

Thermal effects of tissue optics in symbiont-bearing reef-building corals

Isabel M. Jimenez,^a Anthony W. D. Larkum,^{a,b} Peter J. Ralph,^a and Michael Kühl^{a,c,*}

^a Plant Functional Biology and Climate Change Cluster (C3), Department of Environmental Science, University of Technology Sydney, Sydney, Australia

^b School of Biological Sciences, Heydon-Laurence Building A08, University of Sydney, Sydney, Australia

^c Marine Biological Section, Department of Biology, University of Copenhagen, Helsingør, Denmark

Abstract

Reflectance spectroscopy and microscale temperature measurements were used to investigate links between optical and thermal properties of corals. Coral tissue heating showed a species-specific linear correlation to the absorbance of incident irradiance. Heat budgets estimated from absorbance and thermal boundary layer measurements indicated differences in the relative contribution of convection and conduction to heat loss in *Porites lobata* and *Stylophora pistillata*, and a higher heat conduction into the skeleton of the thin-tissued branching *S. pistillata* as compared to the massive thick-tissued *P. lobata*. Decreasing absorbance associated with bleaching resulted in decreased surface warming of coral tissue. Action spectra of coral tissue heating showed elevated efficiency of heating at wavelengths corresponding to absorption maxima of major zooxanthellae photopigments. Generally, energy-rich radiation (< 500 nm) showed the highest heating efficiency. Species-specific relationships between coral tissue heating and absorbance can be strongly affected by differences in the thermal properties of the skeleton and/or tissue arrangement within the skeletal matrix, indicating a yet unresolved potential for coral shape, size, and tissue thickness to affect heat dissipation and especially the conduction of heat into the coral skeleton.

Symbiont-bearing (hermatypic) reef-building corals are efficient light collectors, capable of intercepting a large amount, if not most, of the incident photosynthetically active radiation (PAR; 400–700 nm) (Enriquez et al. 2005; Stambler and Dubinsky 2005; Wangpraseurt et al. 2012). Light utilization by photosynthesis of their endosymbiotic dinoflagellate, *Symbiodinium* (zooxanthellae) is ultimately responsible for the success of scleractinian corals in oligotrophic waters (Falkowski et al. 1990). However, high irradiance and elevated water temperature can lead to photoinhibition of the zooxanthellae and oxidative stress (Lesser 2006). This can result in coral bleaching, i.e., the expulsion of the zooxanthellae and/or loss of photosynthetic pigments from the coral host tissue (Lesser 1997; Coles and Brown 2003). A newly recognized additional effect of the elevated light absorbing capacity of corals is the risk of increased coral surface temperature, particularly under conditions of high irradiance and low water flow in shallow environments (Fabricius 2006; Jimenez et al. 2008, 2012). This additional source of heat has hitherto largely been ignored in coral stress physiological studies but could have implications for our understanding of the thermal exposure and tolerance of individual corals before and during a bleaching event.

Light absorption by corals is mainly due to the major photosynthetic pigments of the zooxanthellae: light-harvesting pigments (chlorophyll [Chl] *a* and *c*₂, and peridinin) and photoprotective pigments (such as β -carotene, diadinoxanthin, and diatoxanthin) (Jeffrey and Haxo 1968; Lesser et al. 2000). Additionally, fluorescent and nonfluorescent host pigments can contribute to the reflection and/or absorption in the blue-green part of the spectrum (Dove et al. 1995; Salih et al. 2000; Mazel and

Fuchs 2003) and are responsible for the spectacular range of coral color hues (e.g., blue, green, pink). Variations in light absorbing capacity among corals in shallow reef environments can create intercolonial differences in temperature up to ~ 1°C (Fabricius 2006; Jimenez et al. 2008, 2012).

Fabricius (2006) showed a positive relationship between a coral's surface warming and its "color darkness" as measured with color chart scores ("Coral Health Chart," Coral Watch), which are qualitative proxies for a coral's light absorbing capacity and may be heavily affected by the color perception of the human eye. However, such indices cannot quantify the continuous range of coral pigmentation, nor can they be used in a coral heat budget model. Instead, the heat influx into coral tissue, and its effect on coral temperature, is best described using a quantitative optical parameter such as the absorbance (*A*), defined as the fraction of incident irradiance intercepted and absorbed by the tissue.

Spectral reflectance measurement is a simple and noninvasive method to (1) evaluate coral optical characteristics (Stambler and Dubinsky 2005; Hochberg et al. 2006; Stambler and Shashar 2007), (2) discriminate between reef bottom types (Hochberg et al. 2003), and (3) potentially monitor coral bleaching events (Yamano et al. 2002). In particular, estimates of the fraction of light absorbed by coral tissue, i.e., the absorbance, can be reconstructed from reflectance spectra (Enriquez et al. 2005), allowing estimates of the energy influx into the tissue layer of variously pigmented corals. Most robust absorbance estimates are obtained from reflectance measurements with integrating spheres that take into account all potential scattering errors (Stambler and Dubinsky 2005), but such specialized systems are not generally available and

* Corresponding author: mkuhl@bio.ku.dk

absorptance determination frequently rely on simple reflection measurements with fiber-optic probes (Stambler and Shashar 2007). Together with measurements of heat dissipation and transport, such absorptance measurements could ultimately be integrated in a predictive coral thermal model, which describes coral temperature as a function of irradiance and the heat fluxes in and out of the tissue layer (Jimenez et al. 2008).

This study focuses on the thermal consequences of light absorption by coral tissue and the potential for predicting the thermal exposure of corals from reflectance-based optical measurements. The goal was to obtain insights into how coral optical properties affect their thermal microenvironment. Spectral reflectance and temperature microsensor measurements were used to quantify the light absorbing efficiency of coral tissue and its effects on coral surface warming. *Stylophora pistillata* and *Porites lobata* samples were exposed to a thermal bleaching treatment to produce contrasting dark and pale pigmentations, and investigate the heat budgets of bleaching corals. *S. pistillata* and *P. lobata* were chosen as a bleaching-sensitive and -resistant species, respectively (Marshall and Baird 2000; Loya et al. 2001).

Methods

Coral sampling—Hemispherical colonies of *P. lobata* and branching colonies of *S. pistillata* were collected from the shallow reef flat adjacent to Heron Island Research Station and transported to the permanent coral holding facility at the University of Technology, Sydney. The corals were allowed to acclimate for at least 4 months in a 500 liter aquarium supplied with recirculating artificial seawater (salinity 32) made out of carbonate (2.5 mmol L^{-1}) and synthetic sea salt (Coral Pro, Red Sea) in reverse-osmosis water. Water temperature was kept at $25 \pm 1^\circ\text{C}$ and corals were exposed to actinic light with a downwelling quantum irradiance of $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ as provided by a 400 W metal halide light source (Ablite) during a 12:12 light:dark cycle. Three replicate colonies of *P. lobata* (brown morph) and three fragments (5 cm) of *S. pistillata* (brown morph) were used in each of the control and bleaching treatments.

Microscale temperature measurements and heat flux calculation—The temperature of the coral tissue surface was measured with temperature microsensors (TP50, Unisense AS) for each coral before and after the bleaching treatment, using the microprofiling equipment and experimental setup described in Jimenez et al. (2008). Corals were placed in a custom-built recirculating flow chamber (Plexiglas, $10 \times 5 \times 36 \text{ cm}$) under a flow rate of 0.75 cm s^{-1} , and exposed to a downwelling quantum irradiance of $1800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (corresponding to an irradiance of 450 W m^{-2}) as provided by a fiber-optic light source (Schott KL-2500) equipped with a collimating lens and a heat filter.

