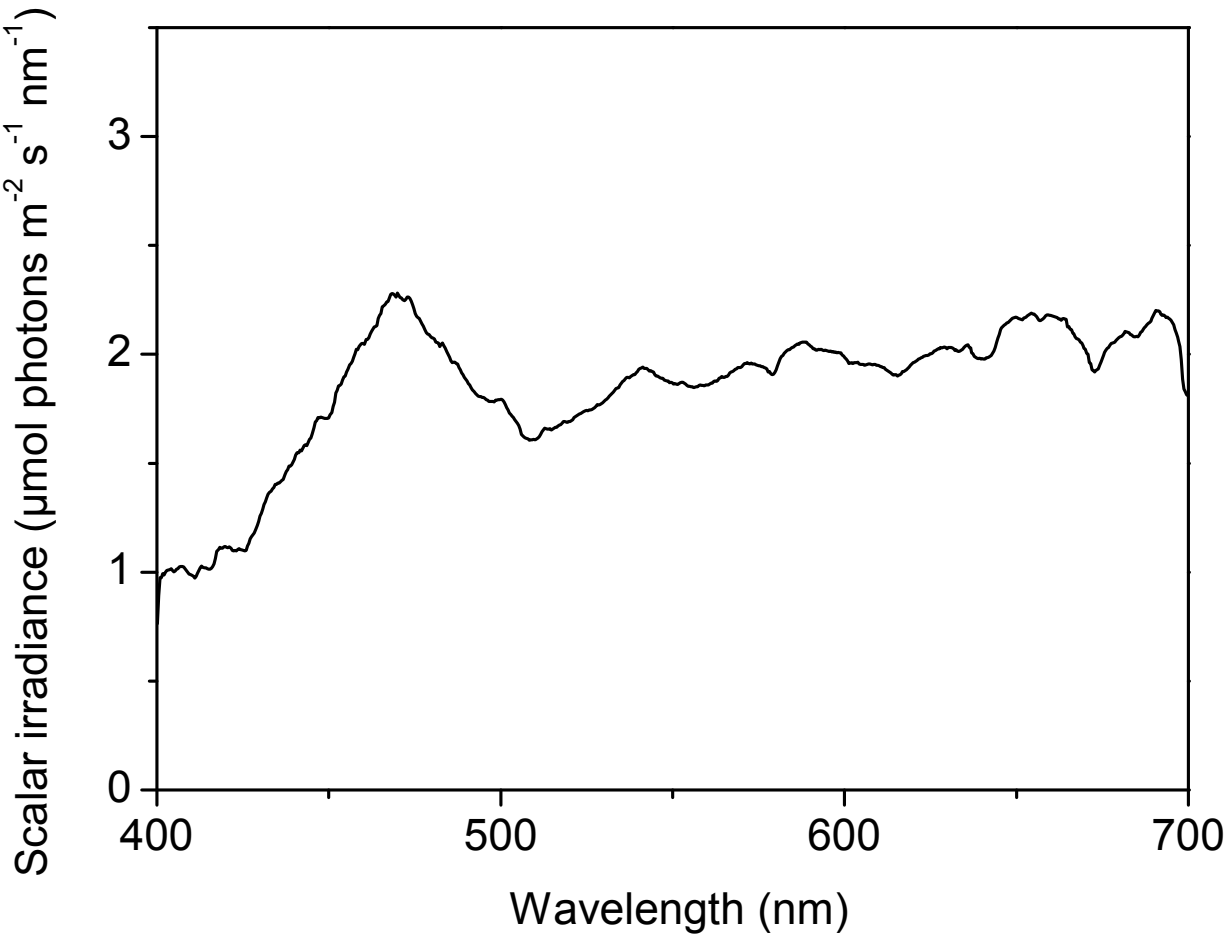


**Fig. S2.** Typical incident downwelling irradiance spectrum (400–700 nm) from the Heron Island reef flat at ~1 m water depth during mid-day sun on a cloudless day.

