Feeling the Burn: *P. acuta* under heat stress

Aditi Amin, Devin DiMascio, & Oksana Omeltchenko

ABSTRACT

Rising sea surface temperature (SST) caused by anthropogenic stressors poses a global threat to marine ecosystems. Past research has demonstrated severe detriments to tropical corals in particular, which already exist near the top of their thermal tolerance range, such as bleaching events (Hoegh-Guldberg, 2000). This study aims to examine the effects of coral genotype and heterotrophic feeding on the thermal tolerance of *Pocillopora acuta*, a tropical coral found in the central Pacific and Indian Oceans. A common garden experiment was used to assess responses to increasing temperature and nutrient availability among eight *P. acuta* genotypes; photosystem II efficiency was measured as a proxy for coral health. Results indicate a drastic decrease in photochemical efficiency among corals exposed to higher temperatures, with different genotypes having varied levels of thermal tolerance. Heterotrophic feeding did not have a significant effect on response to heat stress. These findings have important implications for future research in this area. Identification of thermally tolerant and intolerant genotypes can be used to better tailor conservation methods to corals' specific needs, and allow for more effective protections against SST rise.

1 | INTRODUCTION

Anthropogenic climate change is having drastic, adverse effects on global ecosystems, economies, and societies (Li et al., 2019). Since the Industrial Revolution of the 18th to 19th centuries, fossil fuel consumption has led to a rapid increase in CO2 emissions, disrupting the carbon cycle and causing planetary warming. Global CO2 emissions increased from 2 billion tonnes in 1900 to over 36 billion tonnes in 2015 (Richie & Roser, 2017). The Earth's oceans, which cover approximately 70% of its surface, contain about 50 times more soluble inorganic carbon than the atmosphere; they have absorbed approximately 30% of anthropogenic CO2 emissions between 1850 and 1996 (Raven & Falkowski, 1999). Global sea surface temperatures (SSTs) have increased 0.11°C per decade from 1971 to 2010, and the mean global ocean temperature is predicted to increase by 1-4°C by the year 2100 (IPCC, 2014), which have the potential to cause devastating impacts for marine ecosystems.

Coral reefs provide habitat for ⅓ of all marine fish species and thousands of other organisms, as well as supplying local and international communities with economic benefits and acting as barriers against wave action and storms (Crabbe, 2008). These tropical ecosystems are particularly sensitive to climate change, as most tropical corals already live near their upper thermal limit (Lough et al., 2018). Many tropical corals have symbiotic algae within their inner

tissue cells (Muscatine, 1973), which provide nutrition to the corals who act as hosts to these symbionts through autotrophy. They provide support corals in the formation of their calcium carbonate skeletons (Muscatine and Porter, 1977). Exposure to elevated temperatures can cause coral bleaching, which presents as a loss of color due to the loss of this endosymbiotic algae. While recovery from bleaching events is possible, continued heat exposure results in mortality. (Douglas, 2003). Mass coral bleaching, which occurs when the phenomenon reaches across entire reefs, has rapidly increased in frequency, intensity, and geographical extent due to increasing SSTs (Hoegh-Guldberg, 2011). Rising temperatures have also been associated with an increase in coral disease incidence; it has been estimated that approximately 76.8% of corals globally will be diseased by the year 2100 (Burke et al., 2023).

Pocillopora acuta is a hermatypic coral with strong ecological importance in the central Pacific and Indian Oceans (Roquis, 2022). It inhabits a relatively wide habitat range, from the upper subtidal to the lower intertidal zone (Shinzato et al., 2015). Prior studies have shown significant genotypic variation in physiological and molecular responses to changing environmental conditions (Pang et al., 2021), which indicates substantial intraspecific variability in stress tolerance (Poquita-Du, 2021). *Pocillopora acuta* relies on both autotrophy via algal symbiont photosynthesis and heterotrophy to sustain its energetic needs; they are suspension feeders that typically consume dissolved organic matter and plankton (Huffmyer et al., 2021). Heterotrophic feeding has been shown to significantly strengthen the photosynthetic efficiency and growth of the coral (Huang et al., 2020).

The objective of this study is to determine how different genotypes of *P. acuta* respond to increasing thermal stress when fed or starved. Its wide habitat range and fast growth rate make *P. acuta* an ideal model organism for this experiment. Its categorization as a reef-building coral makes it more susceptible to rising global temperatures, as these species are heavily reliant on their symbiotic algae for nutrients and are therefore more threatened by bleaching events (Jones et al., 2008). We hypothesize that coral health (i.e., absence of tissue sloughing) and photochemical activity will decrease with rising temperature, an effect which will be influenced by genetic background. We also predict that heterotrophic feeding will mitigate these health decreases and buffer against thermal stress. This research aims to provide a clearer understanding of how a common reef-building coral will respond to the current and future patterns of SST rise in order to better predict reef futures.

2 | MATERIALS & METHODS

2.1 | Genet Procurement

The eight *P. acuta* genets were sourced from multiple locations, but were all acclimated to 25°C in Boston University's Marine Program (BUMP) lab for an extended period of time prior to the experiment. ORA Green and ORAPG genets were harvested by ORA Farms and originated in the South Pacific and Indian Oceans. ECCG, ECG Purple, Jasmine Dragon, Midnight Dreaming,

and Aqua Horizon genets were harvested by Eye Catching Coral, a wholesale service for live corals from several countries in the South Pacific and Indian Oceans. The Pink Green genet is from an unknown location and was obtained from the BUMP lab.

