

In situ thermal dynamics of shallow water corals is affected by tidal patterns and irradiance

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Abstract We studied the diel variation of in situ coral temperature, irradiance and photosynthetic performance of hemispherical colonies of *Porites lobata* and branching colonies of *Porites cylindrica* during different bulk water temperature and tidal scenarios on the shallow reef flat of Heron Island, Great Barrier Reef, Australia. Our study presents in situ evidence that coral tissue surface temperatures can exceed that of the surrounding water under environmental conditions typically occurring during low tide in shallow reef or lagoon environments. Such heating may be a regular occurrence on shallow reef flats, triggered by the combined effects of high irradiance and low water flow characteristic of low Spring tides. At these times, solar heating of corals coincides with times of maximum water temperature and high irradiance, where the slow flow and consequent thick boundary layers impede heat exchange between corals and the surrounding water. Despite similar light-absorbing properties, the heating effect was more pronounced for the hemispherical *P. lobata* than for the branching *P. cylindrica*. This is consistent with previous laboratory experiments showing the evidence of interspecific variation in coral thermal environment and may result from morphologically influenced variation in convective

heat transfer and/or thermal properties of the skeleton. Maximum coral surface warming did not coincide with maximum irradiance, but with maximum water temperature, well into the low-tide period with extremely low water flow in the partially drained reef flat, just prior to flushing by the rising tide. The timing of low tide thus influences the thermal exposure and photophysiological performance of corals, and the timing of tidally driven coral surface warming could potentially have different physiological impacts in the morning or in the afternoon.

Introduction

Diurnal fluctuations in irradiance affect the photophysiology of the endosymbiotic dinoflagellates (zooxanthellae) of corals (Brown et al. 1999; Ralph et al. 1999; Jones and Hoegh-Guldberg 2001; Winters et al. 2003; Levy et al. 2004; Hill and Ralph 2005; Smith and Birkeland 2007). Supra-optimal light intensities at noon result in a loss of photosynthetic efficiency (i.e. photoinhibition) mostly through reversible photoprotective mechanisms rather than long-term damage to the photosynthetic apparatus (Brown et al. 1999; Hoegh-Guldberg and Jones 1999; Ralph et al. 1999; Gorbunov et al. 2001). Elevated temperatures are thought to compromise the repair machinery of photosynthesis (Takahashi et al. 2004), causing oxidative stress (Lesser 1997), chronic damage to the zooxanthellae (Smith et al. 2005) and, for example, a caspase-mediated apoptotic cascade in the coral host (Tchernov et al. 2011). Thus, the combination of intense irradiance and elevated temperature is recognized as the primary cause of mass coral-bleaching events (Iglesias-Prieto et al. 1992; Jones et al. 2000).

In shallow reef environments, elevated temperature and high irradiance often co-occur (Coles 1997), where large

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diel increases in water temperature are caused by prolonged solar heating of the shallow water body and reef flat during low Spring tides (Jones et al. 2000; Jimenez et al. 2008). There is increasing evidence for a pronounced diel variation in bulk water temperature over shallow reefs, which is exaggerated by mid-day low tides and periods of low windspeed and water flow (McCabe et al. 2010; Putnam and Edmunds 2011). Furthermore, a detailed study of the temperature dynamics in a single coral reef patch revealed a complex and dynamic temperature pattern over spatial scales <1 m (Gorospe and Karl 2011). Temperature dynamics in single coral patches is thus due to a complex interaction between microspatial variations in flow, affecting boundary layers and heat exchange with benthic interfaces. Unfortunately, in situ measurement of coral temperature is very scarce, but a first data set showed that low-tide, high-irradiance conditions can indeed cause additional solar heating of coral surfaces in situ of up to ~ 0.6 °C (Jimenez et al. 2008).

The thermal sensitivity of the coral–algal symbiosis is such that an excess in water temperature of just 1–2 °C above long-term summer maxima can trigger bleaching (Podesta and Glynn 2001), and differences of about 1 °C in thermal exposure are known to affect the severity of the bleaching response (Berkelmans and Willis 1999). Therefore, additional solar heating of coral surfaces can potentially affect the bleaching response to elevated seawater temperatures (Fabricius 2006, Jimenez et al. 2008). A better understanding of the spatial and temporal variability in bleaching patterns may be achieved by a more accurate description of the thermal exposure of coral tissue in situ, rather than measurements in the surrounding water.

Jimenez et al. (2008, 2011) highlighted a link between coral surface warming and tide regime and provided the first evidence for differences in the thermal exposure of hemispherical and branching corals. These observations may help explain the large differences in bleaching susceptibility between coral taxa with different growth forms (Marshall and Baird 2000; Loya et al. 2001). A prerequisite for testing such relationships between bleaching susceptibility and coral morphology is a better understanding of the in situ thermal exposure of corals. Jimenez et al. (2008) showed a single preliminary data set (without replication) on the in situ temperature dynamics in the hemispherical coral *Cyphastrea serailia* and the branching coral *Porites cylindrica*. No detailed data on tidal variation or longer replicated time series were presented. In the present study, we present a more comprehensive (and replicated) data set on the in situ temperature dynamics under different tidal and irradiance regimes in the hemispherical coral *Porites lobata* and the branching coral *P. cylindrica*. The study thus expands on the still very few fine-scale data on in situ coral temperature dynamics and investigates possible links between tidal and

diurnal dynamics of the temperature and photophysiology of branching and hemispherical shallow water corals.

