

***Astrangia poculata* modulates heterotrophic strategy in response to thermal and lighting stressors**

Allison Cinelli, Marisa DeJesus, Atlas Emmanuel, Artem Vazetdinov | December 16, 2025
Marine Physiology and Climate Change, Boston University Marine Program, Boston University, Boston, MA 02215, USA

Abstract

Rising sea surface temperatures globally threaten coral reef survival, driving increasingly frequent and severe bleaching events. Variation in light intensity can exacerbate thermal stress, a response that may be mediated by algal symbiosis dynamics in some coral species. However, it remains unclear how the temperate northern star coral (*Astrangia poculata*), a facultatively symbiotic and environmentally tolerant species, responds to combined stressors. Here, we show that symbiotic state and trophic strategy strongly influence feeding behavior and photosynthetic efficiency under multi-stressor conditions. By experimentally manipulating temperature, light, and food availability, we quantified polyp activity as a proxy for feeding behavior and measured photosynthetic efficiency of algal symbionts to assess coral health over a 12-day experimental period. We found that combinations of heat and light elicited distinct responses between aposymbiotic and symbiotic corals. Combined heat and light treatments had only marginally significant effects on feeding behavior and minimal effects on photosynthetic efficiency, whereas heterotrophy and symbiotic state significantly shaped these physiological responses. Fed corals maintained higher polyp activity than unfed corals across treatments, suggesting that heterotrophy can buffer environmental stress and supplement energetic demands when symbiont photosynthesis is limited. These findings emphasize that facultative corals may rely on autotrophy and heterotrophy to varying extents to cope with fluctuating stressors. Understanding how symbiont dynamics are regulated under stress provides insight into coral resilience under climate change and informs targeted conservation strategies for temperate and facultative species.

Introduction

Coral reefs, among the most biodiverse ecosystems on the planet, support over 35% of known marine species despite occupying less than 1% of the ocean floor (Richards & Hobbs, 2014). They provide essential ecosystem services, offering habitat for countless marine organisms and supporting the food security of millions of people worldwide (Richards & Hobbs, 2014). Most scleractinian (stony) corals form colonies of interconnected polyps that serve as the building blocks of reef ecosystems (Todd, 2008). The mutualistic relationship between these reef-building corals and their dinoflagellate endosymbionts is a key factor in their evolutionary success (Muller-Parker et al., 2015).

Coral reef survival, however, is increasingly threatened by rising sea surface temperatures, driving more frequent and severe bleaching events in which the host expels its symbionts under stress (Muller-Parker et al., 2015). While mass bleaching events, such as that observed in the Indo-Pacific in 1999, can cause widespread mortality, many affected reefs demonstrate resilience and recovery (Muller-Parker et al., 2015). Developing effective conservation strategies to predict

reef resilience requires a thorough understanding of coral responses to environmental stressors. Although research predominantly focuses on tropical corals due to their role in reef structure and function, temperate corals, which naturally experience a broader range of environmental conditions, offer valuable insight into coral physiology and tolerance to stress (Sweet & Brown, 2016).

Astrangia poculata, commonly known as the northern star coral, is one such temperate scleractinian species native to the western Atlantic with a broad distribution from the Gulf of Mexico to Massachusetts (Dimond et al., 2013). The species exhibits considerable morphological plasticity, forming encrusting, mound, or digitate colonies, and is characterized by the star-like appearance of extended polyps within compact, well-defined corallites (Peters et al., 1988). Colony coloration reflects variation in symbiont density associated with facultative symbiosis, primarily with the dinoflagellate *Breviolum psygmophilum* (LaJeunesse et al., 2018; Lajeunesse et al., 2012). In the absence or low density of algal symbionts, aposymbiotic colonies appear pale and rely on heterotrophic feeding of zooplankton and suspended organic material, whereas symbiotic colonies supplement heterotrophy with algal photosynthesis (Dimond & Carrington, 2008; Sharp et al., 2017). This dynamic relationship, combined with the species' tolerance for broad environmental variation, makes *A. poculata* an ideal model for investigating coral responses to external stressors, particularly those influencing energetics (Dimond & Carrington, 2007; Thornhill et al., 2008).