2.2 | Experimental Design

A common garden experiment (Fig.1) using eight *P. acuta* genotypes was conducted where two tanks were maintained at control conditions (constant temperature of 25°C throughout the duration of the experiment) and two tanks were heated (temperatures were increased by 1°C per day from 25˚C until reaching 32°C, where it was maintained for six additional days). The total duration of the experiment was 12 days. Given that genets were previously acclimated at 25˚C, this temperature was chosen as the baseline for the control treatment. Each pair of tanks shared a common sump. Within each system, fragments in one tank were fed "Benereef" powdered food every three days, while fragments in the other tank were not fed. Water flow to the 'fed' tanks was turned off for 30 minutes to allow for feeding. A filter sock was used to divide the 'fed' and 'unfed' tanks to prevent food particles from flowing between them.

Temperature and salinity were checked three times each day throughout the experiment to ensure that the water quality did not deviate from intended conditions. All tanks were subject to a 12:12 hour dark:light cycle at a light level of 80-95 lux.

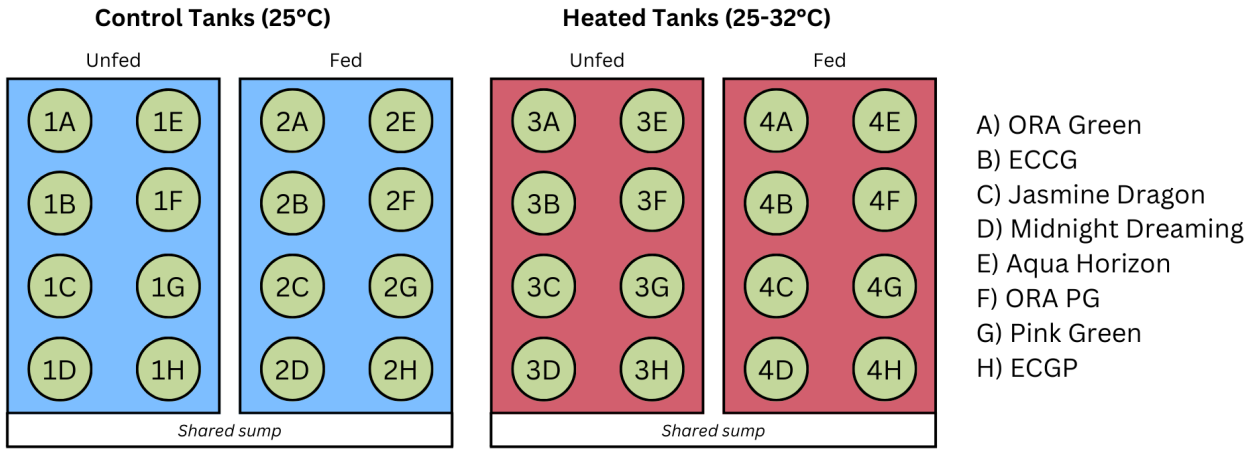

Figure 1: Common garden experimental setup. Two systems of two tanks each contained eight Pocillopora acuta fragments of different genotypes in the same organized arrangement. Control tanks were maintained at 25°C throughout the experiment, and heated tanks were increased by 1°C per day starting from 25℃ to 32°C and remained at 32℃ for six additional days. Each system consisted of one 'fed' tank and one 'unfed' tank.

2.3 | Data Collection & Analysis

(a) Photosynthetic Efficiency Assessments

Photosystem II efficiency of algal symbionts was measured daily using pulse-amplitude modulation (PAM) via a Heinz-Walz JUNIOR-PAM chlorophyll fluorometer. The resulting ratio

of Fv/Fm (change in fluorescence over maximum fluorescence) was used as an indicator for coral health. Each fragment was measured three times daily to obtain an average ratio and reduce error. PAM measurements were taken at least 2.5 hours after the beginning of the dark cycle to ensure dark acclimation. Each triplicate measurement was taken at a different location on the fragment.

(b) Red Channel Intensity (Bleaching)

Red channel intensity was measured from photographs taken before and after the experiment (days 1 and 12, respectively). A Coral Watch coral color health chart with color blocks corresponding to varying levels of coral health was used as our basis for red channel measurements. Photographs were taken inside a white lightbox setup with spotlights on both sides to minimize shadows and glare. Photographs were taken on an iPhone placed on a tripod. The iPhone camera settings, tripod height, and position of both spotlights were kept identical on both day 1 and day 12. Genet photographs were white-balanced using Adobe Photoshop to eliminate light differences that would hinder our analysis. These white-balanced photographs were analyzed using the Image Intensity Analysis Package in MATLAB. Ten random points were selected on each genet photograph to analyze their red, green and blue (RGB) channel intensities in RStudio. A higher value for red channel intensity suggests lighter coral color, indicative of coral bleaching.

(c) Statistical Analysis

All statistical analyses used to compare photosystem II efficiency and red channel intensity were conducted in RStudio 4.4.2. For photosystem II efficiency of symbiont algae, Fv/Fm values were analyzed between 1) control and heated treatments and 2) fed and unfed tanks. Specifically, the differences between control and heated treatments were analyzed using an unpaired t-test. Two-way analyses of variance (ANOVAs) and Tukey's HSD tests were used to compare results in each specific treatment at the end of the 12-day experimental period. For analyzing coral bleaching, percentage difference in red channel intensity before and after the duration of the experiment was analyzed between 1) control and heated treatments and 2) fed and unfed tanks. These differences were also analyzed using an unpaired t-test, two-way analyses of variance (ANOVAs) and Tukey's HSD test in a similar manner to the photosynthetic efficiency analysis. A p value of 0.05 or less was considered statistically significant.

(d) Tissue Sloughing

When a coral undergoes bleaching, the peeling of its tissue from its calcium carbonate skeleton is referred to as sloughing. Because coral genets were exposed to elevated temperatures throughout this experiment, we expected to observe some level of tissue sloughing as a response. We compared photographs of individual coral genets on days 1 and 12 of the experiment to visually assess the prevalence of tissue sloughing. It generally presents as a loss of tissue, exposing the white skeleton underneath, beginning from the base of the coral.