Materials and methods

Site and sampling periods

Coral surface temperature dynamics was monitored on the reef flat adjacent to Heron Island Research Station (151°55'E, 23°26'S) during three periods, representing two contrasting tidal situations. During the first two sampling periods (14–17 January 2007 and 21–24 November 2007), low Spring tides drained the reef flat for approximately 5 h during the daylight period, creating shallow pools ~ 20 –50 cm deep between 10:00 and 16:00 h. In the third experiment (28–30 November 2007), high tide occurred around noon and water depth ranged from 2 to 3 m between 10:00 and 16:00 h. Tidal heights for Heron Island were provided by the Bureau of Meteorology (Australia) for the January 2007 sampling period (30-min intervals) and the Environment Protection Agency (Australia) for the November 2007 sampling period (10-min intervals).

Coral specimens

In the January and November 2007 experiments, hemispherical colonies of *P. lobata* (~ 150 mm diameter) and branching colonies of *P. cylindrica* (branch thickness ~ 10 mm) were collected from the shallow reef flat ($n = 4$ and $n = 5$ in January and November, respectively). A 2-mm-wide hole for mounting of thermistor probes (see below) was drilled vertically through each of the coral skeletons with the corals in seawater, and the colonies were left to recover for at least 24 h in continuously flowing aerated seawater (25 °C—ambient lagoon temperature) before redeployment on the reef flat.

Coral optical properties

The light-absorbing capacity of the *P. lobata* and *P. cylindrica* specimens was assessed as the absorptance (A , fraction of light absorbed by the tissue) in the spectral range 400–750 nm. This was estimated from spectral reflectance measurements taken using a fibre optic spectrometer (USB2000, Ocean Optics, USA) and a deuterium–halogen light source (DH-2000-BAL, Ocean Optics, USA).

Downwelling quantum irradiance at the depth of corals was measured as PAR (photosynthetically active radiation, 400–700 nm) in units of $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ with a submersible downwelling irradiance data logger (Odyssey Dataflow Systems Pty Ltd, New Zealand) using a 5-min integration time.

Coral temperature measurements

The temperature of coral skeletons and the surrounding water was measured every 5 min with custom-made miniature thermistors (tip diameter 1.5 mm, accuracy ± 0.1 °C) connected to a battery-driven submersible data logger (Lothlorien Pty Ltd, Australia) and calibrated against a type T thermocouple in a well-mixed 10-L thermostated water bath (Jimenez et al. 2008). Thermistor accuracy was tested in a slowly varying temperature-controlled bath, and readings proved consistent to within 0.1 °C over a temperature range of 22–35 °C. The thermistors were fed through the holes into the skeleton, in order to ensure that the sensor tips were in thermal contact with the skeleton and level with the sun-exposed surface of the coral colonies (Fig. 1). For *P. cylindrica*, horizontally oriented branches were chosen. In situ water temperature was monitored by a set of thermistors placed in the water column 10 cm away from the coral surfaces.

Photosynthetic capacity of corals

During the November 2007 experiments (daytime low and high tide), variable chlorophyll fluorescence measurements of the photochemical efficiency of the zooxanthellae in the experimental corals were taken in situ using an underwater, pulse amplitude-modulated fluorometer (Diving-PAM, Walz, Germany) (Ralph et al. 1999). The effective quantum yield of photochemistry in PSII in the light-adapted state (Φ_{PSII}) was assessed as $\Delta F/F'_m = (F'_m - F)/F'_m$, where F'_m is the maximum fluorescence yield (measured after the application of a 0.8-s saturating light pulse of $>4,500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and F is the steady-state fluorescence yield (measured under non-actinic weak

0.3 μs pulses from a blue light-emitting diode). $\Delta F/F'_m$ was measured daily around noon (between 12:00 and 15:00), and at night-time (between 22:00 and 04:00), when low tide permitted easy access to the site.

Statistical analysis

Repeated-measures analysis of variance (rm-ANOVA) was used to assess changes in the daytime and night-time quantum yields of PSII over the duration of the November experiment. The time of significant changes was identified using Tukey's post hoc comparisons. Two-tailed Student's *t* tests were used to compare the values of absorptivity (α), surface warming (ΔT) at 10:00, 12:00, 14:00 and 16:00 h and PSII effective quantum yields ($\Delta F/F'_m$) between the *P. lobata* and *P. cylindrica* specimens. All data were tested for normality and homogeneity of variance prior to testing, using Kolmogorov–Smirnov and Levene's tests, respectively.