Coral surface warming (ΔT) was calculated as the temperature difference between measurements at the coral tissue surface and measurements in the mixed water column beyond the 1–3 mm-thick thermal boundary layer.

The convective heat flux between coral tissue and the surrounding water, Q_{conv} , was calculated as $Q_{\text{conv}} = \Delta T \times k/\delta$, where k is the thermal conductivity of water ($0.616 \text{ W m}^{-2} \text{ K}^{-1}$; Denny 1993) and δ is the effective thickness of the coral thermal boundary layer determined from temperature microprofiling (Jimenez et al. 2008).

Bleaching experiment—Treatment: Three replicate colonies of *S. pistillata* and *P. lobata* were placed in a temperature-controlled recirculating tank filled with 100 liters of artificial seawater (see above) and the temperature was ramped up from $25 \pm 1^\circ\text{C}$ to $32 \pm 1^\circ\text{C}$ over 3 d at approximately $+0.2^\circ\text{C h}^{-1}$ during the daylight period. Corals were exposed daily to a downwelling quantum irradiance of $300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (400–700 nm) for 12 h followed by 12 h of darkness. Treatment corals were maintained at the above irradiance and temperature (equivalent to bleaching conditions) up to 3 d following the ramping period. Three replicate control colonies of each species were maintained at $25 \pm 1^\circ\text{C}$ under a quantum irradiance of $200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$. At the end of the treatment period, the samples (control and treatment) were sacrificed for determination of zooxanthellae density. The *S. pistillata* samples in the bleaching treatment experienced severe and sudden discoloration by the end of the temperature ramping period, and were thus sacrificed immediately (before mortality could occur). For *P. lobata*, the bleaching treatment was maintained until a 50% decline in photochemical efficiency (see below) and clear visible signs of bleaching were observed, i.e., after 3 d at 32°C .

Variable chlorophyll fluorescence measurements: The progression of bleaching was monitored by visual observation, reflectance spectra (see below) and variable chlorophyll fluorescence measurements of the zooxanthellae's photochemical efficiency. Triplicate measurements of the dark-adapted maximum quantum yield of photosystem II ($F_v:F_m$) were performed daily (after 11 h of darkness) on adjacent points within a 2 cm^2 area of each coral, using a Diving-PAM fluorometer (Walz GmbH) fitted with a 1.5 mm acrylic fiber optic.

Coral reflectance spectra: Coral reflectance spectra were used to monitor the variation in optical characteristics of coral tissue during and immediately after the temperature ramping period (days 4 and 5, respectively), and for *P. lobata* after 2 and 3 d at 32°C (days 7 and 8). The reflectance spectrum of each coral was measured between 400 and 750 nm (at 0.35 nm spectral resolution) using a fiber-optic spectrometer (USB2000, Ocean Optics) equipped with a 1.5 mm-diameter bifurcated fiber-optic reflectance light probe (Ocean Optics). For measurements, each coral sample was submersed in filtered seawater in a small glass beaker and the tip of the probe was positioned at a distance of $\sim 5 \text{ mm}$ and perpendicular to the coral surface. To be consistent with the boundary layer analyses, reflectance measurements were performed on the apical surface of the hemispherical *P. lobata* samples, and along the length of the horizontal *S. pistillata* branches. Triplicate

spectra were collected from adjacent points within an area of 2 cm² for each coral.

Incident light (400–800 nm) was provided by a deuterium-halogen light source (DH-2000-BAL, Ocean Optics) connected to the output branch of the light guide, whereas the reflected light was collected through the input branch of the spectrometer. Based on a numerical aperture of 0.22 of the collecting fiber optic (cf., Ocean Optics), the input branch thus collected light over a solid angle of ~ 0.1 steradian (sr), which at the measuring distance projected to a circular area (field of view) of ~ 2 mm². The chosen mode of illumination (through the small fiber optic) created a small light spot on the coral surface. Observation of the spread of the light spot over the coral surfaces indicated differences in skeletal scattering properties between the hemispherical *P. lobata* and the branching *S. pistillata* samples. This is consistent with recent observations of differences in forward scattering among branching pocilloporids and massive growth forms (Daniel Wangpraseurt pers. comm.). As a result, and to account for variations in tissue optical properties only, clean coral skeletons were used as reference standards for reflectance calculations. Thus, coral spectral reflectance (R_λ) was estimated as the ratio of light collected from the coral surface to that reflected from a clean airbrushed skeleton sample of each species.

Spectral absorptance, i.e., the fraction of incident light absorbed, was estimated as $A_\lambda = 1 - R_{\lambda\text{corr}}$, where $R_{\lambda\text{corr}}$ is the spectral reflectance normalized to the measured reflectance at 750 nm (R_{750}); this calculation assumes that absorption by the skeleton is negligible at 750 nm (Enriquez et al. 2005). Spectral absorptance, A_λ , was then averaged over PAR (400–700 nm) to compare with previously published coral absorptance values, and over the greater spectral range of the light source (400–800 nm) to estimate the fraction, A , of total incident radiative energy absorbed in the coral tissue. The corresponding absorbed irradiance (in W m⁻²), Q_{rad} , was subsequently calculated as $Q_{\text{rad}} = A \times E_d$, where E_d is the downwelling irradiance.

Cell counts: Zooxanthellae density was measured prior to experimentation and after 5 and 8 d for *S. pistillata* and *P. lobata*, respectively, both for the bleaching and control treatments. Coral tissue was collected from the upper, light-exposed region of the colonies using an airbrush and centrifuged in filtered (0.45 μm) seawater at 2000 rotations min⁻¹ for 10 min. The separated algal pellet was resuspended in filtered (0.45 μm) seawater and homogenized. Zooxanthellae density (quantified as cells cm⁻² coral tissue) was estimated from the average of four replicate haemocytometer counts standardized to the coral surface area as measured using the wax weighing method (Stimson and Kinzie 1991).

Coral thermal action spectrum—Coral surface warming as a function of the spectral composition of incident light was measured in a bleached and a control colony of each of *P. lobata* and *S. pistillata*. Monochromatic light (15–20 nm half-band width) was provided by a 500 W Xenon monochromatic light source (Pollilight PL500, Rofin) equipped with interference filters (peak transmission

wavelengths 415, 440, 490, 505, 530, 555, 590, 620, 650, 680 nm) and an 8-mm-diameter liquid light guide with a quartz focusing lens. The light beam was oriented at a 10° angle relative to the water surface so as to illuminate the coral from above. Coral surface temperature was measured after 5 min exposure to each light setting using the micro-profiling equipment and experimental setup described in Jimenez et al. (2008).

Water temperature was monitored continuously in the flow chamber away from the coral using a type K thermocouple ($\pm 0.1^\circ\text{C}$, Omega) connected to an analogue-digital logger (DT-50 DataTaker Pty) and calibrated against the temperature microsensor. Coral surface warming was determined as the temperature difference between the coral surface and the surrounding water.