3 | RESULTS

3.1 | Temperature and Salinity

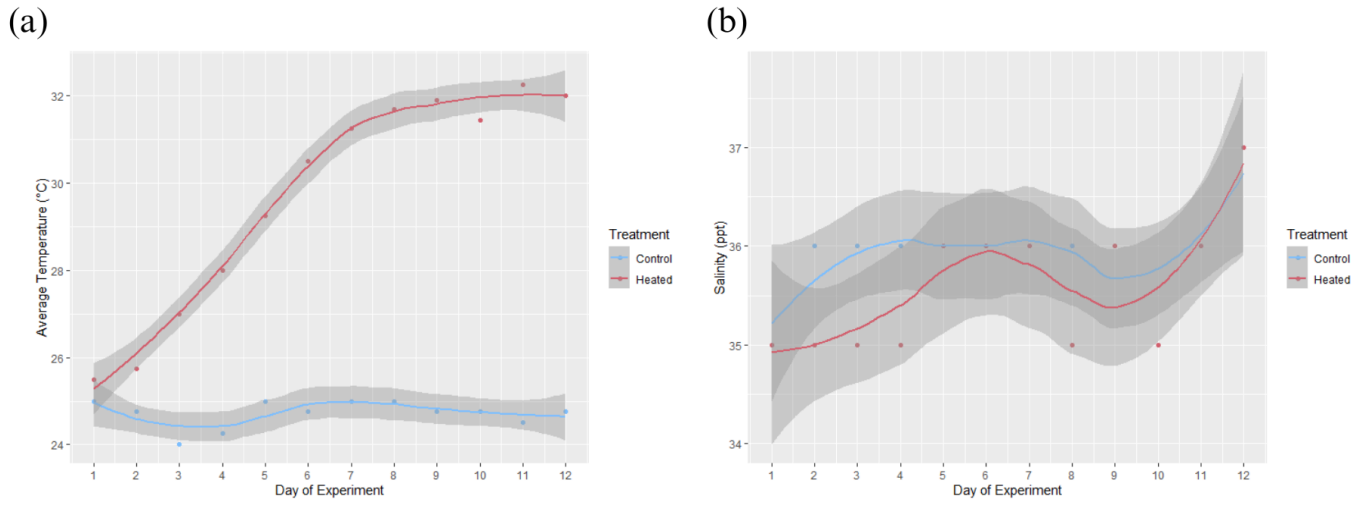

Figure 2: Experimental conditions maintained in each of the four tanks. A) Temperature of control tanks was maintained at 25°C while experimental tanks were ramped from 25 to 32°C. Measured temperatures were always within 1°C of set point. B) Salinity of tanks in both systems was maintained between 35 and 37 ppt for the duration of the experiment. Gray outlines surrounding each line of best fit represent standard error. Blue: Control treatment (25℃); red: Heated treatment (increasing up to 32℃).

Throughout the experiment, the temperature of the two control tanks ranged between 24 and 25°C. The two experimental tanks were steadily ramped from 25 to 32°C, where it remained between 31 and 32°C for six additional days (Fig. 2a). Temperature conditions were always measured within 1°C of the tank set point. The salinity range for both control and heated tanks remained relatively constant throughout the experiment, ranging from 35 to 37 ppt (Fig. 2b). Because there was so little fluctuation, it is assumed that salinity levels did not impact the results.

3.2 | Photosynthetic Efficiency

Statistical analysis of photochemical efficiency (measured as Fv/Fm) data shows a significant difference between control and heated tanks (Fig. 3). Based on unpaired t-tests comparing the two systems, average Fv/Fm was relatively consistent until day 5 ($p = .049$); control tank temperature was set to 25°C on this day while the heated tank temperature had been ramped to 30°C. After this point, there is a significant linear drop in photochemical efficiency in the heated tank, and control levels stay relatively constant. When comparing Fv/Fm levels for the entire experiment, results are highly significant ($p < 2.2e^{-16}$). Throughout the experiment, there was no statistically significant difference in photochemical efficiency between the fed and unfed tanks in

isolation (Fig. 4). There is a slight and relatively consistent negative linear trend for both groups over time. Unpaired t-tests were used to analyze these results, which show a lack of significance for each day as well as over the entire 12-day experiment ($p = .324$). These results are further supported when conducting a two-way analysis of variance (ANOVA) between average Fv/Fm, temperature, and feeding (Fig. 5). Temperature increase significantly decreased photochemical efficiency, while feeding did not appear to have any significant effect (Tukey's HSD test, $p<0.05$).