Results

Noon-low-tide experiments

Water temperature dynamics

The seawater temperature during the sampling periods 14–17 January 2007 and 21–24 November 2007 exhibited large diel fluctuations (Fig. 2), typical of low Spring tides on the shallow reef flat at Heron Island (Potts and Swart 1984; Jones et al. 2000; Jimenez et al. 2008). On each of the four sampling days of 14–17 January 2007, oceanic water levels dropped to 1.1, 1.0, 0.8 and 0.7 m at 12:00,

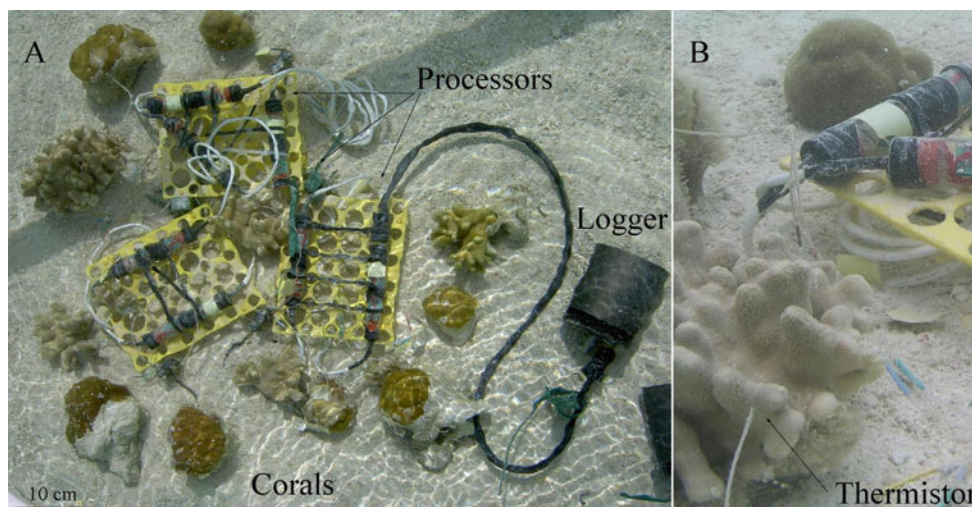


Fig. 1 Experimental set-up for in situ coral temperature measurements. **a** Submersible temperature logging equipment (photograph: I. Jimenez). **b** Close-up of a *P. cylindrica* colony with inserted temperature sensor (photograph: G. Holmes)

13:00, 13:30 and 14:00 h, respectively (Fig. 2a). Low tide during the November 2007 experiment (21–24 November) occurred at similar times: 11:30, 12:30, 13:20 and 14:30 h, but dropped lower to 0.6, 0.5, 0.4 and 0.3 m, respectively (Fig. 2b). The greater tidal amplitude of the November experiment caused a longer residence time of the shallow water body on the reef flat, and this was mirrored by a greater daily seawater temperature variation ($\Delta T_w = 5.3\text{--}7.0\text{ }^\circ\text{C}$) compared to January ($\Delta T_w = 3.9\text{--}5.7\text{ }^\circ\text{C}$) (Fig. 2b, c). Night-time water temperatures were 24–25 $^\circ\text{C}$ on 14–17 January, while daytime temperatures increased to 30.7 $^\circ\text{C}$ on 14 January and were between 28.0 and 29.5 $^\circ\text{C}$ on 15–17 January. In November 2007, water temperatures were 22–24 $^\circ\text{C}$ at night and reached 29.3–30.3 $^\circ\text{C}$ during the day on 21–23 November.

Maximal daily temperatures were reached at approximately 14:30, 15:30, 15:20 and 14:30 h on each of the 4 days on 14–17 January and at 13:30, 14:50, 15:40 and 16:20 h on 21–24 November, respectively. On each

sampling day of the January and November experiments, a sharp decline in water temperature coincided with the flushing of oceanic water into the lagoon, as water levels rose above the reef crest (Potts and Swart 1984, McCabe et al. 2010). This occurred at approximately 17:00, 16:20, 16:00 and 15:50 on the 14–17 January and at 14:30, 15:15, 15:40 and 16:20 on the 21–24 November, respectively.

Coral surface warming

The surface temperature of corals increased above that of the surrounding water (Fig. 2e–h). On the 14–17 January, the surface temperature of the hemispherical *P. lobata* specimens increased above that of the water by +0.3–0.4 $^\circ\text{C}$ between 11:00 and 15:30 h, reaching +0.6 $^\circ\text{C}$ on the 15 January at 14:00 h (Fig. 2e). By contrast, the surface warming of the branching *P. cylindrica* reached only +0.2–0.3 $^\circ\text{C}$ during the same period (Fig. 2g). A similar pattern occurred during the November experiment, whereby

