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Impact of diurnal temperature fluctuations on larval settlement and growth of the reef coral *Pocillopora damicornis*

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Abstract. Diurnal fluctuations in seawater temperature are ubiquitous on tropical reef flats. However, the effects of such dynamic temperature variations on the early stages of corals are poorly understood. In this study, we investigated the responses of larvae and new recruits of *Pocillopora damicornis* to two constant temperature treatments (29 and 31 °C) and two diurnally fluctuating treatments (28–31 and 30–33 °C with daily means of 29 and 31 °C, respectively) simulating the 3 °C diel oscillations at 3 m depth on the Luhuitou fringing reef (Sanya, China). Results showed that the thermal stress on settlement at 31 °C was almost negated by the fluctuating treatment. Further, neither elevated temperature nor temperature fluctuations caused bleaching responses in recruits, while the maximum excitation pressure over photosystem II (PSII) was reduced under fluctuating temperatures. Although early growth and development were highly stimulated at 31 °C, oscillations of 3 °C had little effects on budding and lateral growth at either mean temperature. Nevertheless, daytime encounters with the maximum temperature of 33 °C in fluctuating 31 °C elicited a notable reduction in calcification compared to constant 31 °C. These results underscore the complexity of the effects caused by diel temperature fluctuations on early stages of corals and suggest that ecologically relevant temperature variability could buffer warming stress on larval settlement and dampen the positive effects of increased temperatures on coral growth.

1 Introduction

Scleractinian corals and the reef ecosystems they construct are currently facing environmental changes at unprecedented rates of changes. Of these changes, rising seawater temperature is generally recognized as one of the most immediate and widespread threats (Hoegh-Guldberg, 1999; Hughes et al., 2003). The most conspicuous response of corals to elevated temperatures is to expel their endosymbiotic dinoflagellates and/or photosynthetic pigments, giving the affected colonies a pale appearance, a process known as coral bleaching (Hoegh-Guldberg, 1999). Due to the loss of zooxanthellae, bleached corals usually fail to obtain their key metabolic requirements from photosynthetically fixed carbon (Grottoli et al., 2006). As a result, massive mortality of corals has been frequently observed following bleaching, leading to a serious decline and impaired ecosystem functionality (Hoegh-Guldberg, 2011; Graham et al., 2006).

On average, sea surface temperatures have increased by approximately 0.7 °C since preindustrial times (Feely et al., 2013), and a further increase of 2–3 °C is expected by the end of this century (Bopp et al., 2013), giving rise to increased concerns about effects on corals. The bulk of scientific work addressing the impact of ocean warming on corals has focused on their tolerance and physiological responses to the predicted increases in mean temperature (Stambler, 2010). However, seawater temperatures are characterized by

fluctuations over timescales ranging from minutes to hours to months. Notably, temperature profiles from reef environments typically show diel oscillations of 4–10 °C (Coles, 1997; Dandan et al., 2015; Guadayol et al., 2014; Oliver and Palumbi, 2011; Rivest and Gouhier, 2015). A consistent daily cycle is commonly present, with temperature increasing after sunrise, peaking after noon and then gradually decreasing to the minimum (e.g., Putnam and Edmunds, 2011; Zhang et al., 2013).

It has been long established that the performance of organisms, including a diverse range of marine invertebrates, differs between steady and variable thermal conditions at equivalent mean temperature (Lucas and Costlow, 1979; Sastry, 1979; Orcutt and Porter, 1983; Pilditch and Grant, 1999; Bryars and Havenhand, 2006; Marshall and McQuaid, 2011). These studies have demonstrated that temperature fluctuations can either speed up or retard early development and growth, depending upon the mean temperatures and amplitude of the fluctuations. However, few studies have explored this thermodynamic effect on corals which routinely experience temperature oscillations in nature (e.g., Putnam et al., 2010; Mayfield et al., 2012).

Recently, our understanding of the physiological responses of corals to diurnally fluctuating temperature has advanced, but results have been variable and even conflicting. For instance, the photo-physiology in larval and adult pocilloporid corals is more adapted to fluctuating temperatures (Putnam et al., 2010; Mayfield et al., 2012). Conversely, significant reductions in photochemical efficiency, symbiont density and aerobic respiration were found in corals exposed to fluctuating temperatures compared to those in constant temperatures (Putnam and Edmunds, 2008, 2011). These contrasting results emphasize a clear need to further explore the impact of diurnally fluctuating temperatures, together with the projected increase in temperature on reef corals.

In the context of a global deterioration of coral reefs and climate change, the early life history stages of corals have drawn increasing attention in recent decades, as they are more vulnerable to environmental changes than their adult counterparts and, more importantly, represent a bottleneck for the maintenance of populations (Byrne, 2012; Keshavmurthy et al., 2014). Successful larval settlement, post-settlement survival and growth are of paramount importance to population persistence as well as the recovery of degraded reefs (Ritson-Williams et al., 2009; Penin and Adjeroud, 2013). Mounting evidence suggests that ocean warming poses a serious threat to these early processes (reviewed in Keshavmurthy et al., 2014), but most previous experiments utilized steady temperature treatments, neglecting the temporal variations of in situ temperature (but see Putnam et al., 2010). To date, there is a paucity of knowledge regarding the influence of dynamic temperatures on these crucial early stages of reef corals. The risk imposed by ocean warming on the fitness and development of corals can be best understood by integrating both diel thermocycles and changes in mean temperature (Boyd et al., 2016).