The actual photon flux density at each wavelength was measured as quantum scalar irradiance using an underwater spherical micro quantum sensor (US-SQS/L, Walz GmbH) with a quasi-flat spectral response over 400–700 nm, connected to a light meter (LI-1400, LiCor). The spherical sensor was positioned below the rim of a small dark well positioned in the flow chamber in place of the coral, so as to capture the downwelling irradiance transmitted through water to the coral, and exclude diffuse and upwelling flux reflected from the chamber. For comparison between monochromatic lights, the measured coral surface warming at each wavelength was normalized to a quantum scalar irradiance of 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. As the energy content of monochromatic light is a function of wavelength (λ), coral surface warming was also normalized to equivalent energy fluxes, estimated as $E_\lambda = hc/\lambda$, where h and c are Planck's constant and the speed of light in vacuo, respectively.

Statistical analysis—Repeated-measures analysis of variance (rm-ANOVA) was used to test for changes in Fv:Fm over the duration of the experiment ($\alpha = 0.05$). Comparisons of zooxanthellae density, absorptance, and surface warming between the pretreatment, control, and treatment corals were performed using one-way ANOVA. Kolmogorov–Smirnov normality test and Levene's homogeneity of variance test were used to verify that the data satisfied the assumptions of the parametric ANOVA.

Results

Physiological response to the bleaching treatment—Exposure to bleaching conditions of elevated temperature and irradiance (32°C and 300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) resulted in an $\sim 40\%$ reduction in symbiont photochemical efficiency measured as the maximal quantum yield of photosystem II, Fv:Fm (Fig. 1), and an ~ 3 -fold reduction in zooxanthellae density within the tissue of *S. pistillata* and *P. lobata* (Table 1). This occurred by the end of the temperature ramping period (day 5) for *S. pistillata*, and more progressively during the following 3 d in *P. lobata*. The Fv:Fm values of the control treatments remained constant over the duration of the experiment, at ~ 0.70 in *S. pistillata* and 0.59 in *P. lobata* (rm-ANOVA, $p = 0.20$ and 0.49, respectively).

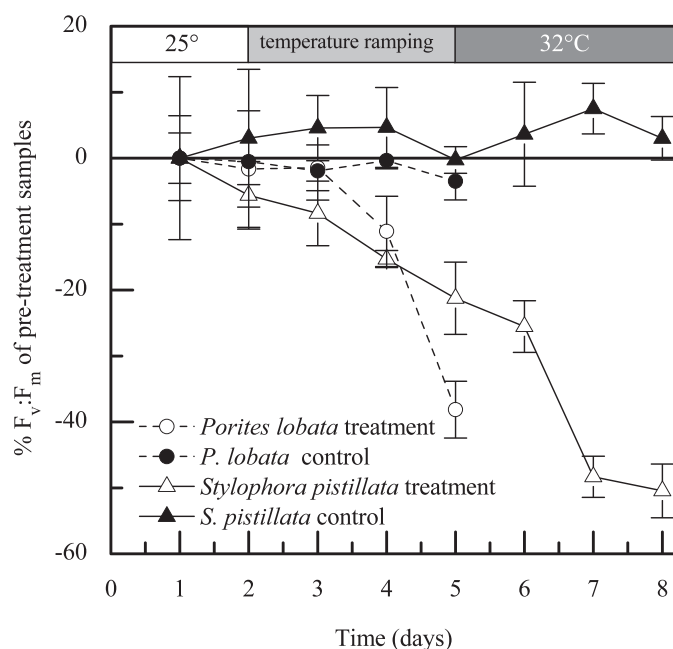


Fig. 1. Relative change of photochemical efficiency ($F_v:F_m$) in relation to pretreatment responses ($n = 3 \pm \text{SE}$) of the control (solid symbols) and treatment (open symbols) of brown color morphs of *Stylophora pistillata* (triangles) and *Porites lobata* (circles), respectively. For the treatment samples, the 3 d of temperature ramping from the control temperature (25°C) are indicated as the light gray bar, and the treatment temperature (32°C) as the dark gray bar. Control samples remained at 25°C.

Coral optical characteristics: Reflectance spectra—The *S. pistillata* specimens were visibly bleached (white) by day 5, with no visible paling occurring the day before. This qualitative and subjective visual assessment of the bleaching response of *S. pistillata* was mirrored by a sudden increase in spectral reflectance between 400 and 700 nm from day 4 to 5 (Fig. 2). In contrast, bleaching of the *P. lobata* samples exposed to 32°C was characterized by a gradual paling over the 3 d following the end of the temperature ramping period (Fig. 2).

The reflectance spectra of the healthy corals (controls and pretreatment) had a similar shape for both species (Fig. 2): a depression between 450 and 550 nm, followed by a rise between 550 and 650 nm with a triple-peak pattern near 575, 600, and 650 nm, and a conspicuous Chl *a* absorption feature near 675 nm. R_λ increased rapidly above 680 nm and reached a maximum value close to 100% at 700 nm. The bleaching treatment resulted in an increased R_λ at all wavelengths in the visible range of the spectrum (400–700 nm), while the overall shape of the triple-peak pattern was preserved.

The spectrally averaged absorbance (A) of the coral tissue in the control and pretreatment corals were similar for both species, with coral tissues absorbing $\sim 70\%$ of incident PAR (400–700 nm) (Fig. 2), and on average 50% of the energy provided by the light source between 400 and 800 nm (Table 1). The *S. pistillata* specimens exposed to the bleaching treatment experienced an overnight 3-fold reduction in A , and by day 5 the tissue layer absorbed only 17% of the total incident irradiance ($A = 0.17$; Table 1), or 24% of incident PAR. In contrast, the reduction in A for the *P. lobata* specimens was slower and after 3 d at 32°C, the tissue was still absorbing 30% of total incident irradiance, or 43% of incident PAR.

Coral thermal exposure and heat budget—The decrease in absorbance and zooxanthellae density was associated with a decrease in the surface warming of the tissue of both species when exposed to a quantum irradiance of $1800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and a flow velocity of 0.75 cm s^{-1} (Table 1). For all treatment groups, *P. lobata* experienced a higher surface warming compared to *S. pistillata* (Table 1). Even the surface temperature of the bleached *P. lobata* samples was higher than that of the control *S. pistillata*.

The estimated heat loss by convection from the coral tissue to the surrounding water was larger for *P. lobata* than *S. pistillata*, under a similar heat influx, i.e., similar absorbed incident irradiance (Table 2). Convective heat loss thus contributed $\sim 60\%$ and $\sim 30\%$ of the total heat flux out of the tissue for *P. lobata* and *S. pistillata*,

Table 1. The effects of temperature-induced bleaching on coral optics and tissue warming. Measurements were taken from the end of the control treatment (control), the first measurement prior to exposure to bleaching conditions (pretreatment), and the end of the exposure period (treatment). Numbers represent averages \pm standard error ($n = 3$), and significant differences ($p < 0.05$) are denoted with superscript letters. ns, not significant.