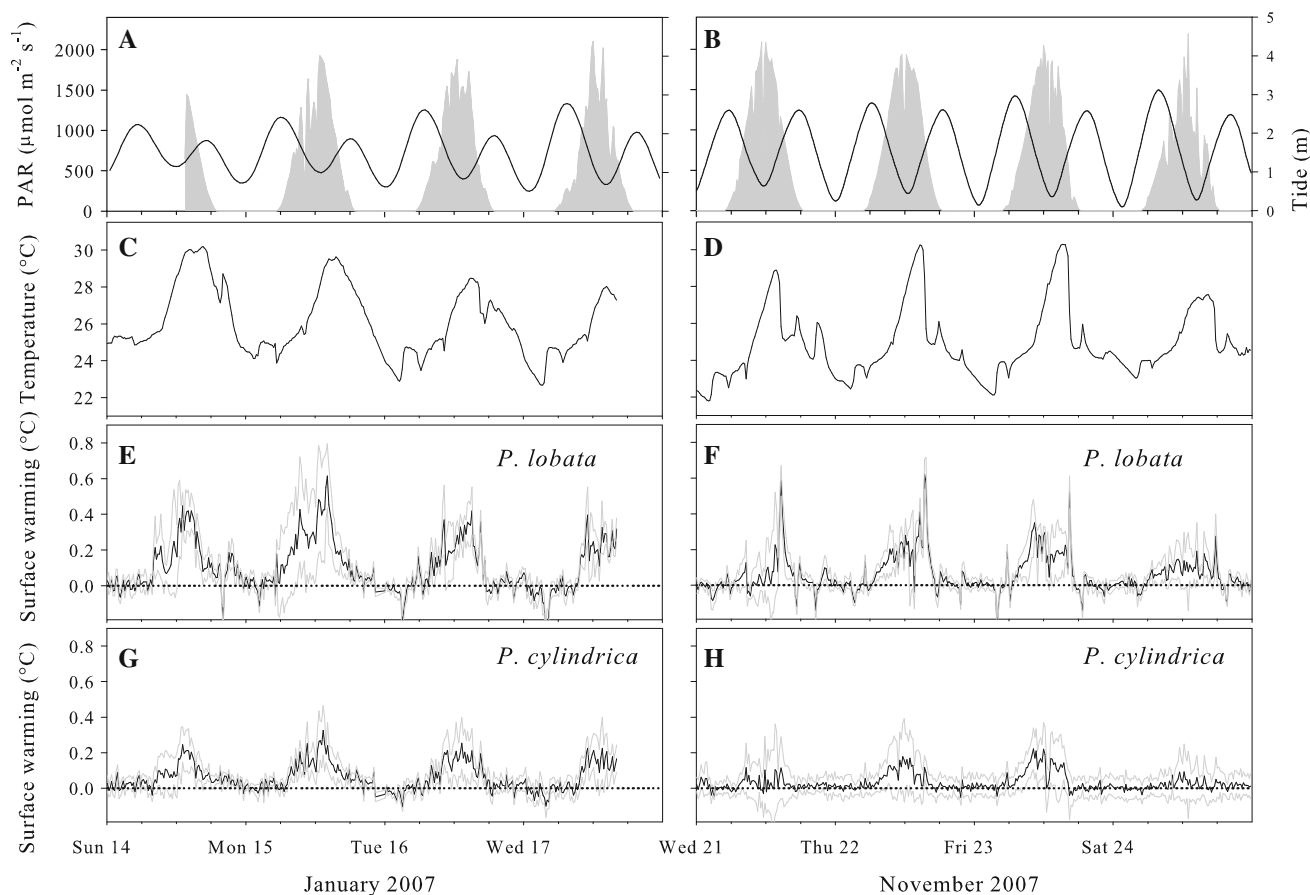


Fig. 2 In situ irradiance and temperature dynamics of hemispherical *P. lobata* and branching *P. cylindrica* colonies on the Heron Island reef flat during 4-day periods of noon low Spring tide in January and November 2007. **a, b** Tidal height (black line, right y axis) and in situ underwater downwelling irradiance (PAR, 400–700 nm) (grey curve,

left y axis) measured at the depth of corals. **c, d** Ambient seawater temperature. **e–h** The relative temperature difference between the coral surface and the surrounding seawater for *P. lobata* (**e, f**) and *P. cylindrica* (**g, h**) specimens (Mean \pm SE, $n = 4$ and 5 in January and November, respectively)

the temperature of the hemispherical *P. lobata* increased by +0.3–0.8 °C above that of the surrounding water (Fig. 2f), while temperature of the branched *P. cylindrica* was only by +0.2–0.3 °C warmer than that of the surrounding seawater (Fig. 2g). In the January experiment, significant differences in the surface warming of *P. lobata* and *P. cylindrica* were detected at 14:00 h on the 15th (0.54 ± 0.09 °C and 0.23 ± 0.04 °C, $p = 0.02$) and the 16th (0.33 ± 0.04 °C and 0.18 ± 0.04 °C, $p = 0.045$) and at 16:00 h on the 16th (0.15 ± 0.02 °C and 0.08 ± 0.02 °C, $p = 0.02$) and the 17th (0.26 ± 0.02 °C and 0.16 ± 0.02 °C, $p = 0.01$). In the November experiment, the surface warming of *P. lobata* was significantly greater than that of *P. cylindrica* at 16:00 h on the 22nd (0.25 ± 0.04 °C and 0.03 ± 0.01 °C, $p < 0.01$) and the 23rd (0.15 ± 0.03 °C and 0.04 ± 0.02 °C, $p < 0.05$).

In the January 2007 experiment, the maximal coral surface warming was reached simultaneously with the daily maximum in water temperature (Fig. 2c, e, g). This occurred at the end of the low-tide period between 14:30 and 15:30 h and thus later than the noon maximum in irradiance. In November, maximal water temperatures were also mirrored by a maximum in coral surface warming, but for the hemispherical *P. lobata* specimens, this was followed by a spike caused by a sharp decline in water temperature and a delayed response in coral surface temperature (Fig. 3).