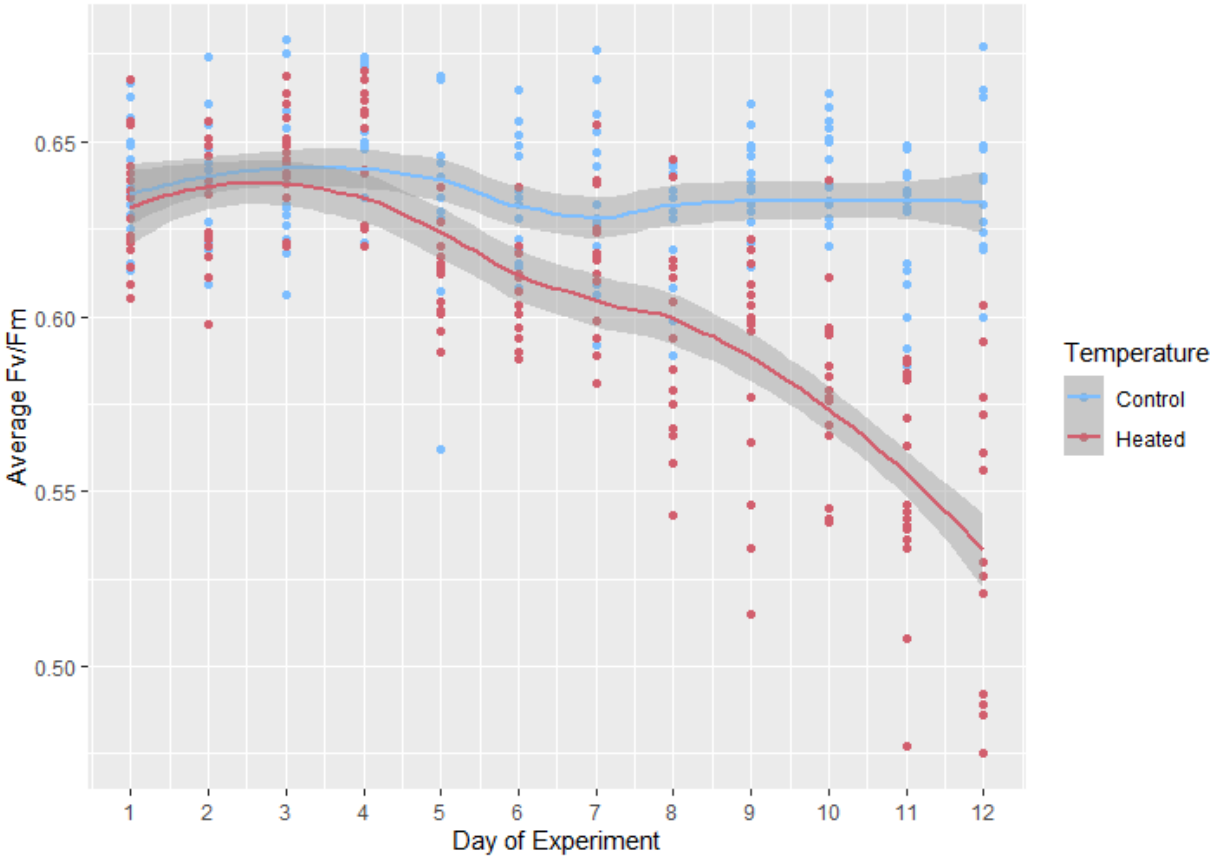

Figure 3: Photosynthetic efficiency of *P. acuta*, measured as Fv/Fm, in control and heated tanks over the course of the 12-day experimental period. Each point represents the average measurement for each genet, recorded daily. Gray outlines surrounding each line of best fit represent standard error. There was a significant difference between treatments beginning on day 5. Blue: Control treatment (25℃); red: Heated treatment (increasing up to 32℃).

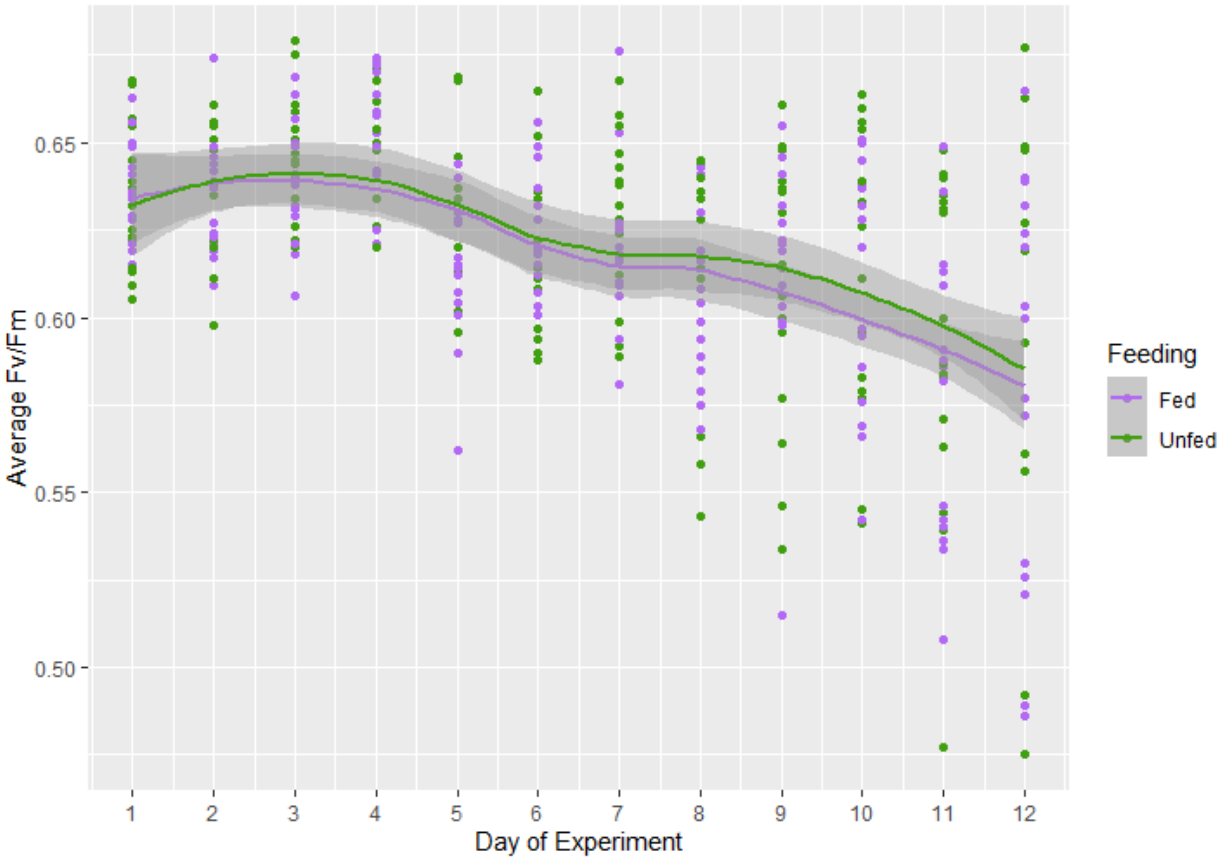

Figure 4: Photosynthetic efficiency of *P. acuta*, measured as Fv/Fm, in fed and unfed tanks over the course of the 12-day experimental period. Each point represents the average measurement for each genet, recorded daily. Gray outlines surrounding each line of best fit represent standard error. There was no statistically significant difference.

