‘Burning *Pocillopora*’: Coral bleaching and recovery in response to a heat stress gradient

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Abstract

As a result of climate change, warming temperatures threaten the livelihood of coral reef habitats around the world. Heat stress leads to bleaching, the expulsion of the corals’ symbiotic algae, depleting the coral hosts of the source of the majority of their nutrition. The present study examines the bleaching, growth, and recovery response of the widespread reef-building coral *Pocillopora sp.* to a heat stress gradient (nine days of ramping up the temperature and seven days of ramping it down). When compared to corals kept at an ambient and constant temperature, the heat-stressed corals experienced a decline in photosynthetic efficiency and color (both indicators of bleaching) but were able to make a full recovery as the temperature returned to ambient conditions. Heat-stressed corals also exhibited a slightly different, but insignificant, growth pattern when compared to controls. Altogether, our results indicate that *Pocillopora sp.* has the capacity to make a short-term recovery to a short-term heat stress gradient.

Introduction

Coral reefs, habitats constructed by colonial reef-building corals, provide homes for hundreds of thousands of species, subsequently creating biodiversity hotspots around the world (Roberts *et al.*, 2002). On a much smaller scale, each individual coral polyp comprising the reef typically provides an endosymbiotic home for algae of the genus *Symbiodinium* (Stat *et al.*, 2006; Trench, 1979). The coral host benefits from the products of the algae’s photosynthesis while the corals supply refuge and compounds needed by these symbionts (Muscatine & Porter, 1977; Pearse and Muscatine, 1971; Trench, 1979).

Unfortunately, warming temperatures due to climate change imperil the relationship between corals and their symbiotic algae (Roberts *et al.,* 2002; Stat *et al.*, 2006). Increasing water temperatures leads to ‘coral bleaching,’ in which the corals’ zooxanthellae either leave or are expelled from the coral, causing the coral to lose its color (Hoegh-Goldberg & Smith, 1989; Yonge & Nichols, 193l). Without the photosynthetic activity of the symbiont, obligately symbiotic corals have a harder time obtaining nutrients and become more susceptible to disease and death (Banin *et al.*, 2000; Stat *et al.,* 2006). In the long run, the adverse effects of bleaching events can lead to a slow recovery and a potential shift in coral resilience and species diversity (Johns *et al.,* 2014). Therefore, bleaching events have the potential to harm those that rely on healthy reefs for fishing and tourism industries (Roberts *et al.*, 2002).

Bleaching events occurring in the tropics have severely impacted reef-building corals, including those belonging to the genus *Pocillopora* (Adjeroud *et al.,* 2009). Native to the Indian and Pacific Oceans, this genus is particularly sensitive to elevated temperatures as it consists of branching coral species with high metabolic rates and skeletal growth (D’Croz & Mate, 2004). Therefore, *Pocillopora sp.* can be used as an effective model to study bleaching events in tropical

corals. Previous studies applying heat stress to *Pocillopora sp.* in order to observe bleaching have done so abruptly (*e.g.* ramping up the temperature from control conditions to heat treatment immediately) and subsequently sacrificed their colonies (Camaya *et al*., 2016; Hill *et al.*, 2014; Putnam *et al.,* 2013, Rodríguez-Troncoso *et al.,* 2010). This does not replicate climate change conditions in nature accurately, considering the ocean does not warm by 3-9˚C immediately.

Although occurrences of bleaching are well documented in tropical coral species around the world, much less is known about their recovery post-bleaching (Johns *et al.,* 2014). Studies that have observed coral recovery have done so over long timescales (*i.e.* months), leaving the question of a colonies' ability to recover to shorter-term events unclear (Johns *et al.,* 2014; Osborne *et al.,* 2017; Thomas & Palumbi, 2017). On the other hand, Schönberg *et al.* (2008) observed no symbiont activity recuperation within 12 hours of recovery time after heat stress in an *Acropora* coral, leaving recovery time periods in between 12 hours and months for *Pocillopora* in question.