Coral absorptance

No differences were detected in the light-absorbing efficiencies of the *P. lobata* and *P. cylindrica* specimens in the

January experiment ($\alpha = 0.49 \pm 0.04$, $p > 0.05$). However, in the November experiment, the absorptance of the *P. lobata* specimens ($\alpha = 0.67 \pm 0.06$) was significantly greater than that of the *P. cylindrica* specimens ($\alpha = 0.45 \pm 0.04$, $p = 0.02$).

Noon-high-tide experiment

Water temperatures

In contrast with the prolonged light exposure of the reef flat during daytime low-tide experiment, the noon-high-tide experiment (28–30 November 2007, Fig. 4) showed smaller seawater temperature variations ($\Delta T_w \sim 4$ °C) and maxima (27 °C on the 29 November). The temperature of the corals differed little from that of the water, at the most by +0.15 °C on 29 November for the *P. lobata* specimens (Fig. 4c, d).

Variable Chlorophyll *a* fluorescence measurements

Throughout the November sampling period (noon low and noon high tide, Fig. 5), both coral species exhibited large diurnal fluctuations in the effective quantum yield of PSII, consistent with the well-known depression of photosynthetic activity under mid-day maximum irradiance (Brown et al. 1999; Ralph et al. 1999). The noon value of $\Delta F/F'_m$ for both coral species was significantly lower on 21 November (0.15 ± 0.04) as compared to 30 November (0.33 ± 0.05) (rm-ANOVA, $p < 0.05$), indicating greater photic stress at noon low tide compared to noon high tide (Fig. 5).

Fig. 3 In situ temperature dynamics of *P. lobata* on 22 November 2007 (Mean \pm SE, $n = 5$) quantified as the relative temperature difference between the coral and the ambient seawater. Inset: temperature of the ambient seawater (solid line) and corals (dashed line). Maxima in coral surface warming are indicated by arrows: **a** 14:30 h, **b** 15:30. The “sun” symbol indicates solar noon

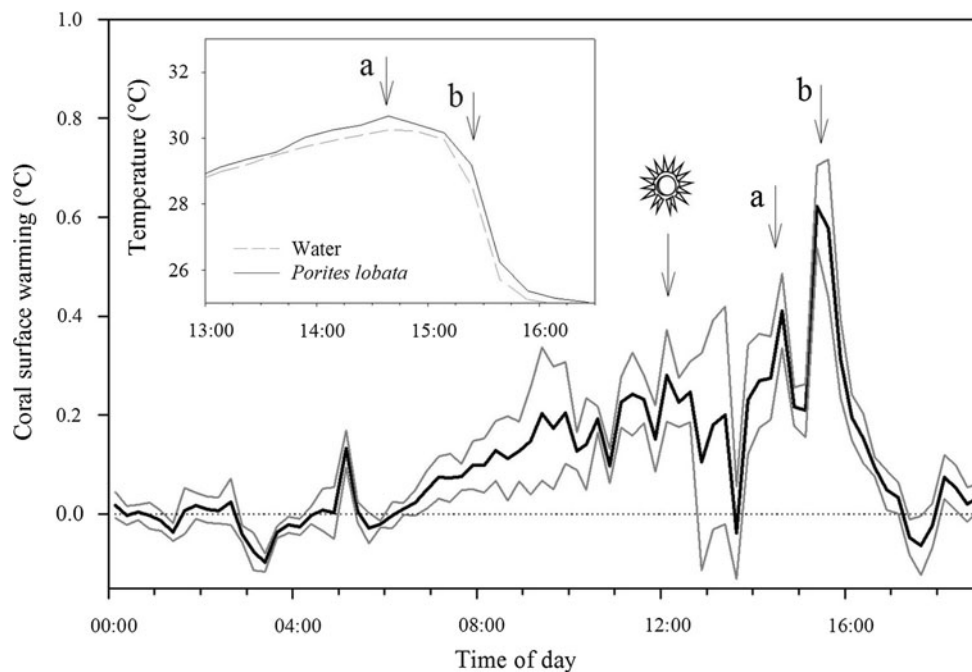
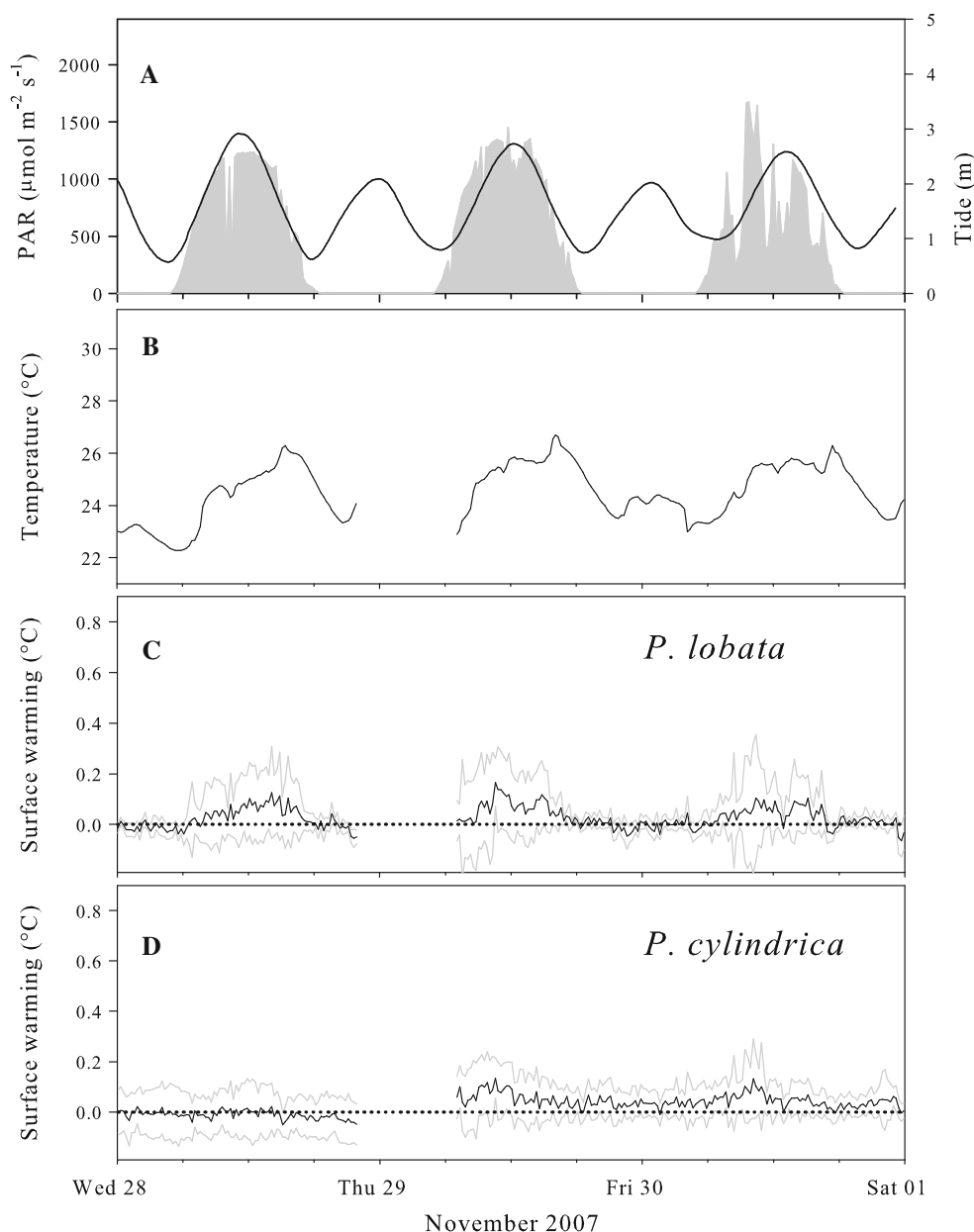