A. poculata has been widely used to study the relationship between symbiosis, physiology, and temperature variation (Wuitchik et al., 2021; Sharp et al., 2017; DeFilippo et al., 2016). As a temperate coral with a broad geographic distribution, it has been observed to survive temperatures ranging from -2°C to 27°C in the field and up to 31°C, or potentially higher, under laboratory conditions (Wuitchik et al., 2021). Given its considerable thermal tolerance, studies have focused on how this species thrives across diverse temperatures as well as how it responds to thermal stress (Trumbauer et al., 2021; Brennan et al., 2018). Heat stress has been a prevalent focus due to projected ocean warming under climate change (Wuitchik et al., 2021). Observed responses to heat stress tend to vary in intensity, ranging from minimal physiological stress (Wuitchik et al., 2021) to rapid adaptation at temperatures several degrees above *A. poculata*'s optimal range (Chen et al., 2019). This broad thermal niche has been attributed not only to its wide geographic distribution (Aichelman et al., 2019) but also to its facultative symbiosis (Wuitchik et al., 2021) and, most notably, its flexible trophic strategy (Aichelman et al., 2016; Trumbauer et al., 2021). Several studies have noted that energy availability plays a significant role in temperate corals' ability to mitigate heat stressors, with both symbiotic state and trophic strategy impacting storage and utilization of energy reserves (Rivera et al., 2023). Heterotrophy, in particular, appears to buffer environmental stress responses by supplementing energetic demands when algal symbionts are scarce or absent (Aichelman et al., 2016). Beyond physiological factors, variation in responses can also result from multi-stressor effects, including interactions between temperature and other environmental variables (Alvarez et al., 2022).

Light intensity has emerged as an intriguing factor influencing coral sensitivity under heat stress, as variations in light spectrum and intensity can affect coral health, coloration, and growth (Alvarez et al., 2022). In *A. poculata*, light intensity is often used to assess symbiont

photosynthetic capacity or as a proxy for the balance between heterotrophy and autotrophy (Lindsay et al., 2025). Changes in light conditions can, therefore, modulate how corals acquire and allocate energy. For example, low light may inhibit symbiont photosynthesis, reducing autotrophic input and potentially leading to dysbiosis or stress-induced symbiont loss (Lindsay et al., 2025), while high light may act as a compounding stressor under elevated temperatures (Alvarez et al., 2022). To better understand these interactions, researchers at Boston University investigated the interactive effects of heat and light on *A. poculata* physiology (Alvarez et al., 2022). Their findings revealed that heat combined with darkness elicited increased immune responses, whereas heat and high light intensity enhanced cell-cycle regulation and decreased carbohydrate metabolism in symbiotic corals. In aposymbiotic corals, this multi-stressor treatment increased immune and stress responses and reduced protein metabolism (Alvarez et al., 2022). The mechanisms underlying these divergent responses are still unknown, and it is unclear how symbiosis influences these responses. Previously, it has been assumed that *A. poculata*'s broad temperature and depth range, along with low exposure to photosynthetically active radiation (PAR), must shape its responses to thermal and light stressors; however, no study has proven it for certain (Lindsay et al., 2025). Additionally, facultative symbiosis produces variation in symbiotic state, which influences trophic strategy and likely shapes response to external stressors. Overall, we expect trophic strategy (autotrophy or heterotrophy) to be the most influential factor in coral's response to external stressors.

The combination of thermal and light stressors, whether darkness or high light, triggers varying responses in *A. poculata* (Alvarez et al., 2022). This study aims to further investigate the mechanisms underlying these responses through exposure to controlled thermal and light stressors and evaluation of photosynthetic efficiency (varying with symbiotic state) and feeding behavior. By analyzing the coral's trophic strategy, we seek to determine whether heterotrophy can act as a buffer against environmental stress in this species. The coral's access to food, whether reliant on autotrophy, fed with *Artemia*, or "starved" in an unfed, dark system, is expected to strongly influence our findings (Martinez et al., 2022). We hypothesize that under heat and high light conditions, *A. poculata* uses cell-cycle regulation to control symbiont density (Gorman et al., 2022; Tivey et al., 2020), allowing symbionts to contribute photosynthetic products to the host while preventing overpopulation. On the contrary, under heat and dark conditions, we hypothesize that, as symbiont photosynthesis is rendered unproductive, symbionts may adopt a parasitic role, instigating an immune response from the coral host (Baker et al., 2018), with the simultaneous heat and light stress amplifying the effect. This work will advance understanding of *A. poculata*'s responses to combined heat and light stressors and inform the development of models that predict not only the species' response to future environmental changes but also the processes influencing symbiosis maintenance and loss. Integrative models of coral symbiosis will improve predictions of reef resilience in a shifting climate, providing crucial guidance for conservation and mitigation efforts.