The present study aimed to investigate how the early stages of the reef coral *Pocillopora damicornis* will be affected by the diurnally oscillatory temperatures, together with ocean warming. *P. damicornis* is a widely distributed and major reef-building coral on reef flats in the Indo-Pacific region (Veron, 1993). This species planulates almost every month, and the release of free-swimming zooxanthellate planula larvae follows a lunar cycle (Fan et al., 2002). Brooded larvae and new recruits were exposed to two temperature levels (29 and 31 °C) crossed with two temperatures regimes (constant and 3 °C diel fluctuations). Diurnal patterns of temperature fluctuations were based on temperature records from our study site, the Luhuitou fringing reef in Sanya, China. Larval condition and juvenile growth after incubation were assessed to compare the larvae's responses to constant and oscillatory temperatures.

2 Materials and methods

2.1 Field seawater temperature monitoring

Seawater temperatures at 3 m depth on the Luhuitou fringing reef (18°12′ N, 109°28′ E) were recorded at 30 min intervals from 2012 to 2016, using Hobo Pendant data loggers (Onset, USA). The temperature profiles showed large seasonal and diurnal fluctuations, with a maximum of 33.1 °C and a minimum of 20.3 °C (Fig. S1a in the Supplement). The mean annual temperature was 27 °C, and the mean monthly temperature ranged from 22 to 30.2 °C (Fig. S1b). The diurnal range in temperature variation during summer (June–September) was between 0.6 and 5.4 °C, with a mean value of 1.76 °C (Fig. S1c). Each day, seawater temperature began to rise at around 08:00 LT, reached the maximum at 13:00 LT, often remained constant for about 2 h and then gradually decreased (Fig. S1d).

2.2 Sampling of corals and larval collection

Eight *P. damicornis* colonies were collected at a depth of 3 m on 20 August 2015. Colonies were transported to the Tropical Marine Biological Research Station and placed individually into 20 L flow-through tanks at ambient temperature (28.7 ± 0.5 °C) under partially shaded light conditions (noon irradiance, ~ 300 µmol photons m^{-2} s^{-1}). The outflow of each tank was passed through a cup fitted with a 180 µm net on the bottom to trap larvae. Larvae released from these colonies were collected at 07:00 LT on 22 August 2015 and then pooled. Two groups of larvae were haphazardly selected for the following settlement and recruit experiments.

2.3 Experimental setup

The two temperature regimes, constant and fluctuating, were set for the target temperature levels of 29 and 31 °C each. The later temperature value was 2 °C above the ambient and 1 °C above the bleaching threshold for coral communities on the Luhuitou reef (30 °C, Li et al., 2012) and within the range of projected increases (Bopp et al., 2013). The pattern and range of temperatures in the two fluctuating treatments were based on in situ records obtained during larval release of *P. damicornis* (Fig. S1d) and the assumption that the predicted 2 °C increase in mean temperature would entail a 2 °C shift in the overall temperature time course (Burroughs, 2007). The 29 °C treatment, corresponding to the ambient temperature at the collection site of adult *P. damicornis*, was used as the control treatment.

All incubations were carried out in 40 L tanks which were filled with sand-filtered seawater. Seawater in each tank was partially exchanged (30 %) with temperature-equilibrated seawater at 22:00 LT every day. Temperature regimes were set using digital temperature regulators (Sieval, TC-05B, China) and 50 W heaters. The seawater was gently aerated and well mixed using submerged pumps (350 L h^{-1}). The water temperature in each tank was recorded with a Hobo Pendant logger at 15 min intervals throughout the experiment. In the two fluctuating treatments (Fig. 1), temperatures were programmed to increase from 28 to 30 °C at 08:00 LT, reach the plateau of 31/33 °C around 13:00 LT and stabilize for 2 h. At 15:00 LT, temperatures were allowed to decrease gradually to 28/30 °C around 22:00 LT and remained stable until 09:00 LT the next morning. Mean (±SD) daily temperatures of the two stable treatments were 29 ± 0.2 and 30.8 ± 0.2 °C, and the mean temperatures of the two fluctuating treatments were 28.9±1.3 and 30.7±1.3 °C, respectively. Salinity in each tank was checked using an Orion 013010MD conductivity probe twice a day and remained stable at 33 psu during the experiment.

Each tank was illuminated by an LED lamp (Maxspect, 10 000 K, China) on a 12–12 h light–dark cycle. Light was measured with a LI-COR 4-π quantum sensor below the water surface. Light intensity was similar in all tanks ($F_{3,96} = 0.32$, $P = 0.81$), averaging 183 ± 3 µmol photons m^{-2} s^{-1} (mean ± SE, $n = 100$), which was close to the irradiance in crevices where coral recruits were found at 3–4 m depths at our study site (Lei Jiang, unpublished data). Facility and logistical constraints precluded the replication of treatments, but salinity and light were carefully controlled to eliminate any possible artifact (Underwood, 1997).