Fig. 4 In situ irradiance and temperature dynamics of hemispherical *P. lobata* and branching *P. cylindrica* colonies on the Heron Island reef flat during a 4-day period of noon high tide in November 2007. **a** In situ downwelling quantum irradiance (PAR, 400–700 nm) measured at the depth of corals (grey curve, left y axis) and tidal height (black line, right y axis) at Heron Island. **b** Ambient seawater temperature. **c, d** The relative temperature difference between coral surface and water for the *P. lobata* (**c**) and *P. cylindrica* (**d**) specimens (Mean \pm SE, $n = 5$)



At noon on 26 November, $\Delta F/F_m'$ of *P. cylindrica* (0.27 ± 0.05) was significantly higher than that of *P. lobata* (0.15 ± 0.02) (t test, $p = 0.01$). No changes were detected in the night-time dark-adapted maximum quantum yields (rm-ANOVA, $p > 0.05$), suggesting that no chronic photoinhibition occurred on those days.

Discussion

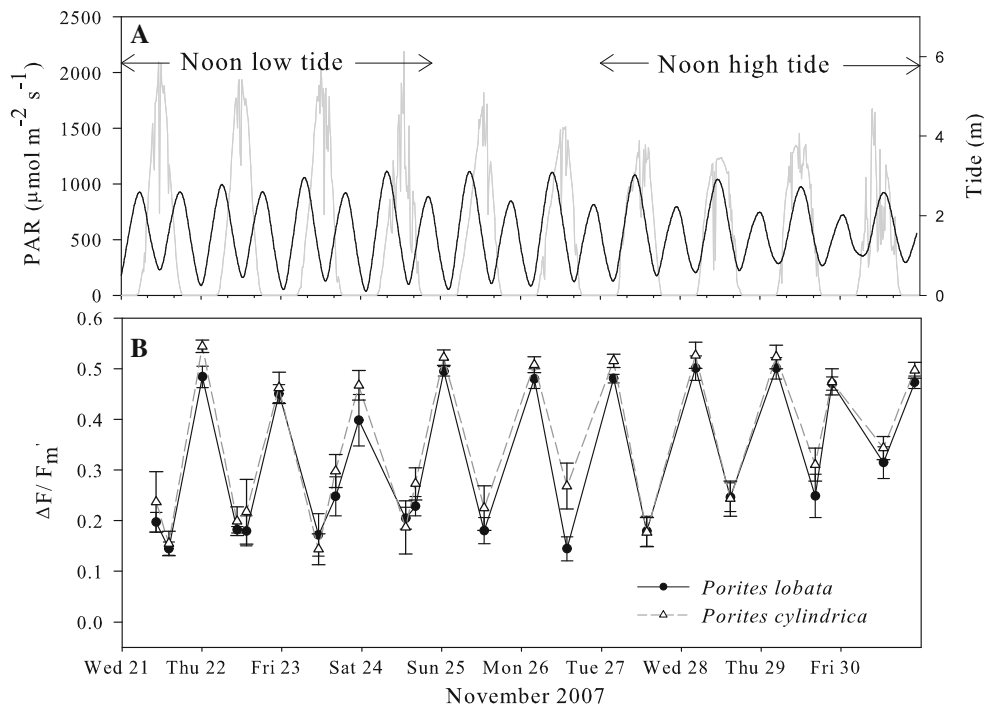
Coral thermal dynamics

Our measurements of bulk water temperature in relation to tidal shifts and daily irradiance patterns largely followed

the same trends reported in a recent detailed study of water temperature and flow of a shallow reef flat (McCabe et al. 2010), showing pronounced water heating at daytime low tide and abrupt changes in water temperature as, for example, the reef flat was flooded during incoming tides during daytime. A discussion of mechanisms affecting such larger-scale spatio-temporal variations on coral reefs is, however, outside the scope of the present paper, and here, we mainly focus on the temperature dynamics and physiological responses of corals.

The temperature of corals increased above that of the surrounding water during both sampling periods of noon low tide (14–17 January and 21–24 November 2007, Fig. 2), but remained within less than ~ 0.2 °C of water

Fig. 5 Plots of **a** tidal height (black line, right y axis) and in situ underwater downwelling irradiance (PAR, 400–700 nm) (grey line, left y axis) during the noon-low- and noon-high-tide sampling periods (November 2007) and **b** effective quantum yield of PSII for *P. lobata* and *P. cylindrica* (Mean \pm SE, $n = 5$)



temperature during the noon-high-tide sampling period (28–30 November 2007, Fig. 4). This is consistent with preliminary data shown in Jimenez et al. (2008) and indicates that low Spring tides in the shallow reef flat at Heron Island provide conditions of low flow and high irradiance conducive to recurring solar heating of shallow water corals. The present study, together with Jimenez et al. (2008), has thus far documented three periods of daytime low Spring tide, during which coral surface temperature increased up to $+0.8$ °C above that of the water, suggesting this may not be a rare occurrence restricted to unusual weather conditions.

Intermittent ponding of shallow water bodies, causing a reduction in water circulation combined with elevated irradiance and seawater temperature, has been documented for reef systems in American Samoa (Smith and Birkeland 2007), Japan (Kraines et al. 1998), French Polynesia (Putnam and Edmunds 2011) and the Great Barrier Reef including Heron Island (Counihan et al. 2001; Jimenez et al. 2008), One Tree Island (Ludington 1979) and Lady Elliot Island (McCabe et al. 2010). Thus, shallow water corals may be regularly exposed to higher temperature than previously thought. This has implications for our understanding of the history of thermal exposure during both bleaching and non-bleaching periods. In particular, through acclimatization or adaptation, exposure to temperature extremes may influence the thermal tolerance of corals (Jokiel and Coles 1990; Marshall and Baird 2000; Coles and Brown 2003).

Coral heating during low-tide, high-irradiance scenarios may not occur to the same extent and as frequently as in

reef habitats, where water flow is predominantly driven by wind rather than tidal currents (e.g., Genovese and Witman 2004). In these cases, low tide and high irradiance may coincide with daily maxima in flow velocity, which could alleviate coral surface warming as flow velocity is an important parameter affecting coral heating under high irradiance (Jimenez et al. 2011).

Further in situ work is required to assess the exact range of flow and irradiance under which the temperature of corals is increased, and the magnitude of this effect across coral taxa, morphologies and pigmentations. This is not an easy task as, for example, difficulties in underwater measurements of surface temperatures pertain to the high thermal conductivity and heat capacity of water. Imperfect contact of the thermosensor with tissue, for example, due to a small water pockets between tissue and the relatively large thermocouple may thus lead to a mixed temperature signal and a lower spatial resolution. It is therefore possible that the sensors deployed in this study underestimated the temperature of corals, and this may be improved through finer-scale measurements using, for example, temperature microsensors in situ together with recently developed diver-operated underwater instrumentation for microsensor measurements (Weber et al. 2007, Hansen et al. 2011; Wangpraseurt et al. 2012).

Interspecific differences in coral warming

The hemispherical *P. lobata* specimens experienced a greater surface warming, and therefore a higher in situ temperature, than the branching *P. cylindrica*. This agrees

with results from Jimenez et al. (2008) showing that branching corals had a smaller surface warming than hemispherical corals. In the January 2007 experiment, this difference occurred despite similar light-absorbing efficiencies, as estimated from our reflectance measurement. This indicates differences between hemispherical and branched corals in how their heat budget is affected by the skeleton, and/or convective heat loss to the surrounding water; these processes and the effects of coral morphology remain to be explored in more detail (see e.g. Jimenez et al. 2011).