Methods

Sample Collection and Acclimation

This study explored the stress ecology of *Astrangia poculata* by evaluating coral-symbiont physiological responses to multiple environmental stressors, including thermal stress, light stress, and starvation. Samples were collected on October 16, 2025, from Fort Wetherill, Jamestown, Rhode Island, located on Conanicut Island within Narragansett Bay. This location is representative of the northern extent of the species' range (Dimond et al., 2013; Fig. 1). Forty colonies were sampled via hammer and chisel on scuba (20 aposymbiotic and 20 symbiotic).



Figure 1 – Sampling Site. Aerial view of Fort Wetherill, Jamestown, Rhode Island, showing the study site where *Astrangia poculata* samples were collected. Imagery acquired on August 25, 2024.

Immediately following collection, samples were transported to the Boston University Marine Invertebrate Research Facility (Boston, MA). Each colony was fragmented into 84 nubbins (~2.5 cm diameter), which were mounted onto ceramic pucks and labeled according to symbiotic state and fragment identification (“AX” for aposymbiotic and “SX” for symbiotic, where “X” denotes the nubbin’s assigned numerical identification). All nubbins were maintained at 19°C ($\pm 0.5^\circ\text{C}$), with light levels set at ~30 PAR for aposymbiotic fragments and ~40 PAR for symbiotic fragments (Lindsay et al., 2025). Lighting adhered to a long-term photoperiod of 6 hours light, 18 hours dark, reflecting seasonal light levels, and was adjusted a week before the start of the experiment to 12 hours light, 12 hours dark to standardize lighting conditions with previous experiments (Alvarez et al., 2022). Nubbins were then transferred to the experimental systems for stress exposure.