2.4 Larval settlement assay

To explore the impact of temperature treatments on larval settlement, 240 larvae were randomly selected for the settlement experiment. Settlement assays were conducted in 5.5 cm diameter petri dishes on 22 August 2015, starting at around 09:00 LT. The crustose coralline algae (CCA) *Hydrolithon reinboldii*, one of the most abundant CCA species and an effective settlement cue for *P. damicornis* larvae at our study site, was collected at 2–3 m depths and cut into uniformly sized (5 mm × 5 mm × 3 mm) chips 4 days before the settlement experiment. Each dish contained 15 mL seawater and a CCA chip. Fifteen actively swimming larvae were introduced into each dish, which was then floated and partially (80 %) submerged in seawater to ensure temperature control. Preliminary measurements showed that the difference in seawater temperature between dishes and tanks was less than 0.4 °C. Four replicate dishes were used for each treatment. Larvae were allowed to settle for 24 h, after which settlement success was assessed under a dissecting microscope following the criteria of Heyward and Negri (1999). Larvae were categorized as belonging to four conditions: (i) dead; (ii) swimming; (iii) metamorphosed and floating in the water, i.e., premature metamorphosis (sensu Edmunds et al., 2001); and (iv) metamorphosed and firmly attached to CCA or dish, i.e., successful settlement.

2.5 Recruit experiment

To test the effects of temperature treatments on the photophysiology, growth and survival of recruits, a second batch of larvae were transferred to 10 cm diameter petri dishes which were left floating in a flow-through tank at ambient temperature. Twenty hours later, four dishes with a total of 30–35 newly settled recruits were assigned to each treatment tank and placed at the bottom of treatment tanks. Only recruits that settled individually and at least 1 cm apart from others were use for the experiment in order to avoid possible contact between recruits during growth. Dishes were rotated daily to avoid the potential positional effects within each tank.

Twenty 3-day-old recruits were randomly selected and marked in each treatment. Diving-pulse-amplitude modulation (PAM) fluorometry (Walz, Germany) was used to measure the maximum quantum yield of photosystem II (PSII) (F_v/F_m), a proxy for potential photochemical efficiency of symbionts (Genty et al., 1989). Measurements were conducted at 05:30 LT on 4 consecutive days to allow enough time for dark adaption. Both the measuring light and gain of PAM settings were adjusted to 7 to give optimal fluorescence signals.

To better assess the photo-physiological performance of symbionts, effective quantum yield ($\Delta F/F'_m$) was also measured for 15 recruits from each treatment four times on the last day of the experiment (08:00 LT, 11:00 LT, 14:00 LT, 17:00 LT). The maximum excitation pressure over PSII (Q_m) was calculated using the equation $Q_m = 1 - [(\Delta F/F'_m \text{ at } 14{:}00)/(F_v/F_m)]$ (Iglesias-Prieto et al., 2004).

The bleaching response was assessed photographically following Siebeck et al. (2006) with some modifications. At the end of the experiment, recruits were photographed with a digital camera under the dissecting microscope and identi-

cal illumination (35 µmol photons m^{-2} s^{-1}). The camera was set to manual mode with constant ISO settings (12800). The saturation of each coral picture, a good proxy for symbiont or chlorophyll density during bleaching, was measured by taking the average value of 30 randomly placed quadrats (100×100 pixels each) on each coral picture using Photoshop's histogram function (Siebeck et al., 2006). The total chlorophyll or symbiont content of each recruit was determined by multiplying the mean saturation by surface area (as measured below) to account for differences in the size of recruits. The bleaching response was quantified as the reduction in the chlorophyll or symbiont content of each recruit relative to the recruit yielding the maximum value. Recruits were checked daily under a dissecting microscope throughout the experiment and scored as alive or dead based on the presence of polyp tissue. At each census, the number of living recruits was recorded for each treatment. Digital images of recruits with scale calibration were also analyzed for lateral growth using ImageJ software (National Institutes of Health). The number of polyps for each recruit was counted visually. Juvenile growth was estimated as the rates of change in planar area and the number of new polyps over time (Dufault et al., 2012; Jiang et al., 2015).

Calcification was calculated as the dry skeletal weight deposited per day (Dufault et al., 2012). The tissue of recruits was removed with a water pick at the end of the experiment. Skeletons were weighed individually using an ultramicrobalance at an accuracy of ±1 µg. Furthermore, the temperature coefficient (Q_{10}), which is widely used to express the sensitivity of metabolism, development and growth to temperature changes (Howe and Marshall, 2001; Hochachka and Somero, 2002; Rivest and Hofmann, 2014), was calculated using the equation $Q_{10} = (R2/R1)^{(10/(T2-T1))}$, where R is the growth rate at temperature $T2$ or $T1$. Q_{10} values of enzyme-catalyzed reactions often double with a 10 °C increase in temperature.

2.6 Data analyses

Data were tested for homogeneity of variances, using Cochran's test, and normality was assessed using Q–Q plots. Percent data in settlement assays and budding rates were square root transformed to meet the requirements of homogeneity of variances. Larval settlement, Q_m and growth parameters were compared among treatments using two-way analyses of variances (ANOVAs) with mean temperature and temperature variability as fixed factors, each with two levels (29 and 31 °C; constant and fluctuating regimes). When the main effects were significant ($P < 0.05$), planned multiple comparisons were conducted using Fisher's least significant difference (LSD) tests, which are more powerful than the original ANOVA (Day and Quinn, 1989; Lesser, 2010). Recruits were divided into three categories according to the number of polyps: 1 polyp, 2–4 polyps and 5–6 polyps. A chi-square test was used to compare the differences in bud formation among treatments. The survivorship of coral recruits was analyzed using a Kaplan–Meier (KM) log-rank analysis. Two-way ANOVAs with repeated measures were used to test for the effects of temperature treatments on F_v/F_m or $\Delta F/F'_m$ over sampling time points. All statistical analyses were performed with STATISTICA version 12.0 (Statsoft).