Species and treatment	Cell density (cells $\text{cm}^{-2} \times 10^6$)	PAR absorbance. A (400–700 nm)	Total absorbance, A (400–800 nm)	Surface warming, ΔT (°C)
<i>Porites lobata</i>				
Pretreatment	1.27 ± 0.56^a	0.73 ± 0.01^a	0.53 ± 0.01^a	0.29 ± 0.03^a
Control	0.94 ± 0.27^a	0.70 ± 0.03^a	0.51 ± 0.02^a	0.31 ± 0.04^a
Treatment	0.32 ± 0.11^b	0.37 ± 0.07^b	0.27 ± 0.05^b	0.16 ± 0.02^b
<i>p</i> -value	0.020	0.010	0.010	0.030
<i>Stylophora pistillata</i>				
Pretreatment	0.71 ± 0.17^a	0.66 ± 0.06^a	0.48 ± 0.04^a	0.04 ± 0.02
Control	0.74 ± 0.32^a	0.71 ± 0.05^a	0.51 ± 0.03^a	0.05 ± 0.01
Treatment	0.22 ± 0.14^b	0.25 ± 0.08^b	0.18 ± 0.06^b	0.01 ± 0.01
<i>p</i> -value	0.002	0.009	0.009	ns

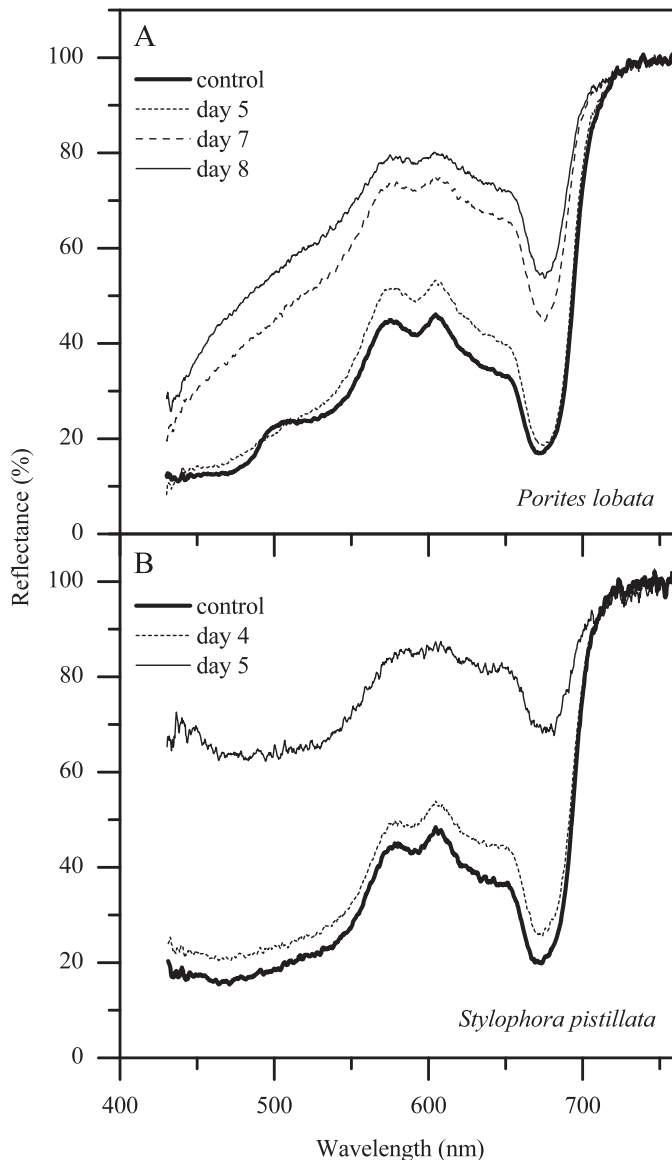


Fig. 2. Spectral reflectance of (A) *P. lobata* and (B) *S. pistillata* measured during the bleaching treatment. For each species, measurements of backscattered light from the tissue surface of intact corals were normalized to the measured backscattered light from clean coral skeletons of the respective species. Curves show average spectra ($n = 3$). Relative standard errors of all spectra were $< 5\%$.

respectively. Bleaching caused a reduction in the total heat influx but did not affect the relative proportions of convection and conduction heat losses (Table 2).

Coral thermal action spectrum—The thermal action spectra of coral tissue heating (Fig. 3) showed that blue light (400–500 nm) caused the highest surface warming. A slight peak and shoulder at 620–680 nm and 490–550 nm, respectively, indicated a contribution to coral heating by light-absorbing symbiont pigments such as Chl *a* and *c*₂, as well as protein-bound peridinin. However, these features disappeared in the bleached samples, where the contribution of wavelengths > 500 nm to coral heating were

reduced to almost zero. The bleached *P. lobata* samples conserved a higher spectral absorbance in the blue (< 500 nm) as compared to 500–700 nm, and their action spectrum showed that the shorter wavelengths contributed most to coral surface warming.

Discussion

The optical absorption properties of coral tissue have long been recognized as an important determinant of coral photophysiology (Shibata and Haxo 1969; Dubinsky et al. 1984; Kühl et al. 1995) but have only recently been linked to the potential increase in coral surface temperature under conditions of low flow and high irradiance (Fabricius 2006; Jimenez et al. 2008, 2011). This study is thus the first to describe coral surface warming as a function of a quantitative estimate of the fraction of absorbed irradiance (absorbance), and we present the very first data on differential thermal effects by the spectral composition of incident irradiance.

Tissue light absorption—The control and pretreatment specimens of *P. lobata* and *S. pistillata* had a similar absorbance of 70–80% of incident PAR (Table 1), consistent with previous findings (Enriquez 2005). Absorption signatures from the light-harvesting pigments of the zooxanthellae were evident from a distinct reflectance minimum near 675 nm (due to Chl *a*), shoulders in reflectance spectra between 450 and 550 nm that can be attributed to peridinin (Hochberg et al. 2003, 2004), and reflectance minima near 590 and 640 nm that indicate absorption by Chl *c*₂ (Shibata and Haxo 1969). Despite the small sample size used in this study ($n = 3$) and the rather large variability in measured symbiont cell density (Table 1), absorbance values were similar between colonies and for both species, and this is consistent with previous findings that absorbance is relatively constant for pigment concentrations > 20 mg Chl *a* m^{-2} (Enriquez et al. 2005).

The loss of symbionts during bleaching leads to different changes in the absorbance (*A*) of the two species; for *S. pistillata*, the reductions in symbiont density and absorbance were equivalent (3-fold, Table 1), whereas for *P. lobata*, a similar reduction in symbiont density was associated with a smaller reduction in absorbance (Table 1). A nonlinear relationship between cell density and absorption efficiency is indicative of greater pigment self-shading (Lesser et al. 2000; Enriquez et al. 2005) in the tissue of *P. lobata* compared to *S. pistillata*. In addition to a greater symbiont cell density (Table 1), *P. lobata* also has thicker tissue and a different skeletal microstructure than *S. pistillata* (Barnes and Lough 1992). The thin (~ 1 mm) layer of tissue of *S. pistillata* lies around an imperforate skeleton and the polyps are arranged in separate corallites. In contrast, the tissue of *P. lobata* interweaves with the skeletal matrix and can penetrate up to ~ 10 mm. The penetration depth of living tissue within the skeletal matrix (Kaniewska et al. 2011; Wangpraseurt et al. 2012), together with light scattering and transmission properties of the skeleton (Magnusson et al. 2007; Reef et al. 2009; Teran

Table 2. The effects of temperature-induced bleaching on coral heat budget. Absorbed irradiance (Q_{rad}) and heat loss by convection (Q_{conv}) in the tissue of *P. lobata* and *S. pistillata* exposed to an irradiance of $1800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (450 W m^{-2}) and a flow velocity of 0.75 cm s^{-1} . Measurements were taken at the end of the control treatment (control) and the exposure period (treatment). Numbers represent averages \pm standard error ($n = 3$).