Experimental Design

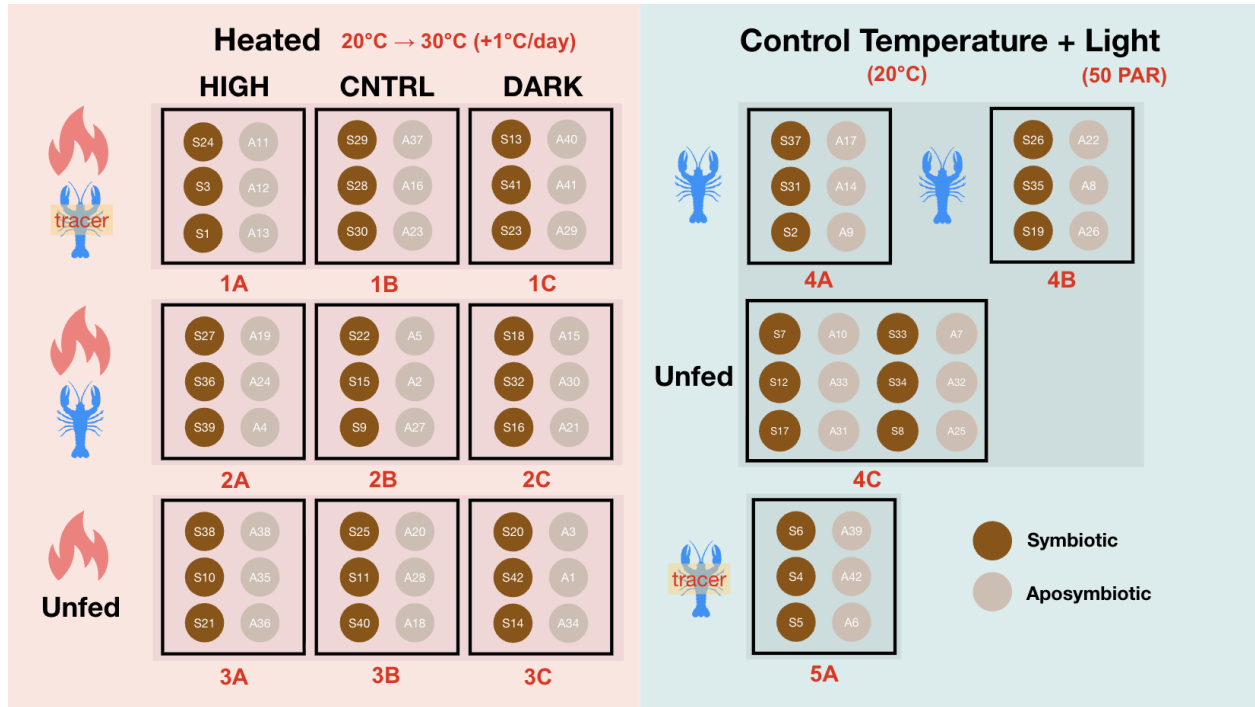


Figure 2 – Experimental Configuration. Five systems with distinct thermal, light, and food treatments were constructed. Each consisted of three equal-sized tanks, except System 5 (one tank). Systems 1-3 (flame symbol) experienced a heat ramp (+1°C daily from 20-30°C over 11 days); Systems 4-5 remained at 20°C (control). The majority of tanks contained $n = 6$ *Astrangia poculata* nubbins ($n = 3$ symbiotic/brown; $n = 3$ aposymbiotic/white), while Tank 4C contained $n = 12$ ($n = 6$ sym; $n = 6$ apo). Light treatments included “HIGH” (400 PAR), “CNTRL” (50 PAR), and “DARK” (no overhead light). Indigo crustaceans indicate *Artemia*-fed tanks, with “tracer” systems receiving isotopically enriched *Artemia*.

The experiment was conducted over a 12-day period, from December 1, 2025, to December 12, 2025. *Astrangia poculata* nubbins were haphazardly distributed across five experimental systems, transferred in uneven groups from the acclimation system and allocated to experimental tanks according to the nearest available position. During placement, nubbin ID was recorded to construct a complete configuration map of the experiment (Fig. 2), enabling accurate data collection and monitoring of individual fragments. Systems 1-4 consisted of three tanks (20 gal each; 80 gal total per system), and System 5 contained a single tank (20 gal). Except for Tank 4C, each tank received 3 aposymbiotic and 3 symbiotic nubbins, characterized by either a white or brown phenotype, respectively. Tank 4C contained 6 nubbins of each phenotype.

All systems were initially set to a target temperature of 20°C (measured 19.62°C ±0.40°C). To assess response under thermal stress, Systems 1-3 were subjected to a daily heat ramp, increasing by 1°C each morning at ~09:30 starting on Day 2 (increasing throughout the experiment from 20°C to 30°C). Systems 4 and 5 remained at control temperature (~20°C) throughout the experiment to reflect average natural conditions at the collection site (Wuitchik et al., 2021). Temperatures were monitored regularly via a standard digital aquarium thermometer (DORHEA), recording system values twice daily (morning and afternoon).

In addition to thermal stress, light availability was manipulated as a secondary stressor. Lighting was scheduled on a timing system, turning on at 03:00 and off at 15:00 daily. Control light tanks (1B, 2B, 3B, and all tanks in Systems 4 and 5) were maintained at 50 PAR. High light treatments (1A, 2A, 3A) received 400 PAR, and nubbins were evenly arranged on a plastic platform (~15.2 x 10.2 x 5.7 cm) constructed out of plastic egg crate panels to achieve the elevation necessary for the target light intensity. Dark treatments (1C, 2C, 3C) received no light throughout the experiment (0 PAR). Lighting was provided by a PAR AI Hydra 26HD system (Apogee Instruments) and measured before the experiment using an MQ-510: Full-Spectrum Quantum Meter with Underwater Sensor (Apogee Instruments). Paneling was used for adequate separation of light conditions between treatments.

Water Quality Monitoring

To ensure consistency in water quality across experimental systems, salinity (ppt) was measured twice daily using a D-D True Seawater Refractometer (The Aquarium Solution). Nutrient concentrations, including nitrate and phosphate (ppm), were measured once daily using handheld colorimeters (Hanna Instruments), following the manufacturer's measurement protocols. Deionized water was added daily to the sump from a top-off jug as needed to maintain the water level in each system and maintain the salinity range of ~34-36 ppt. On Days 4, 8, and 11, sump filters were cleaned by removing the collection cup and filter bags, rinsing them thoroughly with a spray faucet, and reinstalling them in the system.

Coral Color Analysis

On Day 0 of the experiment, all 84 *A. poculata* nubbins were placed on a Coral Health Chart (Coral Watch) and individually photographed to document initial phenotypic coloration and confirm differences in symbiotic state. Images were captured using an iPhone 16 Pro camera inside a black photo box, noting each nubbin's ID. To standardize color across all images, white balance correction was performed in Adobe Photoshop 2024. Using Image-Adjustment-Levels, the white eyedropper tool was used to source a reference area, ensuring all RGB channel values were calibrated to 255. Corrected images were then exported as high-quality JPEG files for further analysis in MATLAB. Each image was processed using the "AnalyzeIntensity" function according to the code by Winters et al. (2009). For each nubbin, 10 points of interest (25 x 25 pixels) were selected haphazardly, avoiding glare, across the coral surface to extract red, green, and blue channel values. The average red channel intensity was calculated for each nubbin and used to classify the fragments based on symbiotic state.