The objective of the present study was to quantify the physiological effects of a nine day heat stress gradient (1˚C/day) on *Pocillopora sp.* and determine whether there is a possibility of short-term recovery from heat stress by removing the stressor and decreasing the temperature along a gradient (1˚C/day) for an additional seven days until the water returns to conditions similar to the first day. To accomplish this, coral color, algal photosynthetic efficiency, and relative weight gain were measured along a sixteen-day period. Declines in pulse amplitude modulated (PAM) fluorometry values, measuring the photosynthetic condition of the symbiont, and coral color both indicate bleaching (Hill *et al.,* 2014; Schönberg *et al.,* 2008). To measure the growth of corals over time, buoyant weight measurements are a technique used in the field or the lab and are an effective way to assess how environmental factors affect coral colony growth (Bak, 1973; Davies, 1989). During heat stress, we expected *Pocillopora sp.* to lose their symbionts and color (*i.e.* bleach), have reduced photosynthetic efficiencies, and calcify at a reduced rates when compared to controls. However, once the heat stress is removed (*i.e.* during recovery), we expect to observe slight recovery of all variables as the *Pocillopora sp.* recover symbionts over time.

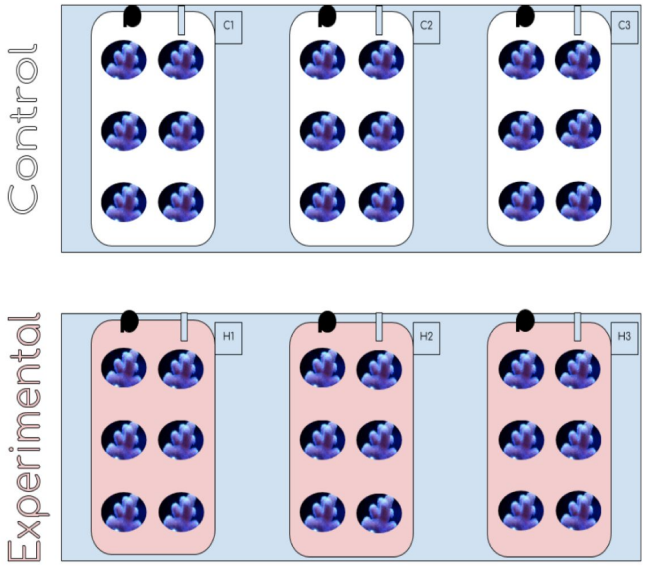

Figure 1. Tank set-up included the random assignment of 36 'nubbins' to one of six tanks. Three tanks were put under control conditions (C) and another three were put under thermal treatment (H). Nubbins were genotypically distinct after they were fragmented from six branching colonies, named a letter (A-F) and number (1-6), and assigned to tanks randomly.

Methods

Experimental Design

Each of six branching coral colonies (defined as one coral genotype, assigned as A-F) was fragmented into six nubbins (labeled 1-6) and glued to individual labeled petri dishes, for a total of 36 'nubbins'. Each petri dish was drilled to allow for buoyant weight measurements. Coral nubbins were allowed to recover from fragmentation and acclimate to holding tank conditions for three weeks. After recovery, nubbins were randomly assigned to one of six tanks, which resulted in six

genotypically distinct nubbins per tank (Fig. 1). Three tanks served as controls and three served as treatment tanks. Three control tanks were maintained at 25˚C for the duration of the experiment. The three thermal stress treatment tanks were subjected to the temperature profile displayed in Fig. 2. Overall, a 1˚C temperature increase occurred daily for six days (from 25˚C to 31˚C; modified from Courtial *et al.*, 2017), temperature was stabilized at 31˚C for three days to induce significant (>90%) bleaching (as demonstrated by Rodríguez-Troncoso *et al.,* 2010), and temperature was decreased 1˚C daily for six days (from 31˚C to 25˚C) with one additional recovery day, for a total experimental timeline of 16 days. Slight variation from the set temperature occurred due to the tank system's inherent error. However, the recorded temperature did not vary from the set temperature by more than ± 1˚C.