Species and treatment	Q_{rad} (W m^{-2})	Q_{conv} (W m^{-2})	Q_{conv} (% of Q_{rad})
<i>Porites lobata</i>			
Control	230 ± 9	149 ± 18	~ 65
Treatment	122 ± 23	74 ± 10	~ 61
<i>Stylophora pistillata</i>			
Control	230 ± 14	72 ± 13	~ 31
Treatment	81 ± 27	22 ± 11	~ 27

et al. 2010), may thus affect the local distribution of light absorption and thus the degree of local heating. This in turn could affect the capacity for the surrounding water to remove excess heat by convection.

Cellular pigment density in coral tissue is known to vary spatially and temporally according to temperature and irradiance conditions (Dubinsky et al. 1990), as well as among species (Dubinsky et al. 1984; Warner et al. 1996; Ulstrup et al. 2008). *P. lobata* may also harbor distinct subpopulations of zooxanthellae characterized by genetic differences, variable pigment contents, different photoacclimation responses, and, possibly, acclimatized to heterogeneous light microenvironments within the host tissue (Apprill et al. 2007; Wangpraseurt et al. 2012). It is thus possible that lighter pigmented endosymbiotic cells were expelled first from the *P. lobata* specimens, while more pigmented symbionts remained in deeper tissue layers, thus leaving partially bleached colonies retaining a significant capacity for light absorption. Our results highlight that light absorption and thus heat influx into coral tissue is strongly influenced by zooxanthellae photophysiology, and can be affected by interspecific differences in symbiont distribution and tissue thickness.

Irradiance absorption is considered here as the only heat flux into coral tissue, while the heating effects of photosynthesis and respiration are considered negligible by comparison. Photosynthesis and respiration do not have a detectable effect on the temperature of terrestrial leaves and are routinely disregarded from their heat budgets (Gates 1980). Similarly, the heat budgets of intertidal invertebrates during air exposure sensibly ignore metabolic heat production, which is all but negligible when compared to irradiance, convection, and conduction (Helmuth 1998). Energy budgets in optically dense microbial mats also showed that heat dissipation from light absorption is predominant (Al-Najjar et al. 2010).

Interspecific differences in coral heat budget—The decrease in coral tissue surface warming (ΔT) during bleaching was equivalent to the reduction in coral tissue absorptance (A) (Table 1), thus indicating that the surface warming of a coral can be described as a linear function of the measured fraction of absorbed incident irradiance. This is consistent with predictions of a model of coral heat budgets, i.e., eq. 13 in Jimenez et al. (2008), as well as previously reported linear relationship between the “color

darkness” of coral tissue and its surface warming (Fabricius 2006). Such a linear relationship can be used in a simple coral thermal model to estimate the extent, to which the temperature of corals can increase under conditions of high irradiance and low water flow (Jimenez et al. 2008, 2011); conditions that occur repeatedly during summer low tides in shallow reef environments (McCabe et al. 2010; Jimenez et al. 2012). However, the relationship is species specific; the ratio between surface warming (ΔT) and absorptance (A) was ~ 0.1 and ~ 0.5 for *S. pistillata* and *P. lobata*, respectively (Table 1); *P. lobata* from all treatment groups reached a higher temperature than even the control and pretreatment *S. pistillata*, despite similar (or lower) absorptance values.

A stronger surface warming of the hemispherical massive coral, *P. lobata*, compared to the thin *S. pistillata* branches is consistent with previous results showing that such differences between branches and massive corals were not attributed to shape-related differences in the thermal boundary layer thickness and heat loss to the surrounding water (Jimenez et al. 2008, 2011). The present study shows that differences in tissue temperature apparently are not due to measurable differences in absorptance either, pointing toward a potential role of the thermal properties of the coral skeleton and/or difference in the thickness and heat capacity of coral tissue. The heat budgets estimated from absorptance and boundary layer measurements (Table 2) indicate that the relative contribution of convection and conduction to heat loss may be different for *P. lobata* and *S. pistillata*, and that heat conduction into the skeleton may be greater for the branching *S. pistillata*.

Bleaching effects on coral tissue thermal exposure—The relationship between optical and thermal properties of corals may have strong implications for our understanding of the severity of the bleaching response of individual corals, as heat exposure is known to affect physiological responses such as photoinhibition (Jones et al. 1998), production of reactive oxygen species and oxidative stress (Downs et al. 2002), host cell apoptosis (Ainsworth et al. 2008), change in heat shock proteins (Coles and Brown 2003), and other repair processes (Obura 2005).

The decreasing light absorbing capacity associated with bleaching resulted in a decreasing surface warming (ΔT) of coral tissue when exposed to high irradiance and low water flow (Table 1). Thus, during a summer bleaching event the

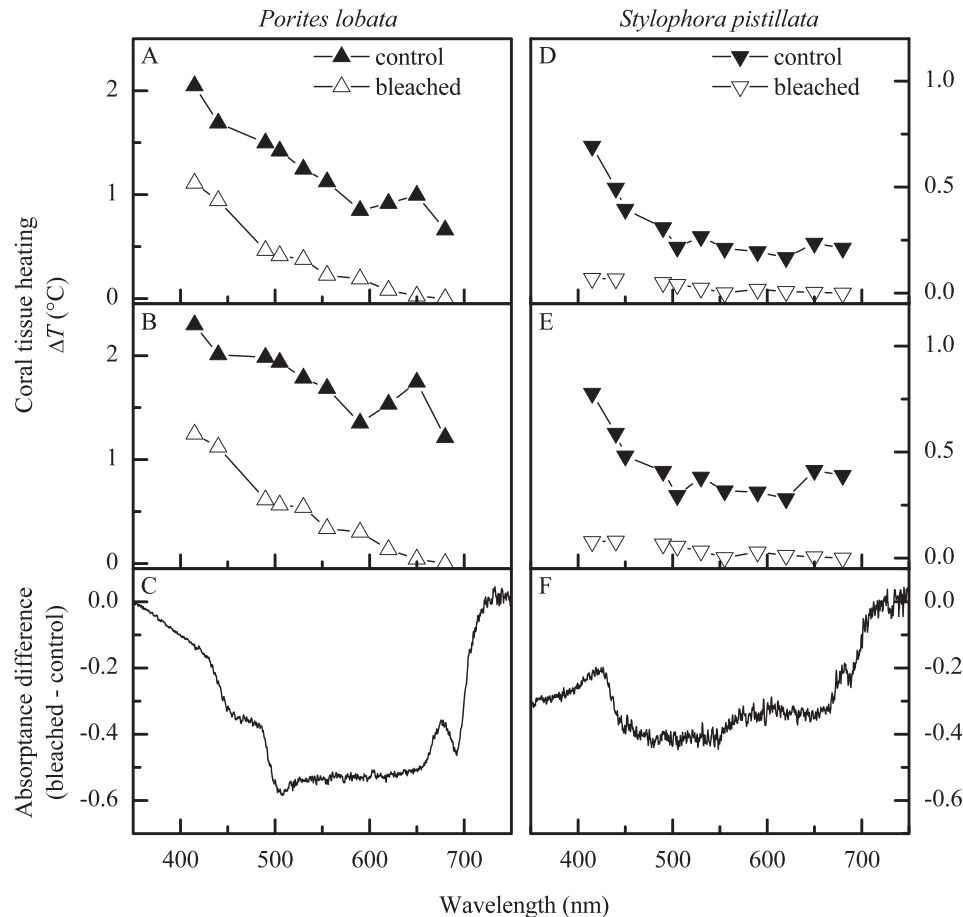


Fig. 3. Action spectra of coral surface warming for bleached and control specimens of (A, B) *S. pistillata* and (D, E) *P. lobata* and (C, F) differences in spectral absorbance between the bleached and healthy coral samples. Coral surface warming at each wavelength was normalized (A, D) to an equivalent quantum irradiance of $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ and (B, E) to an equivalent irradiance of 1000 W m^{-2} .