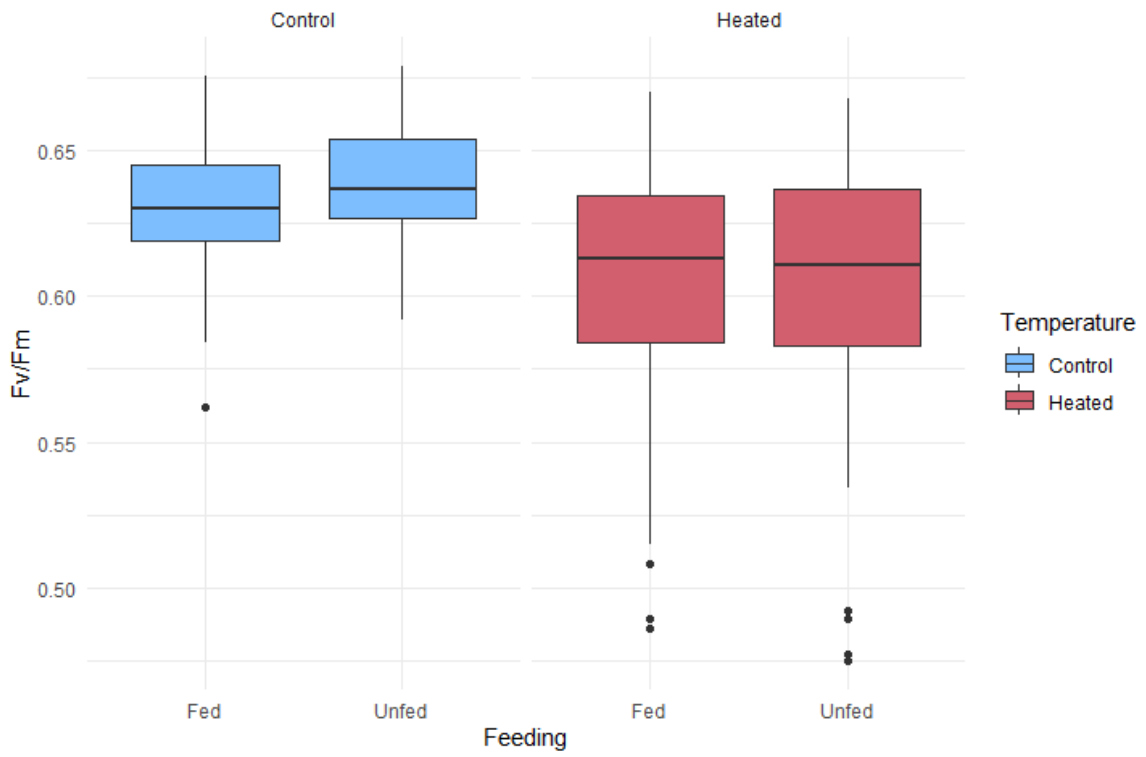

Figure 5: Photosynthetic efficiency, measured as Fv/Fm, for each *P. acuta* treatment group. There was a significant difference between temperature treatment, but heterotrophic feeding did not appear to have any significant effect. Blue: Control treatment (25℃); red: Heated treatment (32℃ on day 12).

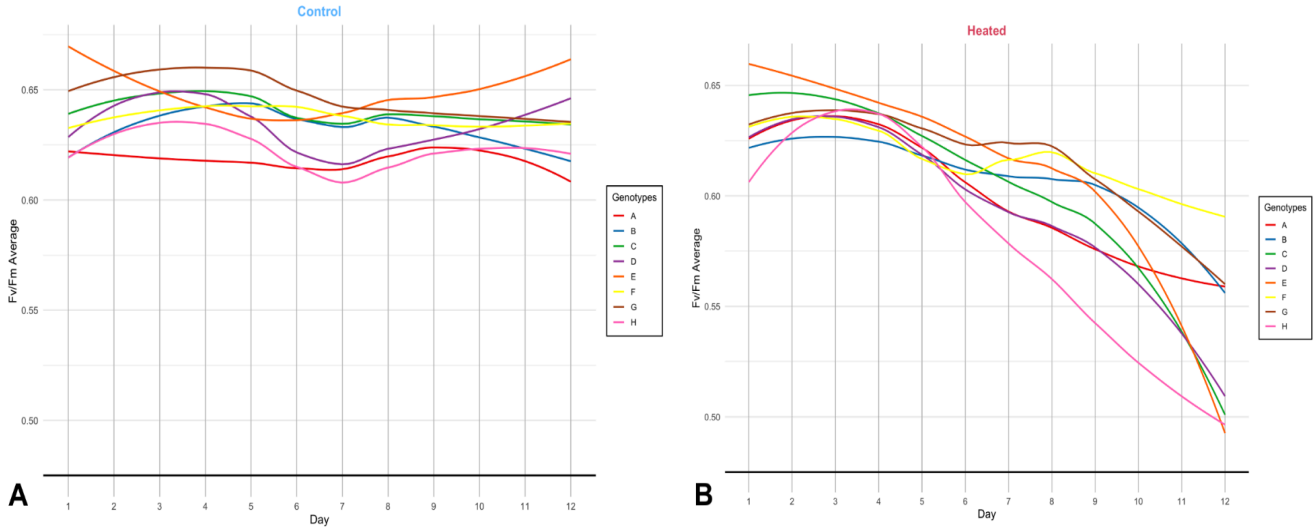

Figure 6: Photosynthetic efficiency measured as Fv/Fm for each *Pocillopora acuta* genet type taken over a period of 12 days. A) Fv/Fm measurements taken in the control tanks. B) Fv/Fm measurements taken in the heated tanks.