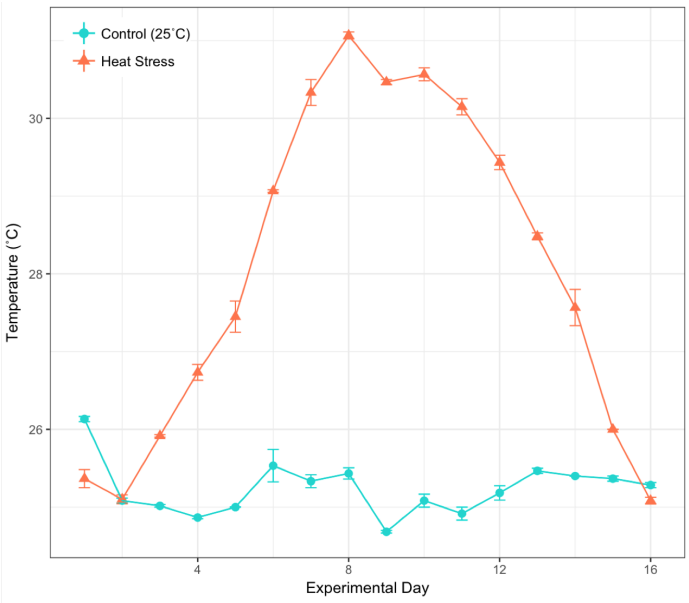

Figure 2. Temperature profile obtained from tank readings taken twice per day.

Tank Maintenance

In order to reduce algal growth, algae were removed using a toothbrush during water changes and coral position rotations. Algae growing on the corals were either pulled off if large enough or scrubbed off as close to the corals as possible without physically touching them. If necessary, algae were gently scrubbed off of the white, non-living sections of the corals. During weekly water changes, a large brush was used to scrub tank walls and then a 10% water change was conducted. To maintain salinity, an auto-top off system refilled tanks from a supply of reverse osmosis (RO) water. All tank conditions (pH, salinity, light levels, flow) remained constant, with the exception of temperature. pH was kept at a range between 7.72 and 8.76, while salinity was kept between 27.0 and 32.0 ppm (though the salinity unexpectedly dropped to 24 ppm on experimental day 10). Corals were fed three times per week to ensure adequate nutrition. Every three days, nubbins were rotated clockwise within the tanks to ensure that all corals experienced the similar light conditions. Light levels were measured in the tanks using a Marine PAR Sensor and average PAR measurements were between 65 and 90 µmol/m^{2}s. Tank temperatures were tested twice daily with a liquid-in-glass thermometer and salinity and pH were recorded daily via a refractometer and pH meter, respectively.

Assessing Coral Bleaching

One bleaching assessment was using the ratio of variable fluorescence to maximum fluorescence (*Fv/Fm*) to measure photochemical activity and efficiency of the corals' *Symbiodinium* in converting light into energy. *Fv/Fm* was measured by Junior Pulse Amplitude Modulated (PAM) fluorometry on days 2 and 4 during the heat stress increase, on days 8 and 9 during the 31˚C heat stress, and on days 12, 14, and 16 during the recovery period (modified from Schönberg *et al.,* 2008). PAM measurements were taken after corals were dark acclimated for at least thirty minutes. Head lamps emitting red light were used to minimize *Symbiodinium* light

exposure. Most *Fv/Fm* measurements are between 0.310-1.000 units (Björkman & Demmig 1987). However, our results and results for *Pocillopora* range between 0.350 and 0.700 units (Hill *et al.*, 2014). Three replicate measurements were taken on three different branches on each coral at each time point. All replicates were within 0.050 units of each other. After all PAM measurements for the day were completed, photographs of each coral nubbin were taken as a second assessment of bleaching. A cylindrical container with a hole in the center of the lid for the camera lens was utilized to standardize camera height approximately 4 inches above the coral. A 2-inch segment of white tape was used as a standard color reference. The red-green-blue (RGB) color intensity of the coral in three tip locations per nubbin was quantified in ImageJ for each nubbin. Photographs were taken each day that PAM fluorometry was carried out, but photos from day 2 were omitted from analyses due to non-standard light conditions.