3 Results

3.1 Larval settlement

During the settlement assays, larval mortality was only observed in the constant 31 °C treatment (Fig. 2a). In all treatments, between 35 and 60 % of larvae metamorphosed whilst in a free-floating polyp state (Fig. S2), and between 2.5 and 15 % were swimming actively (Fig. 2b). Although the differences in these percentages among treatments were not significant (Table S1 in the Supplement), there were more metamorphosed and floating larvae in the constant 31 °C treatment than in other treatments. Settlement was significantly affected by elevated temperature and marginally affected by the interaction between temperature level and regime (Table S1). Specifically, percent settlement was similar between the two temperature regimes at 29 °C but differed between the constant and fluctuating treatments at 31 °C. The settlement rate at fluctuating 31 °C was comparable to that in the control treatment and significantly higher than that in the constant 31 °C treatment (Fig. 2c; Table S2).

3.2 Photo-physiology, growth and survival of recruits

A significant interaction between time, temperature level and regime was observed for maximum quantum yield F_v/F_m (Table S3; Fig. 3a). Separation of the results by time showed that F_v/F_m was consistently lower at higher temperatures, but the effect size was small, only amounting to a 3 % decrease (Table S4). There was also a significant interaction between time, temperature level and temperature regime for effective quantum yield $\Delta F/F'_m$ (Table S3). Further separate analyses revealed that both temperature increase and fluctuations had strong effects except at 08:00 LT (Table S4), with lower $\Delta F/F'_m$ at elevated temperature and higher $\Delta F/F'_m$ under fluctuating conditions (Fig. 3b).

Q_m, the maximum excitation pressure, was not influenced by elevated temperature (Table S5). However, it was considerably reduced under fluctuating regimes (Fig. 3c; Table S5). Recruits at 31 °C exhibited a paler appearance than those at 29 °C, as evidenced by the reduction in saturation and the increase in brightness (Fig. S3). However, the bleaching index which accounts for differences in recruit size, was unaffected by temperature level, regime or their interaction (Fig. 3d; Table S5).

The budding state of recruits differed significantly among treatments (chi-square test, $\chi^2 = 19.4$, DF = 6, $P = 0.004$).

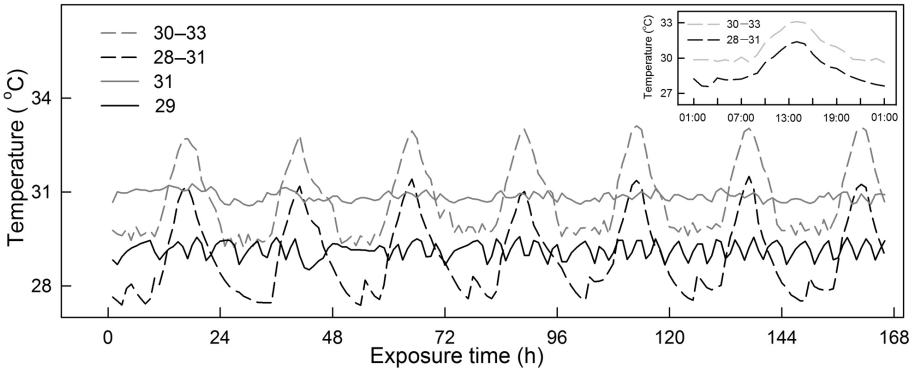

Figure 1. Temperature profiles for each treatment throughout the experiment. The inset shows the 1-day temperature trajectory in the two oscillating treatments. The time course in fluctuating treatments was 10 h at minimum temperature, 5 h of upward ramping, 2 h at maximum temperature and 7 h of downward ramping (passive).

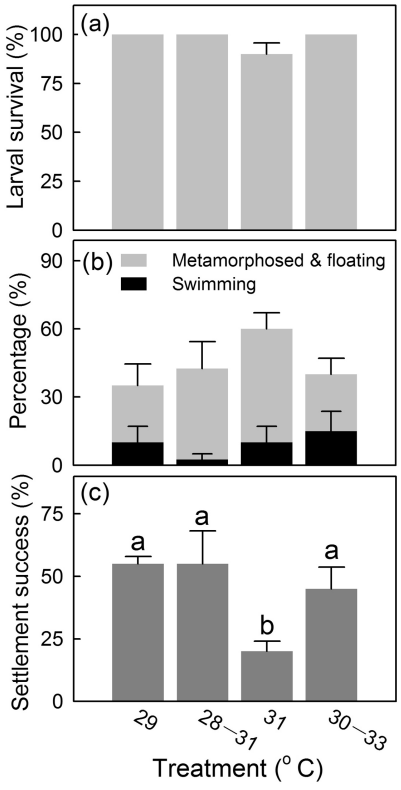

Figure 2. Percentage of *P. damicornis* larvae that **(a)** survived, **(b)** metamorphosed while floating and remained pear-shaped, and **(c)** successfully settled after 24 h exposure to temperature treatments. Error bars represent 1 standard error of the mean (SEM) ($n = 4$). Different letters denote significant differences between treatments.

Seven days after settlement, approximately 70 % of recruits at 31 °C produced at least one bud, compared to less than 50 % of recruits at 29 °C (Fig. 4a). Budding rates at 31 °C were more than twice those at 29 °C (Fig. 4b; Table S5). No significant differences between the constant and fluctuating regimes were observed at either temperature.