Photochemical efficiency (measured as Fv/Fm) for each genotype showing the variability of different genotypes' ability to tolerate thermal stress (Fig. 6). Jasmine Dragon (C), Midnight Dragon (D), Aqua Horizon (E), and ECGP (H) genets have the lowest Fv/Fm values of less than 0.512 by day 12 of the experiment in the heated treatments (Figure 6B). ORA Green (A) and Pink Green (G) genets had the highest Fv/Fm values of higher than 0.558 by day 12 of the experiment in the heated treatments (Figure 6B). The control tank showed relatively consistent genet tolerance with all genotypes Fv/Fm staying over 0.60 throughout the experiment (Figure 6A).

3.3 | Red Channel Intensity (Bleaching)

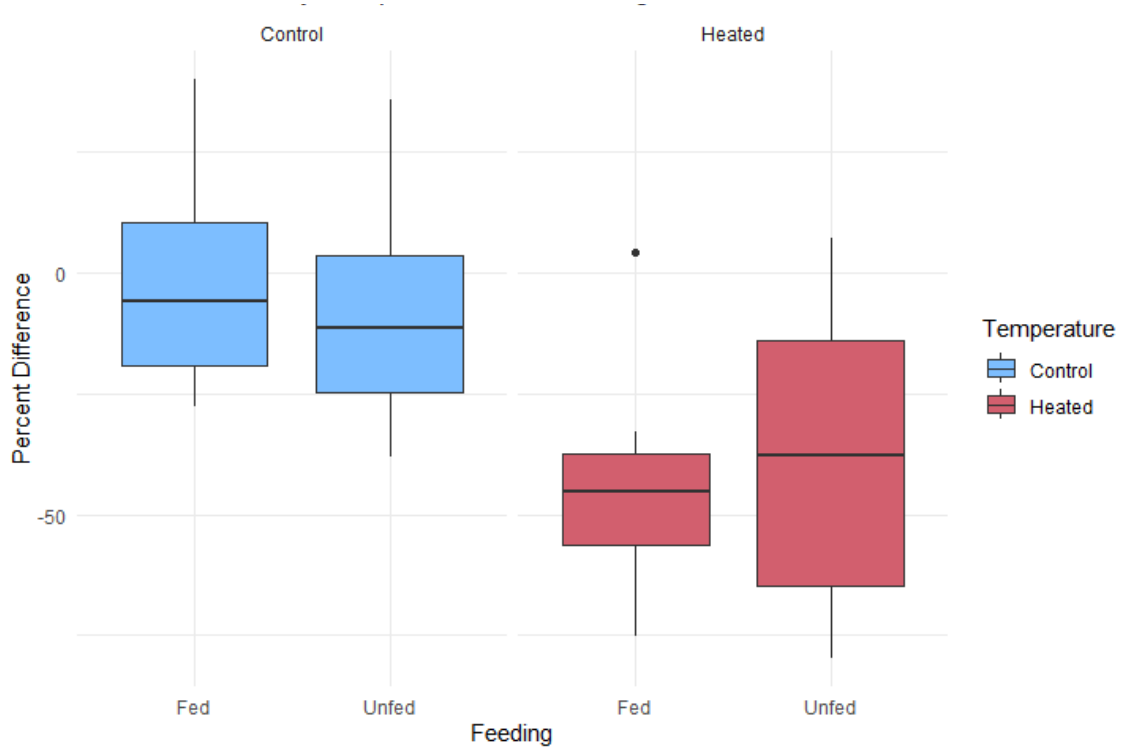

Figure 7: Differences in bleaching were observed between genets in control and heated tanks at the end of the 12-day experimental period. Percentage differences were calculated for average red channel intensity from standardized photographs before and after the experiment for each genet in each treatment. Negative percentage differences represent a higher red channel intensity at the end of the experiment which indicates bleaching. Blue: Control treatment (25℃); red: Heated treatment (32℃ on day 12).

Statistical analysis of red channel intensity data shows significant differences in bleaching responses of *P. acuta* genets in control and heated tanks (Fig. 7). Unpaired t-tests revealed that *P. acuta* genets in the heated system with increasing temperatures of up to 32°C showed significantly lower values of percentage change in red channel intensity ($p=0.0006$), suggesting that they underwent significant levels of bleaching. In contrast, higher values of percentage change in red channel intensity in *P. acuta* genets from control tanks indicate negligible levels of

bleaching. Throughout the experiment, there was no statistically significant difference in red channel intensity between the fed and unfed tanks in isolation (p=0.942) (Fig. 7).