Weight Change

Coral buoyant weights were quantified on days 2, 8, and 16, to observe coral growth during and after treatment. Measurements were taken in the morning after temperature and water quality conditions were confirmed. To weigh, a scale was attached to the top of a 5-gallon glass tank with zip-ties. A thick metal hook was attached to the scale's underside and a thin wire hook hung on the metal hook. Corals were then hung on the wire to assess buoyant weight. Water levels and temperature remained constant at all buoyant weight time points. Three replicate weight measurements per coral were collected at each time point and averaged. Growth over time was then calculated as the percent weight difference per nubbin between days 2 and 8 and between days 8 and 16.

Statistical Analyses

After data collection, all data were placed into statistical program *R* (RStudio Team, 2015). Using *R*, the averages for all three replicates for weight, PAM, and RGB measurements per nubbin were calculated and then grouped and averaged by treatment and experimental day. One way ANOVAs were then used to determine if there was a significant difference between the corals in the heat treatment and corals in the control for each timepoint. Weight comparisons were made between the treatments by finding the change in weight from day 2 to day 8 and from day 8 to day 16 matching the heating and the recovery period, respectively. PAM data was plotted over the experimental time to show the change over time for both the heated treatment and the controls. Color data (RGB measure) was plotted over time showing color change over time for both groups.

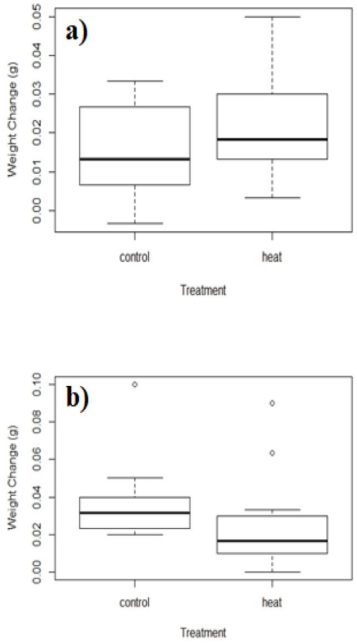

Figure 3: The effect on heat stress on coral growth from day 2 to 8 (a) and from day 8 to 16 (b). The weight change between the two treatments show the weight gained over the heating period were not statistically significant with p= 0.09 for days 2 and 8 (a) and p=0.07 for days 8 and 16.

Results:

Effects of Heat Stress on Weight Gain

Under elevated temperature, heat-treated corals seemed to have had an increased growth rate when compared to control corals for the first 8 days (Fig. 3a). However, the difference between the control and heat treatment was statistically insignificant (p = 0.09). From days 8 to 16, the heat treatment corals appeared to grow slower than the control corals, however, there was no statistical significance (Fig. 3b, p = 0.07).

Effects of Heat Stress on Photosynthetic Efficiency

When comparing results between heat-treated and control corals, photosynthetic efficiency (*Fv/Fm*) was negatively and significantly affected by heat stress on days 8 (temperature set to 31˚C, $p < 0.01$) and 12 (29˚C, $p < 0.01$, Fig. 4a,c). On all other experimental days that *Fv/Fm* was measured, the difference between treatments was statistically insignificant. However, when considering the results through time, between days 2, 4, and 8 (while the temperature increased from 26˚C to 31˚C), the average *Fv/Fm* of the heat-treated corals had not noticeably changed, while the control corals' *Fv/Fm* inexplicably increased. Between days 8, 9, and 12 (treatment changing from 31˚C to 29˚C), the *Fv/Fm* of the heat-treated corals declined, but then made a recovery between days 12 and 14 to become statistically indistinguishable from control coral levels again.

Effects of Heat Stress on Color

Corals put under heat stress showed a large decrease in color intensity (indicative of bleaching) during the heat gradient increase from experimental day 4 (temperature set to 27˚C) to experimental day 8 (31˚C, Fig. 4b,c). Accordingly, control corals kept at 25˚C showed significantly higher RGB levels than heat-treated corals on day 8 ($p < 0.01$). Surprisingly, on the last day of maximum heat stress (31˚C, experimental day 9), treatment corals displayed an increase in coloration to return to the range of control corals' RGB coloration. Then from experimental day 10 to the end of the experiment, both tanks show very similar trends where there are little to no differences in color between treatments and both treatments showed an increase in color until the last day. At the end of the experiment, the amount of coloration was higher in both tanks than when the bleaching assessments began.