Lateral growth rates increased significantly with elevated temperature but were not affected by temperature fluctuations (Fig. 4c; Table S5). The skeletal weight deposited each day was 56 % higher at 31 °C than at 29 °C (Table S5). The effects of temperature fluctuations on calcification depended on the mean temperature (Fig. 4d), even though the interaction between temperature level and regime was not statistically significant (Table S5): at 29 °C, the fluctuating regime had no discernible effect on calcification, while in the fluctuating regime with a mean temperature of 31 °C a significant reduction (20 %) in calcification was observed when compared to the constant 31 °C regime (Table S6).

The survival of recruits remained > 86 % in all treatments after 7 days, with the highest and lowest values at 31 °C (97 %) and 29 °C (86 %), respectively. The survivorship did not vary significantly across treatments ($\chi^2 = 4.49$, DF = 3, $P = 0.21$; Fig. 5), although it was 6–13 % higher at elevated temperature. For juvenile *P. damicornis*, lateral growth, budding and calcification increased 1.19-, 1.91- and 1.68-fold, respectively, between 29 and 31 °C, yielding a Q_{10} of 2.6, 36.8 and 17.8.

4 Discussion

4.1 Larval settlement under elevated and fluctuating temperatures

The pronounced declines in successful settlement at constant 31 °C were consistent with previous findings that reported the effects of thermal stress (> 30 °C) on coral larval settlement (Randall and Szmant, 2009; Humanes et al., 2016). Interestingly, transient exposure to 33 °C in variable conditions did not produce the same negative effect on larval settlement as constant exposure to 31 °C; on the contrary, coral larvae experiencing diurnal shifts between 30 and 33 °C set-

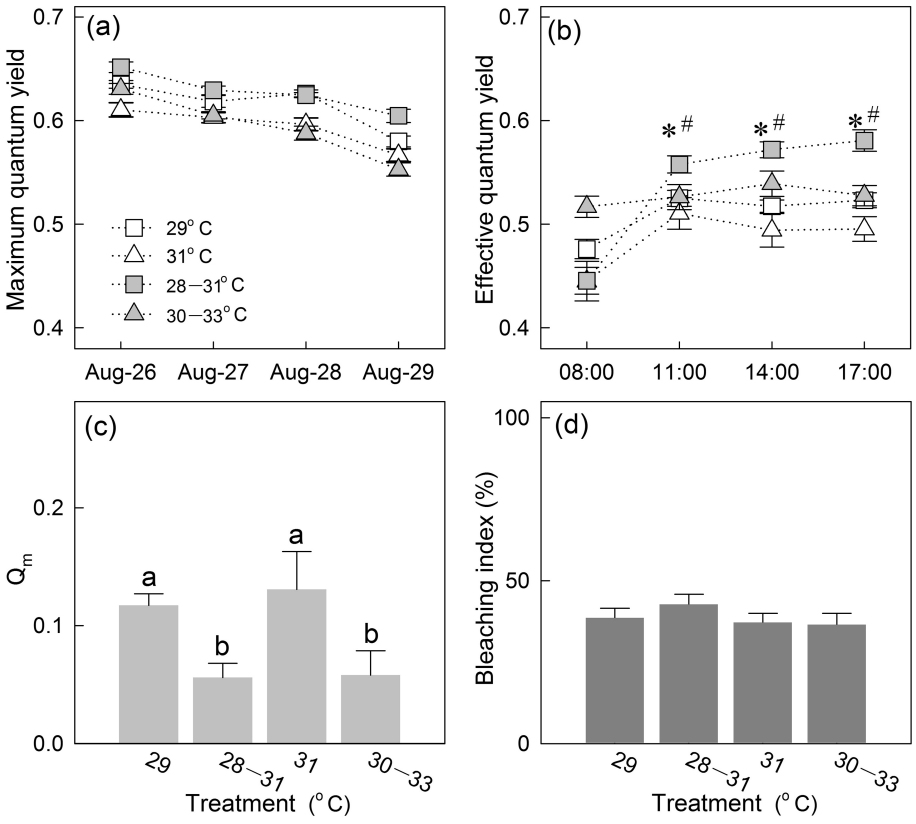

Figure 3. Photo-physiology and bleaching of *P. damicornis* recruits under constant and fluctuating conditions of two temperatures (29 and 31 °C): **(a)** F_v/F_m over 4 consecutive days; **(b)** $\Delta F/F'_m$ throughout the last day of the experiment; **(c)** Q_m and **(d)** bleaching rates. Error bars represent 1SEM ($n = 20$ for F_v/F_m; $n = 15$ for $\Delta F/F'_m$ and Q_m; $n = 25$–33 for bleaching index). Asterisks and hashes indicate significant effects of temperature increase and fluctuations at a specific time, respectively. Different letters represent significant differences between treatments.

tled at a similar rate to those in the control. During daytime exposure to elevated and stressful temperatures, coral larvae may not initiate metamorphosis and settlement because larvae undergoing this complex stage are particularly susceptible to thermal perturbations (Randall and Szmant, 2009), but settlement may proceed as temperature descends to a more tolerable level at night (30 °C in this study). It is likely that the fluctuating temperature conditions could provide some respite for coral larvae, thereby favoring settlement at elevated and fluctuating temperature conditions. A more precise assessment of settlement timing was not possible without disturbing larvae, given the use of small petri dishes. Future studies are needed to regularly observe and establish the dynamics of larval behavior under fluctuating temperatures to confirm this hypothesis.