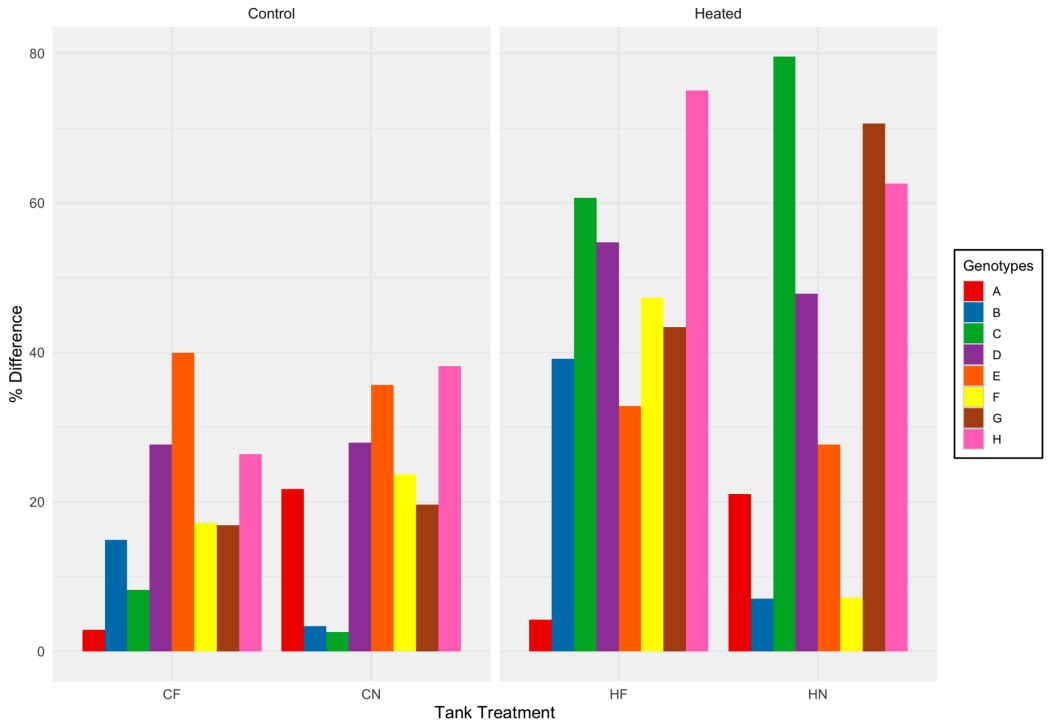

Figure 8: Differences in bleaching were observed between *P. acuta* genotypes in control and heated tanks at the end of the 12-day experimental period. Percentage differences were calculated for average red channel intensity from standardized photographs before and after the experiment for each genet in each treatment. Genotypes are assigned a unique color as shown in the genotypes color key.

We also observed a large variation of average red channel intensity among different genotypes within each treatment. We observed the largest percentage differences in heated treatments, and observed the smallest percentage differences in control treatments (Figure 8). In the control 'fed' treatment, Aqua Horizon (E) genet had the highest percentage difference in average red channel intensity (39.9%) and ORA Green (A) genet had the lowest percentage difference (2.92%). In the control 'not-fed' treatment, ECGP (H) genet had the highest percentage difference in average red channel intensity (-38.1%), and Jasmine Dragon (C) genet had the lowest (-2.58%). The percentage difference value for Jasmine Dragon (C) genets in the control 'not-fed' treatment was also the smallest percentage difference of the overall experiment. In the heated 'fed' treatment, ECGP (H) genet had the highest percentage difference in average red channel intensity (-75.0%) and ORA Green (A) genet had the lowest percentage difference in average red channel intensity (4.27%). In the heated 'unfed' treatment, Jasmine Dragon (C) genet had the highest percentage difference in average red channel intensity (-79.5%) and ECCG (B) genet had the lowest percentage difference in average red channel intensity (7.06%). The percentage difference value for Jasmine Dragon (C) genet in the heated 'unfed' treatment was also the largest percentage

difference of the overall experiment. ECGP (H) genet and Jasmine Dragon (C) genets indicated consistently high percentage differences in the heated treatments. ORA Green (A) genet maintained low percentage differences in the heated treatments.