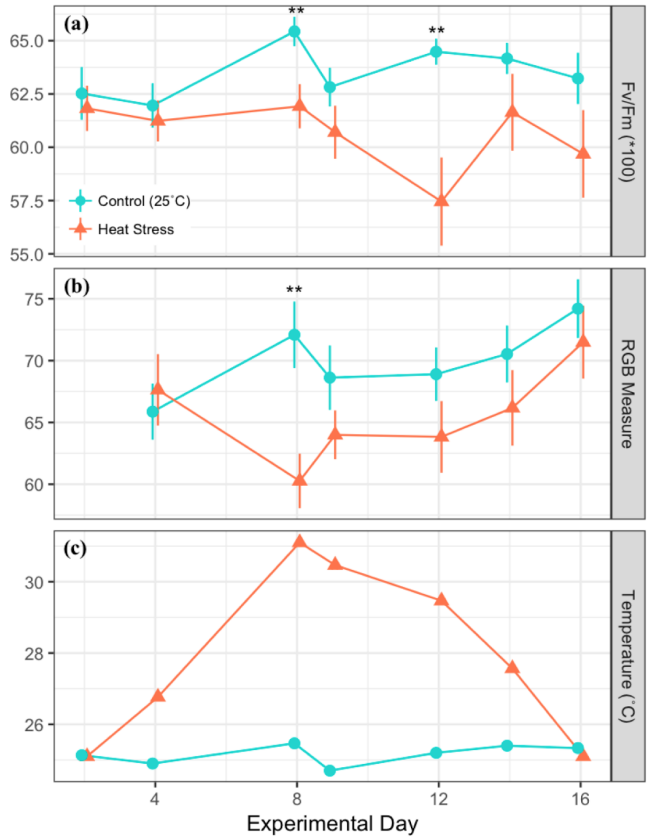

Figure 4. The effect of heat stress on (a) symbiont photosynthetic efficiency (measured as chlorophyll fluorescence *Fv/Fm*) and (b) color when compared to controls on each experimental day (** = $p < 0.01$). (c) Temperature regime experienced by the corals per experimental day.

Discussion

Effects of Heat Stress on Buoyant Weight

Under heat stress from day 2 to 8, corals under the heat stress gained more weight than

the corals in the control but from day 8 to 16, corals under the heat stress gained less weight than the corals in the control (Fig. 3a,b). This means that as the corals grew under heat stress, there was a point when the corals' growth began slowing. Although our analysis indicates that there was no statistical significance, it has been observed that corals do grow faster under elevated temperature (Lough *et al.*, 2000; Cooper *et al.*, 2008; Marshall *et al.*, 2004). However, once the temperature rises above the optimal growing temperature, calcification rates are suppressed and the growth of the coral decreases (Lough *et al.*, 2000; Cooper *et al.*, 2008; A. T. Marshall *et al.*, 2004). Accordingly, as the heat-treated corals in the present study were exposed to an elevated temperature gradient, they had a higher weight gain than controls. Once the conditions surpassed the ideal growth temperature, the corals in the heat treatment had a lower weight gain in the second half of the study. Because measurements were taken on days 2, 8 and 16, the temperature and day where the corals began to decrease in growth was not recorded. More measurements or time may help to better understand how temperature affects growth of *Pocillopora sp.*