Another possible cause for the higher settlement of larvae in the fluctuating 31 °C treatment may be the brief exposure to extreme temperatures around noon. Previous studies have demonstrated that short-term exposure (minutes to hours) of coral larvae to extremely high temperatures (33–37 °C) significantly enhanced the subsequent settlement at a lower temperature, suggesting a strong latent effect (Coles, 1985; Nozawa and Harrison, 2007). Therefore, the 2 h incubation at 33 °C during the daytime may have exerted a latent and stimulatory effect on settlement at night when the temperature was lower.

Metamorphosed and floating larvae, previously noted in corals (Richmond, 1985; Edmunds et al., 2001; Vermeij, 2009; Mizrahi et al., 2014), were more frequent at elevated temperatures. One possible explanation is that premature metamorphosis in coral larvae is a spontaneous response to increased temperatures (Edmunds et al., 2001). The floating polyps, as a result of pelagic metamorphosis, have been shown to have extended longevity, possibly because they can obtain energy from photosynthesis by maternally derived symbionts and heterotrophic feeding using tentacles (Richmond, 1985; Mizrahi et al., 2014). Thus, the plasticity of metamorphosis during the dispersive phase could be a strategy for coping with environmental stress in coral larvae, although it remains to be determined whether these floating polyps are capable of settling and contributing to recruitment in natural conditions.

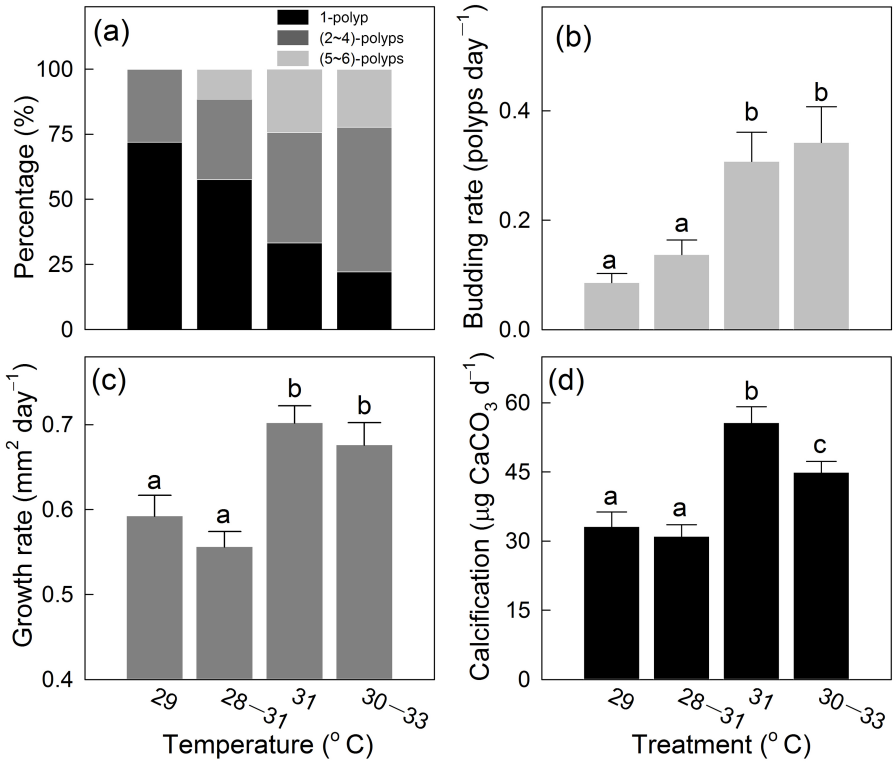

Figure 4. **(a)** Budding state, **(b)** polyp formation rate, **(c)** lateral growth and **(d)** calcification of *P. damicornis* recruits under constant and fluctuating conditions of two temperatures (29 and 31 °C). Error bars represent 1SEM ($n = 25$–33). Different letters denote significant differences between treatments.

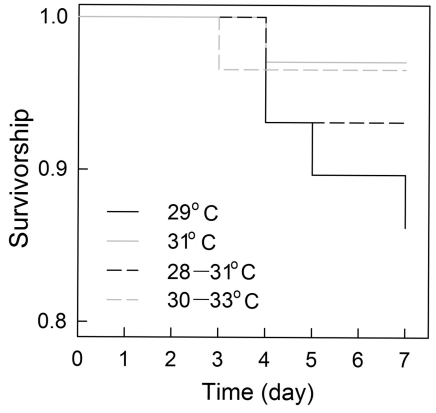

Figure 5. Survivorship of *P. damicornis* recruits estimated using Kaplan–Meier analysis in each treatment over the 7-day experiment. The numbers of recruits at the start of the experiment in each treatment are 30 for the treatments 29, 30–33 and 28–31 °C and 35 for 31 °C.