3.4 | Tissue Sloughing

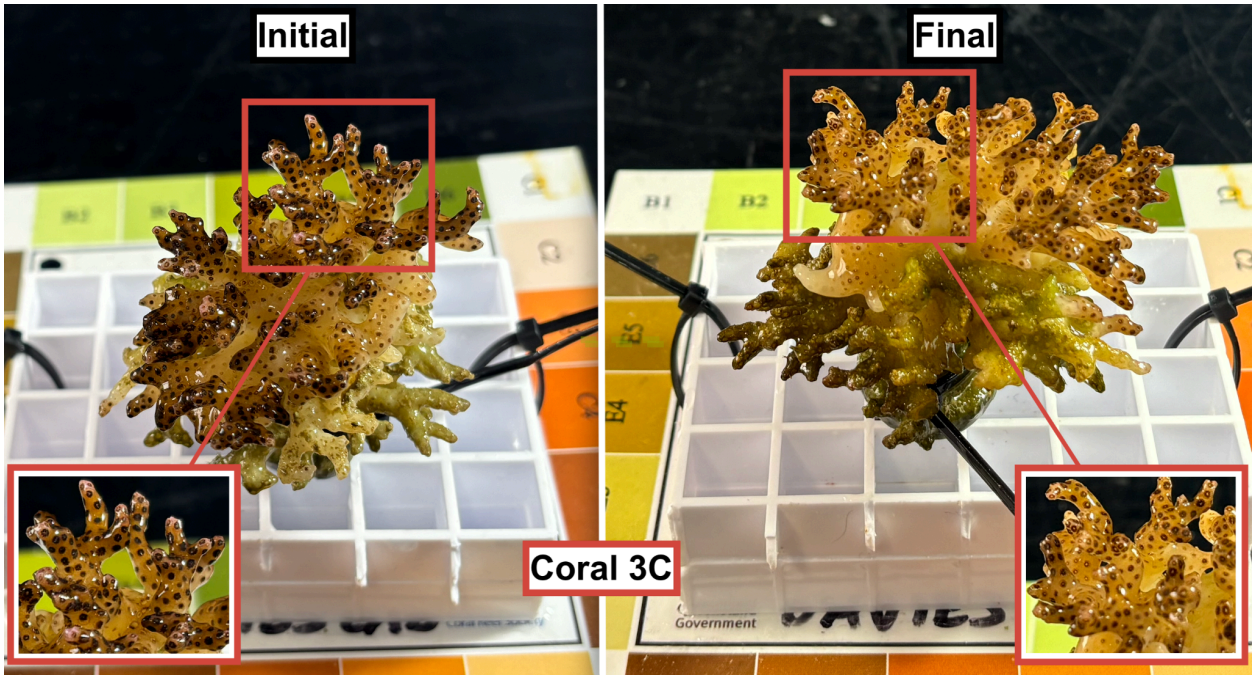

Figure 9: *Pocillopora acuta* photographs were taken against a Coral Watch coral color health chart on the first day of the experiment (labeled initial) and the last (labeled final). Coral 3C is the *P. acuta* genotype Jasmine Dragon in the unfed heated treatment. Initial image taken on November 10th which was the first day of our experiment. The final image was taken on November 12th which was the last day of the experiment.

We did not observe any significant evidence of tissue sloughing in genets regardless of tank treatment. The largest difference in tissue sloughing, which was not significant, was observed in the Jasmine Dragon genet in the unfed heated treatment (Figure 9).

4 | DISCUSSION

The results of our experiment show that *P. acuta* health deteriorates when exposed to increased temperatures. Genets in the control system with a constant temperature of 25°C showed higher photosynthetic efficiencies than genets in the heated system with temperatures of up to 32°C. Red channel intensities stayed relatively consistent among control genets, while there was a significant decrease among heated corals, indicating a loss of color. This supports our hypotheses that photochemical activity and coral health will decrease with rising temperatures. Contrary to Huang et al., (2020), we did not find statistically significant differences in photosynthetic efficiency and red channel intensity between fed and unfed corals. This contradicts our hypothesis that heterotrophic feeding will mitigate health decreases and act as a buffer against

thermal stress. In a study conducted on a similar species *Pocillopora damicornis*, Fong et al. (2021) did not find any significant effects of feeding on endosymbiont density. This could also be the case for our experiment considering that endosymbionts of the coral play a significant role in ensuring photosynthetic efficiency and red channel intensity.

4.1| Genetic variability in thermal stress responses

Genetic variance observed in our results suggests that some genotypes may be better equipped in responding to thermal stress than other genotypes. This supports our hypothesis that genetic background will influence the extent of heat stress experienced. ECGP (H) and Jasmine Dragon (C) genets had low Fv/Fm values with the highest average red channel intensity differences in the heated treatments; this indicates they may be more sensitive to thermal stress. ORA Green (A) genets maintained low percentage differences in red channel intensity and ORA PG (F) genets showed the highest Fv/Fm values in the heated treatments. This suggests that ORA Green (A) and ORA PG (F) genets are the least sensitive and most tolerant to thermal stress. The differences in red channel intensity could arise from the coral host genotype or from the type of symbiotic algae associated with the corals.

4.2| Lack of tissue sloughing under thermal stress

The lack of tissue sloughing on coral genets in the heated system is surprising since we would expect otherwise. Bouchie et al. (2023) conducted a similar study with *P. acuta* following a similar procedure where they observed significant tissue sloughing on coral genets in the heated system at the end of their 12 day experimental procedure. Moreover, in our study, the results of our photosynthetic efficiency analysis indicate a decrease in efficiency and coral symbiont health in the heated system which is commonly associated with physical tissue sloughing. Schlotheuber et al. (2024) studied a similar species *Pocillopora damicornis* where they only observed tissue sloughing after high heat stress at 39℃. Another study conducted on the scleractinian coral *Acropora eurystoma* found tissue sloughing to be evident at 34 °C (Maor-Landaw and Levy, 2016). Since we only assessed thermal resilience up to 32℃, the lack of tissue sloughing in our study could be attributed to the temperature not being high enough to cause physical change. Further research is needed to assess the specific symbiont type and test its responses to thermal stress.

4.3| Sources of error

There are a few potential sources of error that are important to mention and correct in future experiments. Firstly, it was difficult to ensure complete accuracy in PAM measurements of photochemical efficiency, as measurements were taken within the tank systems where corals were not entirely stable. This could be corrected by taking more measurements on each genet to obtain a larger sample size, or by better stabilizing the genets within each tank to prevent movement that would affect results. We were also not able to ensure that every coral fragment received the exact same treatment within the tank. The water intake, output and aerator were

only present on one side of each tank, and due to difficulties with changing the position of each fragment within the tanks, certain fragments were always closer or farther from said tank accessories. However, from our data it does not seem that the corals were significantly affected by this since the ones closest to the stronger water flow did not all have consistent patterns within the data that could signal response due to tank position. Similarly, cross-contamination of nutrients between fed and unfed tanks in each system was possible; a filter sock was used to minimize flow of larger pieces of food, but some small particles may have been able to pass through. Future studies should utilize more tank systems with separate sumps to avoid this issue.

5 | CONCLUSIONS

Overall, our results indicate a consistent decrease in photosynthetic efficiency and increase in levels of coral bleaching under thermal stress. These findings have important implications for future research and conservation efforts. Gaining a clearer understanding of the relationships between coral health and temperature is especially important given the rapidly accelerating SST rise of the current anthropocene. Our findings help better understand coral stress responses through changes in photosynthetic efficiency and red channel intensity; processes that are vital to the survival of corals. As seen in our results, certain genotypes of *P. acuta* are more sensitive to thermal stress than others and these genotypes might require more active conservation efforts. Our findings help identify genotypes with different capacities to withstand thermal stress, creating potential for targeted conservation and restoration efforts. Future studies should be aimed towards understanding specific types of algal symbionts, their relationship with host genotypes, and their effects on coral health under increasing temperatures.

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