loss of zooxanthellae and/or photosynthetic pigments from coral tissue could, as a side effect, reduce the risk of additional heat exposure at low tide, caused by strong light penetration and low water flow (McCabe et al. 2010). The reduction in tissue thermal exposure of *P. lobata* was less pronounced and more gradual than in *S. pistillata* (Table 1), consistent with a more gradual decline in photochemical and light absorbing efficiencies (Figs. 1 and 2, respectively). In the field, this would result in more days, over which the temperature of *P. lobata* tissue could increase at low tide.

On the other hand, following a bleaching event, as corals recover their pigmentation they would progressively be exposed to increased risk of elevated thermal exposure if conditions of high light and low water flow occur repeatedly at low tide (Jimenez et al. 2012). Interspecific differences in the heat exposure of repopulating zooxanthellae may thus influence the thermal acclimatization of recovering corals and such differences should be taken into consideration for accurate monitoring or modeling of heat exposure during extended bleaching events and subsequent recovery.

Spectral effects on coral temperature—Thermal effects of shortwave radiation: This study demonstrates for the first time that the spectral composition of incident irradiance affects the magnitude of coral surface warming and in particular that the blue region of the visible spectrum ($< 500 \text{ nm}$) is most efficient at heating coral tissue (Fig. 3). Under equal photon doses (Fig. 3A,D), the higher energy content of blue photons caused more efficient heating. Therefore, a unit photon (quantum) flux of blue monochromatic light contains more energy than an equivalent photon (quantum) flux of red monochromatic light, and consequently, if absorbed, generates more heat within coral tissue. When blue and red light were provided at equivalent energy flux (Fig. 3B,E), coral heating efficiency still differed, possibly reflecting differences in absorption maxima of major zooxanthellae photopigments. Such spectral effects on coral tissue heating also imply that the optical characteristics of the water column, by affecting the spectral transmission of downwelling irradiance, have the potential to affect coral surface warming. Optically clear waters typical of oligotrophic coral reefs readily transmit blue light and downwelling PAR peaks around 450–550 nm (Kirk 1994). Scattering and

absorption by phytoplankton and/or dissolved organic material (DOM) can significantly attenuate downwelling irradiance, particularly at shorter wavelengths (< 500 nm) (Maritorena and Guillocheau 1996). This is further affected by the nature and composition of DOM, by the size, shape, and chlorophyll content of phototrophs, as well as the intracellular arrangement of photopigments within the cells (Wozniak et al. 2007). Spectral light attenuation thus varies greatly among reef locations (Maritorena and Guillocheau 1996) and strong penetration of shortwave radiation in optically clear offshore reefs may expose corals to a greater risk of heating at low tide, compared to fringing reefs influenced by terrestrial runoff containing DOM (yellow substance).

Furthermore, the spectral output of light sources should be taken into account when interpreting results from laboratory assessments of coral surface warming. Artificial light sources such as halogen lamps have a relatively weak output in the ultraviolet and blue region of the spectrum as compared to natural sunlight and, e.g., xenon or metal halide lamps, and would thus underestimate the potential surface warming of corals compared to in situ conditions.

Thermal effects of photopigment absorption: The spectral variability displayed by the thermal action spectra normalized to equivalent energy flux instead of photon flux (Fig. 3) is most likely due to the spectral absorption properties of coral tissue. Strong heating caused by shortwave (blue) radiation is consistent with the peak absorption from photosynthetic pigments, in particular Chl *a*, Chl *c*₂, and peridinin, at 400–550 nm and a slight peak and shoulder at 620–680 nm and 490–550 nm, respectively. Despite a shoulder near 520 nm in the reflectance spectrum of healthy *P. lobata* (Fig. 2), which indicates some fluorescence from host pigments (Salih et al. 2000), the spectra are dominated by the triple-peak reflectance pattern (between 550 and 650 nm) symptomatic of the “brown coral mode” (Hochberg et al. 2004). This spectral signature differs from the “blue mode” reflectance of corals exhibiting strong host-pigment absorption and fluorescence and indicates that light absorption by the brown *P. lobata* and *S. pistillata* samples was predominated by the photosynthetic pigments of the zooxanthellae, with little contribution from coral host pigments (Hochberg et al. 2003, 2004).

Host pigments may provide photoprotection in high-light environments (Salih et al. 2000; Dove et al. 2001) and/or enhance photosynthesis in low-light environments (Schlichter and Fricke 1990). They can have different optical properties, where fluorescent host pigments can reemit part of the absorbed light as fluorescence at longer wavelengths, while other chromophores reflect a proportion of the spectrum, typically in the blue (Mazel and Fuchs 2003), or absorb light without fluorescence (Dove et al. 1995). Detailed heat budget models of coral temperature may need to take such different properties into account, as the contribution of host pigments to the heat budget of corals would depend on the relative proportion of absorbed, reflected, and fluoresced light energy. In high-light environments, absorbing or reflecting pigments may have the same function of diverting potentially damaging radiation from

the photosystems (Gilmore et al. 2003). As for the coral’s heat budget, preferential absorption or reflection of short-wave radiation could have opposite effects, by either increasing or decreasing the heat load of the tissue. Furthermore, because they are usually not expelled during bleaching (Jokiel and Coles 1974), host pigments may still influence the heat budget of bleaching and/or recovering corals. In any case, such investigations would need to separate the fluorescence signal from the reflectance spectra in order to facilitate an accurate estimate of the light (and thus heat) absorption by the tissue (Fuchs 2001). Finally, some pigments are extremely sensitive to increased temperature, so that thermal exposure of coral tissue may cause their denaturation and loss of their photo-protective function (Dove 2004). The thermal stability of photo-protective pigments may thus be directly affected by the heat generated locally upon absorption of excess radiation.

In summary, this study shows several close links between the optical and thermal properties of corals. Coral temperature is linearly correlated to the fraction of absorbed irradiance, and we show for the first time that the spectral composition of light is important in determining the magnitude of coral surface warming. Especially, energy-rich radiation at short wavelengths (< 500 nm) had the highest heating efficiency. Besides interactions between symbiont photopigments and the scattering properties of coral tissue and skeleton, coral host pigments may play an important role for the heat budget of corals; dissipating radiative heating by reflecting energy-rich radiation or increasing tissue heating by absorbing blue and ultraviolet light. The relationship between coral temperature and absorbance is species specific, possibly as a result of differences in tissue thickness, the thermal properties of the skeleton, and/or tissue arrangement within the skeletal matrix, indicating a yet unresolved potential for coral shape and size to affect the conduction of heat into their skeleton.