4.2 Symbiont responses to elevated and fluctuating temperatures

The reduction in F_v/F_m at 31 °C does not indicate severe damage to the photosynthetic apparatus or chronic photoinhibition, as the values were still within the healthy range (Hill and Ralph, 2005). The fluctuating regime had positive effects on $\Delta F/F'_m$, suggesting a greater light use efficiency to drive photochemical processes. Q_m, an indicator of the excitation pressure over PSII, was reduced in fluctuating treatments, reflecting a stronger competitiveness of photochemical process for reaction centers over non-photochemical quenching (Iglesias-Prieto et al., 2004). The higher $\Delta F/F'_m$ and lowered Q_m under fluctuating conditions suggest that the diel temperature oscillations could relieve heat stress on corals and corroborate previous findings that temperature fluctuations are favorable to the photo-physiology of corals (Mayfield et al., 2012; Putnam et al., 2010). The positive effect of exposure to fluctuating temperatures on these photophysiological metrics may be associated with the cooling overnight and upregulation of the genes related to photosynthesis (Mayfield et al., 2012).

In contrast to the aforementioned studies, Putnam and Edmunds (2008) found that when incubated at fluctuating temperatures (26–32 °C), F_v/F_m of *P. meandrina* and *Porites rus* nubbins were depressed by ∼ 20 % compared to those maintained at a constant temperature of 28 °C. These contrasting results may be due to methodological differences. Our study and Mayfield et al. (2012) mimicked natural temperature fluctuations by progressively modulating tempera-

tures over time, whereas Putnam and Edmunds (2008) directly transferred corals from low to high temperature in the morning and vice versa at night. This approach could cause instant heat shock and prolonged exposure to extreme temperatures, thereby exaggerating the stressful effects of diurnal thermal fluctuations.

Although juvenile *P. damicornis* at 31 °C exhibited an apparent paling appearance compared to those at 29 °C, the loss of symbionts and bleaching were not indicated, as the faster lateral growth at 31 °C suggests that the paling is instead the result of pigment dilution due to a larger surface area. This outcome contrasts with previous work showing the sensitivity of endosymbionts within coral recruits to elevated temperatures (Anlauf et al., 2011; Inoue et al., 2012). The lack of bleaching response to elevated temperatures in the current study may be linked to the symbiont type. *P. damicornis* predominantly harbored *Symbiodinium* clade D in Luhuitou (Zhou, 2011), which has been found to be particularly thermally tolerant. In addition, the difference in treatment duration could also partially explain these contrasting sensitivities. Albeit ecologically relevant, the exposure duration in this study was much shorter than that in previous studies (Anlauf et al., 2011; Inoue et al., 2012), therefore resulting in less cumulative stress. It is possible that a longer exposure time may cause similar bleaching responses to those found by other studies.

Further, daytime exposure to high temperatures in fluctuating treatments did not induce significant symbiont loss in juvenile *P. damicornis*. This observation is in stark contrast to the observations of Putnam and Edmunds (2011) on adult corals. That study found that ephemeral exposure to 30 °C at noon in fluctuating conditions (26–30 °C) elicited a 45 % reduction in symbiont density of adult *P. meandrina* compared to corals at the steady 28 °C treatment, a larger effect than was elicited by continuous exposure to 30 °C (36 %). The flat structure of juvenile corals has been suggested to provide a higher mass transfer capacity to remove reactive oxygen species than the branching and three-dimensional adults (Loya et al., 2001). Hence, the discrepancy between our results and that of Putnam and Edmunds (2011) may, at least partially, be attributed to the morphology-specific difference in thermal tolerance of juvenile and adult corals.

4.3 Accelerated early development at elevated temperature

The early development of juvenile *P. damicornis*, including budding, lateral growth and calcification, was accelerated at 31 °C, which is 2 °C above the local long-term summer mean and 1 °C above the local bleaching threshold (Li et al., 2012). Growth stimulation by temperature increase also occurred in a pilot study which showed that lateral growth and budding of *P. damicornis* after 2 weeks at 31 °C were 10 and 41 % higher, respectively, than that of those at 29 °C (Fig. S4). Moreover, recruits with increased growth rates at elevated temperatures showed higher survivorship, consistent with previous field observations that survival in early stages of reef corals was strongly dependent on colony size and growth rates (Hughes and Jackson, 1985; Babcock and Mundy, 1996). In contrast to our study with a tropical coral, a previous study reported that calcification of symbiotic polyps of *Acropora digitifera* in subtropical Okinawa was highest at 29 °C (2 °C above the local summer mean) and was reduced at 31 °C (Inoue et al., 2012).

It has been widely accepted that warming is likely to be more deleterious to early stages of tropical corals than subtropical species (Woolsey et al., 2014). Clearly, thermal tolerance of corals depends on the ambient temperature at a particular location. Given the large seasonal temperature fluctuations and ranges in our study site (Fig. S1), it is not surprising that *P. damicornis* grew faster at 31 °C. The positive effects of the 2 °C temperature increase on the early development of *P. damicornis* suggest that tropical corals dwelling in thermally dynamic habitats may also have the capacity to modify their thermal limits, thereby enhancing physiological performance and tolerance under increasing temperatures (Clausen and Roth, 1975; Dandan et al., 2015; Schoepf et al., 2015).

There are two possible explanations for the increases in growth and development at elevated temperature in our study. Firstly, the paling of recruits at elevated temperatures as a result of pigment dilution will enhance their internal light fields, which could bring about a 2- to 3-fold increase in symbiont-specific productivity (Wangpraseurt et al., 2017) and in turn support skeletal growth and asexual budding. Secondly, since coral calcification is positively correlated with carbon translocation between *Symbiodinium* and the host (Tremblay et al., 2016), the elevated calcification and growth at 31 °C indicates more efficient nutritional exchange, sustaining the metabolic expenditure of faster development. This interpretation is further supported by the excessive deviation of Q_{10} from the kinetic expectations (2–3): this signifies a strong amplifying effect through changes in fundamental biochemical systems along with the acceleration of functional enzyme activities at increased temperatures (Hochachka and Somero, 2002).