Feeding Behavioral Assessment

Feeding treatment varied among experimental systems in terms of food type, isotopic labeling, and feeding frequency. Systems 1 and 6 received $^{13}\text{C}/^{15}\text{N}$ -labeled *Artemia salina* to quantify heterotrophic carbon and nitrogen incorporation in both the coral host and its symbionts. Preparation began by culturing the microalga *Dunaliella sp.* in f/2 medium enriched with 2 mmol L^{-1} $\text{NaH}^{13}\text{CO}_3$ and 1 mmol L^{-1} $^{15}\text{NH}_4\text{Cl}$. Newly hatched *A. salina* nauplii were fed this algal culture for two days, then isolated by filtration through a 20- μm mesh, divided into equal portions, freeze-dried, and stored at 20°C until use.

System 2 and Tanks 4A and 4B of System 4 received unenriched *A. salina*, grown in parallel using *Dunaliella* sp. cultured in standard (unlabeled) f/2 medium. System 3 and Tank 4C served as unfed controls. Feeding was conducted every other day in the afternoon, around 14:00, beginning on Day 0 of the experiment.

Prior to feeding, water pumps in all tanks, regardless of treatment, were temporarily turned off to minimize water flow. After approximately 2-3 minutes of still water, tanks designated to receive food were provided with 10 mL of the prepared *Artemia* solution per tank, containing 10 mg (dry weight) of either labeled or unlabeled *A. salina*. Food was evenly distributed across samples using a pipette, positioning the tip directly above each nubbin to deliver a steady flow over all polyps, acknowledging the sessile nature of *A. poculata*. Behavioral observations were conducted 30 minutes post-feeding, recording the percentage of fully extended tentacles for each nubbin to quantify feeding activity. Percentage estimates were made by visually assessing the proportion of polyps on each nubbin with extended tentacles relative to the total number of polyps present. Each nubbin was scored separately to capture variation in feeding behavior. Daily values were then averaged across nubbins within each treatment and symbiotic phenotype (aposymbiotic “white” or symbiotic “brown”). To reduce observer bias, the same two individuals performed all behavioral assessments throughout the experiment. Following measurements, pumps were restored to normal operative settings for standard water circulation.

Photosynthetic Efficiency (PAM)

Photosynthetic efficiency of the symbiotic algae within *A. poculata* nubbins were quantified using a pulse-amplitude modulated (PAM) fluorometer (JUNIOR-PAM, Walz) to determine the maximum quantum yield of photosystem II (Fv/Fm) for all 84 experimental nubbins. Measurements were conducted every other day, beginning on Day 1 of the experiment at 15:30, following a 30-minute dark acclimation period to allow photosystem acclimation, resulting in a total of six sampling points (Days 1, 3, 5, 7, 9, and 11). During each measurement, the fiber-optic probe was positioned perpendicular to the coral polyp surface, and short, saturated light pulses were applied to stimulate photosystems. At least three polyps per nubbin were measured, and Fv/Fm values were recorded and averaged to represent the photosynthetic efficiency of each fragment. To minimize potential external light stress during the procedure, red headlamps were used for illumination, as red light did not interfere with fluorescence (Harman et al., 2025). During all handling of coral nubbins, gloves were worn to preserve coral health and prevent cross-contamination between the systems. Throughout PAM testing, only polyps exhibiting the observed dominant trophic characteristics were measured, consistent with the symbiotic state originally identified for each nubbin.

Statistical Analyses

All data were recorded in Google Sheets and analyzed using RStudio version 2024.12.0+467. Shapiro-Wilk tests were conducted to evaluate the distribution of variables, including red channel intensity values. When assumptions of normality were met ($p > 0.05$), two-sample t-tests were used to assess significant differences in mean red intensity between aposymbiotic and symbiotic nubbins. Relative photosynthetic efficiency was calculated as the proportional change in maximum quantum yield (Fv/Fm) between Day 1 and Day 11 ((Day 11 - Day 1) / Day 1).

Photosynthetic efficiency and feeding behavior (polyp activity) were analyzed using three-way ANOVAs to test the main effects of light x heat treatment combination, symbiotic state, and feeding condition, as well as the two-way and three-way interactions among these factors. When statistical differences ($p < 0.05$) were detected across groups, Tukey HSD post-hoc tests were used to assess pairwise interactions among variables.