Effects of Heat Stress on Photosynthetic Efficiency

As expected, the heat-treated corals displayed reduced photosynthetic efficiency when compared to control corals during the peak of our heat stress experiment, on day 8 (31˚C, Fig. 4a). However, when analyzing the results over time, the average *Fv/Fm* values did not decline between days 4 and 8 for the treatment corals, rather the control corals *Fv/Fm* values unexpectedly increased. According to our tank temperature data (Fig. 4c) there was also a very slight temperature increase from 25 to 25.5˚C between days 4 and 8, providing a possible explanation for the control corals' response. On the other hand, support for the result of reduced photosynthetic efficiency on day 8 stems from Fig. 4b, which shows that were was a significant drop in color on this day, indicating a loss of symbionts. After day 8 in the *Fv/Fm* values, there is a decline in *Fv/Fm* over time, until day 12's heat-treated corals performed significantly worse than control corals during PAM measurements (29˚C, Fig. 4a). This supports our hypothesis that the photosynthetic efficiency of the *Pocillopora* would decline in response to the heat stress. Strangely, this result did not correlate with a significantly reduced RGB measure in treatment corals on day 12 in Fig. 4b. Lastly, we observed a recovery in the heat-treated corals' photosynthetic efficiency between days 12 and 14, supporting our prediction that the corals would be able to recover from the effects of the heat stress. Day 14's average *Fv/Fm* for the heat-treated corals had returned to pre-heat stress levels, exceeding our expectation of a slight recovery. There was a slight decline again into day 16 for the treatment corals, however it was not significantly different from the controls, indicating that the *Pocillopora*'s photosynthetic efficiency successfully recovered.

Effects of Heat Stress on Color Change

After analyzing our results, it can be concluded that *Pocillopora sp*. bleached while the water temperature was ramped up 1˚C per day until experimental day 8, when a significant color difference between control and heat stress corals was noted (Fig. 4b). From then on, experimental corals experienced increased coloration (*i.e.* no longer displayed characteristics of bleaching) from day 9 to day 16, with day 9 being the last day being held at 31˚C (the highest temperature applied) and days 10 to 16 being the recovery period where temperature was

decreased 1˚C per day. When comparing day 4 (pre-heat stress) to the last day of the experiment, the color of the treatment corals showed recovery after bleaching. We had expected control corals to experience little to no color change because they would not be under any stress. Although temperature, pH, salinity, and flow conditions were kept as consistent as possible, our control corals still changed color over time. By the end of the experiment, the coloration of all corals were much higher compared to day 4.

Overall, these results support the part of our hypothesis that predicted that symbionts would leave *Pocillopora sp.* when under heat stress. These tropical corals were stressed and bleached in color from loss of symbionts in response to being put under thermal conditions that they did not normally experience. At the same time, these same results do not support the part that said we would observe a slight recovery in coloration during the period in which heat is removed. Instead, the heat-stressed corals made a full recovery by the last day. Though these corals experienced bleaching up to the second day at 31˚C, they were able to gain back their color over time. This means that *Pocillopora sp.* has the ability to recover from bleaching after applied heat stress along a gradient within a short experimental period of sixteen days. This took us by surprise as we expected the heat-stressed corals to only recover slightly with such a short time span allowed for recovery. Many studies done previously show coral bleaching recovery from thermal stress occurring after much longer timescales (*i.e.* months) and no recovery within 12 hours, therefore we did not expect our corals to make a full recovery in coloration within seven days of removed heat stress (Johns *et al.,* 2014; Osborne *et al.,* 2017; Thomas & Palumbi, 2017). Another unexpected result is that both treatment and control tanks showed increased coloration after day 12. While it would make sense for the treated corals to regain symbionts because the temperature during the recovery period fell back within the normal range for *Pocillopora sp.*, it is not known why control corals also gained symbionts after day 12 when their water temperature was kept at ambient conditions throughout the entire experiment.

Conclusions

Our findings provide evidence that *Pocillopora sp.* can recover from heat stress and associated bleaching within a matter of days. However, variation in desired temperature, pH, and salinity may have confounded the results, considering the day by day variability in measurements that we observed in the control corals. On the other hand, this variability could reflect natural variation rather than experimental error. Future studies assessing bleaching in *Pocillopora sp.* taking place over a longer timescale, with more time-points assessed within the experimental period, and/or with more experimental replicates would provide further insight. A long time-period would also be better suited to assess the effects on coral growth over time. Finally, the relevance of such laboratory studies to environmental conditions should be taken into consideration, and would perhaps encourage variability within the experimental conditions to replicate the natural world. Studies effectively assessing the impacts of temperature on these ecologically and economically vital coral species become imperative as the climate continues to warm.

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