Acknowledgments

We acknowledge the help and assistance of staff at Heron Island Research Station, University of Queensland, during the field component of this study. We thank the two anonymous reviewers for their constructive criticism and suggestions for improvements. This study was supported by grants from the Australian Research Council (P.J.R., A.W.D.L.) and the Danish Natural Science Research Council (M.K.). The research was conducted under the Great Barrier Reef Marine Park Authority permits G05/16166.1, G03/12019.1, and G06/178151.

References

- AINSWORTH, T. D., O. HOEGH-GULDBERG, S. F. HERON, W. J. SKIRVING, AND W. LEGGAT. 2008. Early cellular changes are indicators of pre-bleaching thermal stress in the coral host. *J. Exp. Mar. Biol. Ecol.* **364**: 63–71, doi:10.1016/j.jembe.2008.06.032
- AL-NAJJAR, M., D. DE BEER, B. B. JØRGENSEN, M. KÜHL, AND L. POLERECKY. 2010. Conversion and conservation of light energy in a photosynthetic microbial mat ecosystem. *ISME J.* **4**: 440–449, doi:10.1038/ismej.2009.121
- APRILL, A. M., R. R. BIDIGARE, AND R. D. GATES. 2007. Visibly healthy corals exhibit variable pigment concentrations and symbiont phenotypes. *Coral Reefs* **26**: 387–397, doi:10.1007/s00338-007-0209-y

- BARNES, D. J., AND J. M. LOUGH. 1992. Systematic variations in the depth of skeleton occupied by coral tissue in massive colonies of *Porites* from the Great Barrier Reef. *J. Exp. Mar. Biol. Ecol.* **159**: 113–128, doi:10.1016/0022-0981(92)90261-8
- COLES, S. L., AND B. E. BROWN. 2003. Coral bleaching—capacity for acclimatization and adaptation. *Adv. Mar. Biol.* **46**: 183–223, doi:10.1016/S0065-2881(03)46004-5
- DENNY, M. W. 1993. Air and water: The biology and physics of life's media. Princeton Univ. Press.
- DOVE, S. 2004. Scleractinian corals with photoprotective host pigments are hypersensitive to thermal bleaching. *Mar. Ecol. Prog. Ser.* **272**: 99–116, doi:10.3354/meps272099
- , O. HOEGH-GULDBERG, AND S. RANGANATHAN. 2001. Major colour patterns of reef-building corals are due to a family of GFP-like proteins. *Coral Reefs* **19**: 197–204, doi:10.1007/PL00006956
- , M. TAKABAYASHI, AND O. HOEGH-GULDBERG. 1995. Isolation and partial characterization of the pink and blue pigments of Pocilloporid and Acroporid corals. *Biol. Bull.* **189**: 288–297, doi:10.2307/1542146
- DOWNES, C. A., J. E. FAUTH, J. C. HALAS, P. DUSTAN, J. BEMISS, AND C. M. WOODLEY. 2002. Oxidative stress and seasonal coral bleaching. *Free Radicals Biol. Med.* **33**: 533–543, doi:10.1016/S0891-5849(02)00907-3
- DUBINSKY, Z., P. G. FALKOWSKI, J. W. PORTER, AND L. MUSCATINE. 1984. Absorption and utilization of radiant energy by light- and shade-adapted colonies of the hermatypic coral *Stylophora pistillata*. *Proc. R. Soc. Lond. B* **222**: 203–214, doi:10.1098/rspb.1984.0059
- , N. STAMBLER, M. BEN-ZION, L. R. MCCLOSKEY, L. MUSCATINE, AND P. G. FALKOWSKI. 1990. The effect of external nutrient resources on the optical properties and photosynthetic efficiency of *Stylophora pistillata*. *Proc. R. Soc. Lond. B* **239**: 231–246, doi:10.1098/rspb.1990.0015
- ENRIQUEZ, S., E. R. MENDEZ, AND R. IGLESIAS-PRieto. 2005. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnol. Oceanogr.* **50**: 1025–1032, doi:10.4319/lo.2005.50.4.1025
- FABRICIUS, K. E. 2006. Effects of irradiance, flow, and colony pigmentation on the temperature microenvironment around corals: Implications for coral bleaching? *Limnol. Oceanogr.* **51**: 30–37, doi:10.4319/lo.2006.51.1.0030
- FALKOWSKI, P. G., P. L. JOKIEL, AND R. A. KINZIE. 1990. Irradiance and corals, p. 109–131. *In* Z. Dubinsky [ed.], *Coral reefs. Ecosystems of the world*. Elsevier.
- FUCHS, E. 2001. Separating the fluorescence and reflectance components of coral spectra. *Appl. Opt.* **40**: 3614–3621, doi:10.1364/AO.40.003614
- GATES, D. M. 1980. *Biophysical ecology*. Courier Dover Publications.
- GILMORE, A. M., A. W. D. LARKUM, A. SALIH, S. ITOH, Y. SHIBATA, C. BENA, H. YAMASAKI, M. PAPINA, AND R. VAN WOESIK. 2003. Simultaneous time resolution of the emission spectra of fluorescent proteins and zooxanthellar chlorophyll in reef-building corals. *Photochem. Photobiol.* **77**: 515–523, doi:10.1562/0031-8655(2003)077<0515:STROTE>2.0.CO;2
- HELMUTH, B. S. T. 1998. Intertidal mussel microclimates: Predicting the body temperature of a sessile invertebrate. *Ecol. Monogr.* **68**: 51–74, doi:10.1890/0012-9615(1998)068[0051:IMMPTB]2.0.CO;2
- HOCHBERG, E. J., A. APPRILL, M. J. ATKINSON, AND R. BIDIGARE. 2006. Bio-optical modeling of photosynthetic pigments in corals. *Coral Reefs* **25**: 99–109, doi:10.1007/s00338-005-0071-8
- , M. J. ATKINSON, AND S. ANDRÉFOUËT. 2003. Spectral reflectance of coral reef bottom-types worldwide and implications for coral reef remote sensing. *Remote Sens. Environ.* **85**: 159–173, doi:10.1016/S0034-4257(02)00201-8
- , ———, A. APPRILL, AND S. ANDRÉFOUËT. 2004. Spectral reflectance of coral. *Coral Reefs* **23**: 84–95, doi:10.1007/s00338-003-0350-1
- JEFFREY, S., AND F. HAXO. 1968. Photosynthetic pigments of symbiotic dinoflagellates (zooxanthellae) from corals and clams. *Biol. Bull.* **135**: 149–165, doi:10.2307/1539622
- JIMENEZ, I. M., M. KÜHL, A. W. D. LARKUM, AND P. J. RALPH. 2008. Heat budget and thermal microenvironment of shallow-water corals: Do massive corals get warmer than branching corals? *Limnol. Oceanogr.* **53**: 1548–1561, doi:10.4319/lo.2008.53.4.1548
- , ———, ———, AND ———. 2011. Effects of flow and colony morphology on the thermal boundary layer of corals. *J. R. Soc. Interface* **8**: 1785–1795, doi:10.1098/rsif.2011.0144
- , A. W. D. LARKUM, P. J. RALPH, AND M. KÜHL. 2012. In situ thermal dynamics of shallow water corals is affected by tidal patterns and irradiance. *Mar. Biol.* **8**: 1773–1782, doi:10.1007/s00227-012-1968-8
- JOKIEL, P. L., AND S. L. COLES. 1974. Effects of heated effluent on hermatypic corals at Kahe Point, Oahu. *Pac. Sci.* **28**: 1–18.
- JONES, R. J., O. HOEGH-GULDBERG, A. W. D. LARKUM, AND U. SCHREIBER. 1998. Temperature-induced bleaching of corals begins with impairment of the CO₂ fixation metabolism in zooxanthellae. *Plant Cell Environ.* **21**: 1219–1230, doi:10.1046/j.1365-3040.1998.00345.x
- KANIEWSKA, P., S. H. MAGNUSON, K. R. N. ANTHONY, R. REEF, M. KÜHL, AND O. HOEGH-GULDBERG. 2011. The importance of macro versus micro structure in modulating irradiance inside coral colonies. *J. Phycol.* **47**: 846–860, doi:10.1111/j.1529-8817.2011.01021.x
- KIRK, J. T. O. 1994. *Light and photosynthesis in aquatic ecosystems*. Cambridge Univ. Press.
- KÜHL, M., Y. COHEN, T. DALSGAARD, B. B. JØRGENSEN, AND N. P. REVSBECH. 1995. Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with micro-sensors for O₂, pH and light. *Mar. Ecol. Prog. Ser.* **117**: 159–172, doi:10.3354/meps117159
- LESSER, M. P. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. *Coral Reefs* **16**: 187–192, doi:10.1007/s003380050073
- . 2006. Oxidative stress in marine environments: Biochemistry and physiological ecology. *Annu. Rev. Physiol.* **68**: 253–278, doi:10.1146/annurev.physiol.68.040104.110001
- , C. MAZEL, D. PHINNEY, AND C. S. YENTSCH. 2000. Light absorption and utilization by colonies of the congeneric hermatypic corals *Montastraea faveolata* and *Montastraea cavernosa*. *Limnol. Oceanogr.* **45**: 76–86, doi:10.4319/lo.2000.45.1.0076
- LOYA, Y., K. SAKAI, K. YAMAZATO, Y. NAKANO, H. SAMBALI, AND R. VAN WOESIK. 2001. Coral bleaching: The winners and the losers. *Ecol. Lett.* **4**: 122–131, doi:10.1046/j.1461-0248.2001.00203.x
- MAGNUSON, S. H., M. FINE, AND M. KÜHL. 2007. Light microclimate of endolithic phototrophs in the scleractinian corals *Montipora monasteriata* and *Porites cylindrica*. *Mar. Ecol. Prog. Ser.* **332**: 119–128, doi:10.3354/meps332119
- MARITORENA, S., AND N. GUILLOCHEAU. 1996. Optical properties of water and spectral light absorption by living and non-living particles and by yellow substances in coral reef waters of French Polynesia. *Mar. Ecol. Prog. Ser.* **131**: 245–255, doi:10.3354/meps131245
- MARSHALL, P. A., AND A. H. BAIRD. 2000. Bleaching of corals on the Great Barrier Reef: Differential susceptibilities among taxa. *Coral Reefs* **19**: 155–163, doi:10.1007/s003380000086