4.4 Differing effects of temperature fluctuations on growth

The growth-related processes, including budding, lateral growth and calcification, differ in their responses to temperature fluctuations, with calcification being more responsive. The lack of statistically significant effects of temperature fluctuations on budding and lateral growth suggests that either these processes were not affected by fluctuating temperatures or the length of exposure to the peak temperatures may be not long enough to trigger a detectable effect (Lucas and Costlow, 1979).

The impact of fluctuating temperatures on calcification was different at ambient and elevated temperatures: the fluc-

tuating treatment did not affect calcification at 29 °C but resulted in a significant decline at 31 °C. In comparison, prior studies with corals did not find that temperature fluctuations influenced skeletal growth (Putnam and Edmunds, 2011; Mayfield et al., 2012). It is likely that the impact of temperature fluctuations depends critically on whether the temperature range encompasses the maximum thermal limits of the species (Vasseur et al., 2014).

The relationship between skeletal growth in corals and temperature is nonlinear and characterized by a parabola with an optimum and threshold, beyond which the stimulatory impact of temperature will be reversed (Wírum et al., 2007; Buddemeier et al., 2008; Inoue et al., 2012; Castillo et al., 2014). Although the optimal temperature for calcification by *P. damicornis* recruits remains unknown, it is possible that the recruits exposed to the fluctuating 31 °C treatment calcified at a slower rate when the temperature was below 31 °C compared to those in the constant 31 °C treatment. However, given the well-established temperature performance curve for coral calcification (Buddemeier et al., 2008; Wírum et al., 2007), daytime exposure to temperatures above 32 °C would have severely impaired the calcification process, thus leading to an overall decrease in calcification. At least two hypotheses from the literature can help explain this inhibitory effect. First, during the warmest part of a daily temperature cycle, metabolic rates will usually be depressed to improve energy conservation (Sastry, 1979; Putnam and Edmunds, 2008; Marshall and McQuaid, 2011). Depression in metabolism and ATP production in this specific "quiescent" period may impose constraints on daytime calcification, as calcification is energetically costly, consuming up to 30 % of the coral's energy budget (Allemand et al., 2011). An alternative and nonexclusive explanation is that daytime exposure to extreme temperature could disturb the function and/or synthesis of skeletal organic matrix (OM) within the calcifying medium. The OM has critical roles in calcification such as calcium binding and providing carbonic anhydrase and the template for crystal nucleation (Allemand et al., 2011). Daytime temperatures of 33 °C may disrupt the function of carbonic anhydrases (Graham et al., 2015), thereby severely inhibiting the conversion of respired CO_2 to bicarbonate for subsequent use in calcification.

Further, since the OM itself is also incorporated into the skeleton, the rate of OM synthesis is a limiting factor for calcification (Puverel et al., 2005; Allemand et al., 2011). Extreme temperatures may impede the production of OM as it is highly sensitive and vulnerable to short-term thermal stress (Desalvo et al., 2008, 2010; Maor-Landaw et al., 2014). Although the exact mechanism has not yet been fully resolved, our study provides evidence that daytime exposure to extreme temperature in variable thermal conditions adversely affects calcification and dampens the stimulation of skeletal growth in *P. damicornis* at elevated temperature.

5 Conclusions and implications

This study was the first to examine the effects of both increased temperature and daily temperature variability on the early stages of a reef coral. We found that realistic diurnal temperature fluctuations considerably tempered thermal stress on larval settlement and had varied effects on the physiology and early development of *P. damicornis*. Diel oscillations in temperature did not induce bleaching but relieved heat stress on photo-physiology. Further, temperature fluctuations had no obvious effects on budding and lateral growth, although 2 h exposure to 33 °C during the daytime apparently caused a reduction in calcification compared to constant exposure to 31 °C. The results reported here emphasize the distinction between the effects of constant and fluctuating temperatures, both for different mean temperatures and on two successive life stages, and highlight the importance of incorporating diurnal fluctuations into research on the influence of ocean warming on coral biology.

The results of this study suggested that coral larvae subjected to diurnal temperature variations, especially at increased temperature, exhibit better settlement competence than those subjected to static thermal treatment. The fluctuating temperatures were favorable to the photo-physiology of endosymbionts and only had minor effects on post-settlement development of coral recruits. Therefore, corals in highly fluctuating environments may have the potential to tolerate and acclimate to the changing seawater temperatures. These findings may also provide clues as to how diverse coral communities can persist and thrive in some thermally variable conditions (Craig et al., 2001; Richards et al., 2015). It is important to note that this study was technically limited to only one fluctuating amplitude, and the extent of thermal variance has as much of an impact on fitness as the changes in mean temperature (Vasseur et al., 2014). Given that there is currently still no consensus on the future temperature variability (Burroughs, 2007), it will be critical to study the impact of a broad range of thermal variations which corals may experience in a warming ocean.

Data availability. The data associated with the present study are available from the corresponding author upon request.

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Author contributions. LJ and HH conceived and designed the experiments; LJ, YFS and YYZ performed the experiments; XBL, LJM, JSL, XML, GWZ, SL and PYQ contributed analysis and materials. LJ wrote the manuscript with comments from all co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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