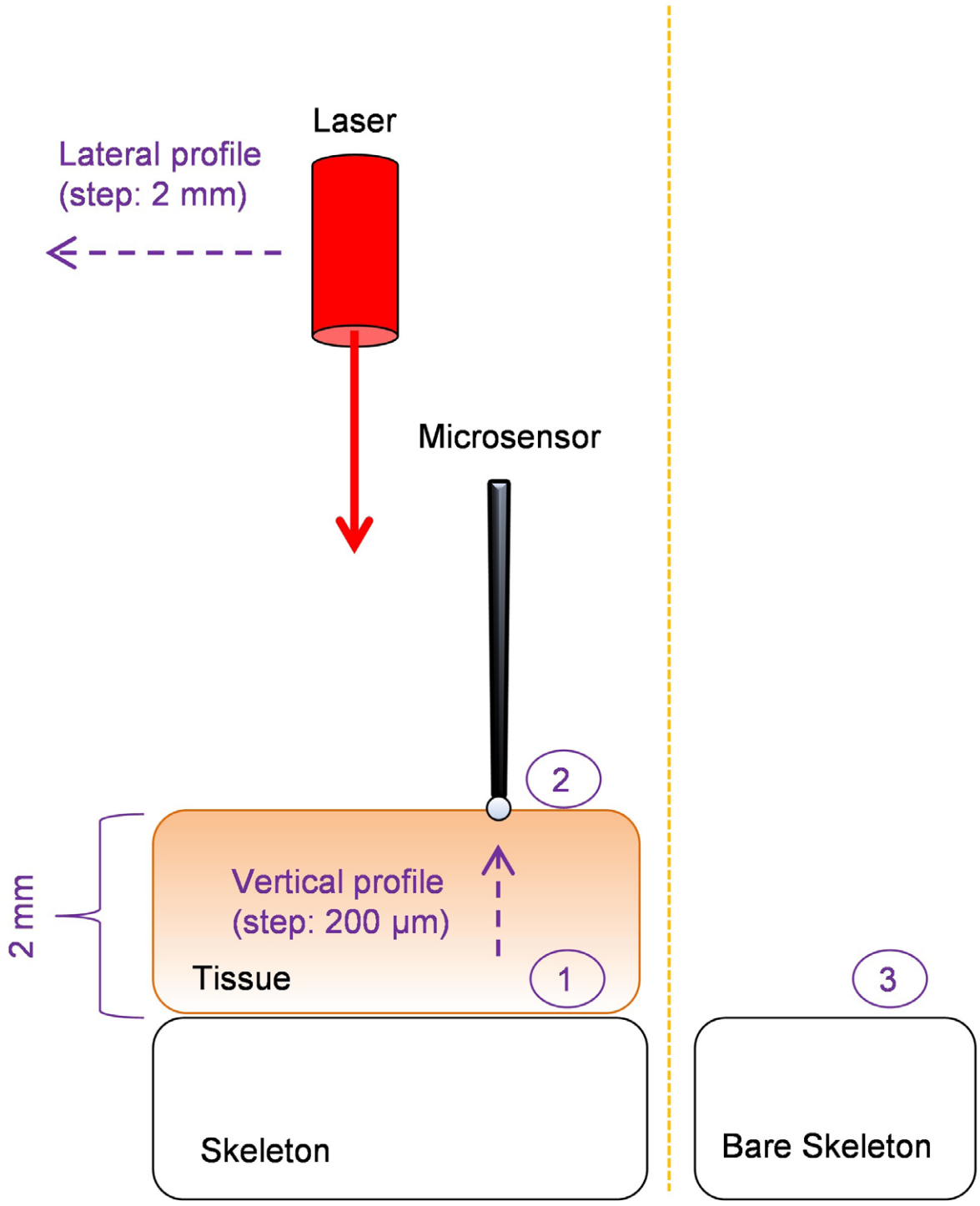


**Fig. S3.** Experimental design and measurement locations. Vertical profiles were done with fibre-optic microsensors (scalar irradiance or field radiance) in steps of 200 µm upwards from the skeleton surface (0 mm) until the tissue surface was reached (~2 mm). At each vertical position, a lateral profile was taken with the laser beam in steps of 2 mm over a lateral distance of ~2 cm. The same measurements were performed on the bare skeleton with coral tissue removed. Numbers (1–3) indicate the measurement locations that were used to estimate lateral light attenuation: 1, skeleton surface of an intact coral (defined as the measurement on the skeleton surface and the next measurement step 200 µm above the surface); 2, tissue surface of an intact coral (defined as the measurement on the tissue surface and the previous measurement step 200 µm below the surface); 3, skeleton surface of the bare skeleton (defined as the measurement on the skeleton surface and the next measurement step 200 µm above the surface). The first step size (i.e. + or – 200 µm) was included in all averages to reduce a potential bias in mispositioning of the sensor.