- MAZEL, C. H., AND E. FUCHS. 2003. Contribution of fluorescence to the spectral signature and perceived color of corals. *Limnol. Oceanogr.* **48**: 390–401, doi:10.4319/lo.2003.48.1_part_2.0390
- MCCABE, R. M., P. ESTRADA, J. H. MIDDLETON, W. K. MELVILLE, M. ROUGHAN, AND L. LENAIN. 2010. Temperature variability in a shallow, tidally isolated coral reef lagoon. *J. Geophys. Res.* **115**: C12011, doi:10.1029/2009JC006023
- OBURA, D. O. 2005. Resilience and climate change: Lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuar. Coast. Shelf Sci.* **63**: 353–372, doi:10.1016/j.eccs.2004.11.010
- REEF, R., P. KANIEWSKA, AND O. HOEGH-GULDBERG. 2009. Coral skeletons defend against ultraviolet radiation. *PLoS One* **4**: e7995, doi:10.1371/journal.pone.0007995
- SALIH, A., A. W. D. LARKUM, G. COX, M. KÜHL, AND O. HOEGH-GULDBERG. 2000. Fluorescent pigments in corals are photo-protective. *Nature* **408**: 850–853, doi:10.1038/35048564
- SCHLICHTER, D., AND H. W. FRICKE. 1990. Coral host improves photosynthesis of endosymbiotic algae. *Naturwissenschaften* **77**: 447–450, doi:10.1007/BF01135950
- SHIBATA, K., AND F. T. HAXO. 1969. Light transmission and spectral distribution through epi- and endozoic algal layers in the brain coral, *Favia*. *Biol. Bull.* **136**: 461–468, doi:10.2307/1539688
- SMITH, D. J., D. J. SUGGETT, AND N. R. BAKER. 2005. Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals? *Global Change Biol.* **11**: 1–11, doi:10.1111/j.1529-8817.2003.00895.x
- STAMBLER, N., AND Z. DUBINSKY. 2005. Corals as light collectors: An integrating sphere approach. *Coral Reefs* **24**: 1–9, doi:10.1007/s00338-004-0452-4
- , AND N. SHASHAR. 2007. Variation in spectral reflectance of the hermatypic corals, *Stylophora pistillata* and *Pocillopora damicornis*. *J. Exp. Mar. Biol. Ecol.* **351**: 143–149, doi:10.1016/j.jembe.2007.06.014
- STIMSON, J., AND R. A. KINZIE. 1991. The temporal pattern and rate of release of zooxanthellae from the reef coral *Pocillopora damicornis* (Linnaeus) under nitrogen-enrichment and control conditions. *J. Exp. Mar. Biol. Ecol.* **153**: 63–74, doi:10.1016/S0022-0981(05)80006-1
- TERAN, E., E. R. MENDEZ, S. ENRIQUEZ, AND R. IGLESIAS-PRIETO. 2010. Multiple light scattering and absorption in reef-building corals. *Appl. Opt.* **49**: 5032–5042, doi:10.1364/AO.49.005032
- ULSTRUP, K. E., R. HILL, M. J. H. VAN OPPEN, A. W. D. LARKUM, AND P. J. RALPH. 2008. Seasonal variation in the photo-physiology of homogeneous and heterogeneous *Symbiodinium* consortia of two scleractinian corals. *Mar. Ecol. Prog. Ser.* **361**: 139–150, doi:10.3354/meps07360
- WANGPRASEURT, D., A. W. D. LARKUM, P. J. RALPH, AND M. KÜHL, M. 2012. Light gradients and optical microniches in coral tissues. *Frontiers Microbiol.* **3**: 316, doi:10.3389/fmicb.2012.00316
- WARNER, M. E., W. K. FITT, AND G. W. SCHMIDT. 1996. The effect of elevated temperature on the photosynthetic efficiency of zooxanthellae *in hospite* from four different species of reef corals: A novel approach. *Plant Cell Environ.* **19**: 291–299, doi:10.1111/j.1365-3040.1996.tb00251.x
- WOZNIAK, B., AND J. DERA. 2007. Light absorption in sea water. Springer.
- YAMANO, H., M. TAMURA, Y. KUNII, AND M. HIDAKA. 2002. Hyperspectral remote sensing and radiative transfer simulation as a tool for monitoring coral reef health. *Mar. Technol. Soc. J.* **36**: 4–13, doi:10.4031/002533202787914205

Associate editor: Dariusz Stramski

Received: 02 March 2012

Accepted: 10 August 2012

Amended: 13 August 2012