Furthermore, the November 2007 experiment indicated that the thermal dynamics of hemispherical corals may in some instances be delayed relative to variations in the water temperature. On November 22, the lag between the water and coral temperature curves was about 5 min. The small hemispherical corals used in Jimenez et al. (2008) (approximately 5 cm in diameter) had response times of approximately 1 min, and based on predictions from the theoretical thermal model in that paper, this should increase proportionally to the coral diameter. The hemispherical *P. lobata* specimens in the present study were ~15 cm in diameter, and according to similar theoretical calculations, they should exhibit a thermal response time of ~3 min. This value is close to the observed response, thus further indicating that coral morphology and size influence the thermal dynamics of coral tissue.

It should be noted that because the sharp increase in surface warming coincided with a decrease in water temperature, this did not increase the coral temperature, but merely slowed the cooling curve by a few minutes (Fig. 3). Furthermore, this was observed only in the November experiment (Fig. 2e, g), and not in January (Fig. 2f, h), where water temperature had a slower rate of cooling (Fig. 2c). Thus, thermal buffering by the skeleton may influence the surface temperature of hemispherical corals, but only occasionally and for a few minutes. It might, however, prove interesting to investigate the potential buffering effect of much larger (metrewide) colonies of massive corals, which often are very resilient to bleaching.

Another, yet unexplored, temperature buffering mechanism may be linked to the thermal properties of coral mucus. To our knowledge, the thermal properties of coral mucus have not been investigated. However, studies of mucoid exopolymers in biofilm communities indicate that they have a thermal conductivity rather similar to water (Characklis 1981), and if coral mucus exhibits similar thermal properties, its role in buffering corals against temperature variations may be limited.

Physiological implications

The mid-day depression in effective quantum yield of PSII (Fig. 5) was associated with active down-regulation as a

photoprotective mechanism, as well as possible photoinhibitory damage under intense noon irradiance (Ralph et al. 1999; Gorbunov et al. 2001; Winters et al. 2003; Levy et al. 2004). Exposure to excessive temperature can exacerbate photoinhibition and impair photosynthesis of the zooxanthellae (Jones et al. 1998; Hill et al. 2004; Takahashi et al. 2004). Thus, the additional heating of corals during low tide may influence the physiological impacts of concurring high irradiance in terms of, for example, higher excitation pressure (Jones et al. 1998; Warner et al. 1999) and production of reactive oxygen species (Lesser and Farrell 2004; Franklin et al. 2004).

Our study confirms the previous observation that maximum coral surface warming did not coincide with maximum irradiance, but with maximum water temperature, well into the low-tide period (Fig. 2, and Jimenez et al. 2008). This possibly coincided with extremely low water flow in the partially drained reef flat, prior to flushing by the rising tide (Ludington 1979; Kraines et al. 1998, McCabe et al. 2010). The timing of low tide thus influences the thermal exposure of corals, and this may have implications for the diel variation in photophysiological performance of corals. The effective quantum yield of PSII in shallow water corals is often lower in the afternoon compared to morning values (Winters et al. 2003; Levy et al. 2004), indicating an afternoon loss in photosynthetic capacity due to photoinhibition (Winters et al. 2003). Thus, the timing of tidally driven coral surface warming could potentially have different physiological impacts in the morning or in the afternoon.

There were no significant differences in the effective quantum yield of PSII between *P. lobata* and *P. cylindrica* during the noon-low-tide sampling period, when the tissues of *P. lobata* were exposed to additional surface warming (Fig. 5). This indicates that the zooxanthellae in *P. lobata* were not adversely affected by exposure to temperatures higher than in *P. cylindrica*. This is not surprising, as exposure temperatures remained lower than the critical bleaching threshold of 32 °C. The $\Delta F/F'_m$ of *P. lobata* was reduced as compared to *P. cylindrica* on the 26 January 2007, when daytime high tide reduced the intensity of noon irradiance. This may arise from numerous other biotic and abiotic factors not investigated in this study, including the prehistory of temperature and light exposure, interspecific differences in the production of heat-shock proteins, symbiont photophysiology (Warner et al. 1996; Hill and Ralph 2005; Ulstrup et al. 2006) and mass transfer (Finelli et al. 2006, 2007). However, considering the differences in thermal exposure caused by additional solar heating of *P. lobata*, the physiological impacts of small intermittent increases in temperature should be further investigated, in particular when water temperatures approach bleaching conditions.

Conclusion

This study presents first detailed in situ evidence that coral tissue surface temperatures can exceed that of the surrounding water under environmental conditions typically occurring during low tide in shallow reef or lagoon environments. Such heating may be a regular occurrence on shallow reef flats, triggered by the combined effects of high irradiance and low water flow, for example, characteristic of low Spring tides. At these times, solar heating of corals coincides with times of maximum water temperature and high irradiance, and the slow flow and consequent thick boundary layers impede gas and heat exchange between corals and the surrounding water, thus promoting coral stress and photoinhibition of the zooxanthellae. The potential implications of such excess temperature stress on coral bleaching await further investigation. Despite similar light-absorbing properties for *P. lobata* and *P. cylindrica*, the temperature effect was more pronounced for the hemispherical *P. lobata* than for the branching *P. cylindrica*. This is consistent with previous evidence of interspecific variation in coral thermal environment (Jimenez et al. 2008) and may result from variation in convective heat transfer and/or thermal properties influenced by the coral morphology and skeleton matrix (Jimenez et al. 2011).

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