Results

Mean salinity remained consistent among treatments, ranging from 34.646 to 34.958 ppt (Table 1). Phosphate concentrations exhibited minor variation among treatments, with mean values ranging from 0.025 to 0.060 ppm, while nitrate concentrations ranged from 0.000 to 0.155 ppm (Table 1). Mean salinity, phosphate, and nitrate across all treatments were 34.768 ± 0.116 ppt, 0.048 ± 0.014 ppm, and 0.034 ± 0.053 ppm, respectively.

Daily temperature variability, expressed as the standard deviation of daily temperatures, was generally low across all systems. Mean standard deviation was higher in heated systems (System 1: 1.09°C , System 2: 0.94°C , System 3: 0.77°C) than in control systems (System 4: 0.47°C , System 5: 0.28°C). Maximum variability occurred in heated systems on Day 8, reaching 4.10°C (System 1), 2.55°C (System 2), and 3.04°C (System 3), coinciding with a system controller malfunction (Fig. 3).

Across symbiotic state, there was a significant difference in average red channel intensity (RBG) ($df = 78.3$, $p < 0.05$), with aposymbiotic nubbins ($n = 42$) exhibiting higher values than symbiotic nubbins ($n = 42$) (187.98 ± 34.23 and 88.08 ± 27.41 , respectively; Fig. 4), suggesting that symbiotic corals were darker in color (i.e., more algal symbionts) than aposymbiotic nubbins.

Polyp activity, a proxy for feeding behavior, varied throughout the experimental period across treatments, symbiotic state, and feeding condition (Figs. 5-6). A three-way ANOVA revealed that polyp activity across the entirety of the experimental period differed significantly with symbiotic state ($F = 4.24$, $p < 0.05$) and feeding treatment ($F = 416.94$, $p < 0.05$), but not with light ($F = 2.17$, $p = 0.12$) or heat ($F = 0.91$, $p = 0.34$). Tukey HSD post-hoc tests indicated that fed *A. poculata* nubbins exhibited significantly higher polyp activity than unfed nubbins (mean difference = 48.17 , $p < 0.05$), and that symbiotic nubbins showed slightly greater polyp extension than aposymbiotic nubbins (mean difference = 4.67 , $p < 0.05$). When considering relative polyp activity comparing observations from Day 0 to Day 10, feeding treatment was the only significant factor ($F = 32.88$, $p < 0.05$), while symbiotic state ($F = 2.59$, $p = 0.11$) and treatment combination ($F = 2.49$, $p = 0.07$) were no longer significant. Tukey HSD post-hoc tests indicated both unfed aposymbiotic and symbiotic nubbins in light x heat conditions had lower polyp activity relative to fed symbiotic nubbins in the control heated treatment ($p < 0.05$).

Photosynthetic efficiency of the algal symbionts associated with the corals, expressed as change in maximum quantum yield (Fv/Fm) from Day 1 to Day 11, varied with symbiotic state (Fig. 7). A three-way ANOVA revealed significant effect of symbiotic state on Fv/Fm ($F = 153.38$, $p < 0.05$), while light x heat treatment ($F = 2.01$, $p = 0.13$) and feeding treatment ($F = 1.34$, $p = 0.27$) were not significant. Interactions between symbiotic state and feeding condition revealed no significant interactions ($p > 0.05$).

Table 1 – Water Quality. Mean water quality parameters and corresponding experimental treatments, including light (control 50 PAR, dark 0 PAR, high 400 PAR) and temperature (control 20 ±1°C, heat ramp 20-30°C). Feeding indicates whether tanks received a prepared *Artemia* solution. Salinity was maintained at 33.0-35.0 ppt, and temperature and salinity were recorded twice daily (morning and afternoon). Nitrate and phosphate concentrations (ppm) were measured daily (afternoon).

Light	Heat	Feeding	Salinity (ppt)	Phosphate (ppm)	Nitrate (ppm)
Control	Control	Fed	34.958	0.027	0.062
Control	Control	Unfed	34.875	0.025	0.155
Control	Heated	Fed	34.646	0.050	0.000
Control	Heated	Unfed	34.792	0.060	0.018
Dark	Heated	Fed	34.646	0.050	0.000
Dark	Heated	Unfed	34.792	0.060	0.018
High	Heated	Fed	34.646	0.050	0.000
High	Heated	Unfed	34.792	0.060	0.018

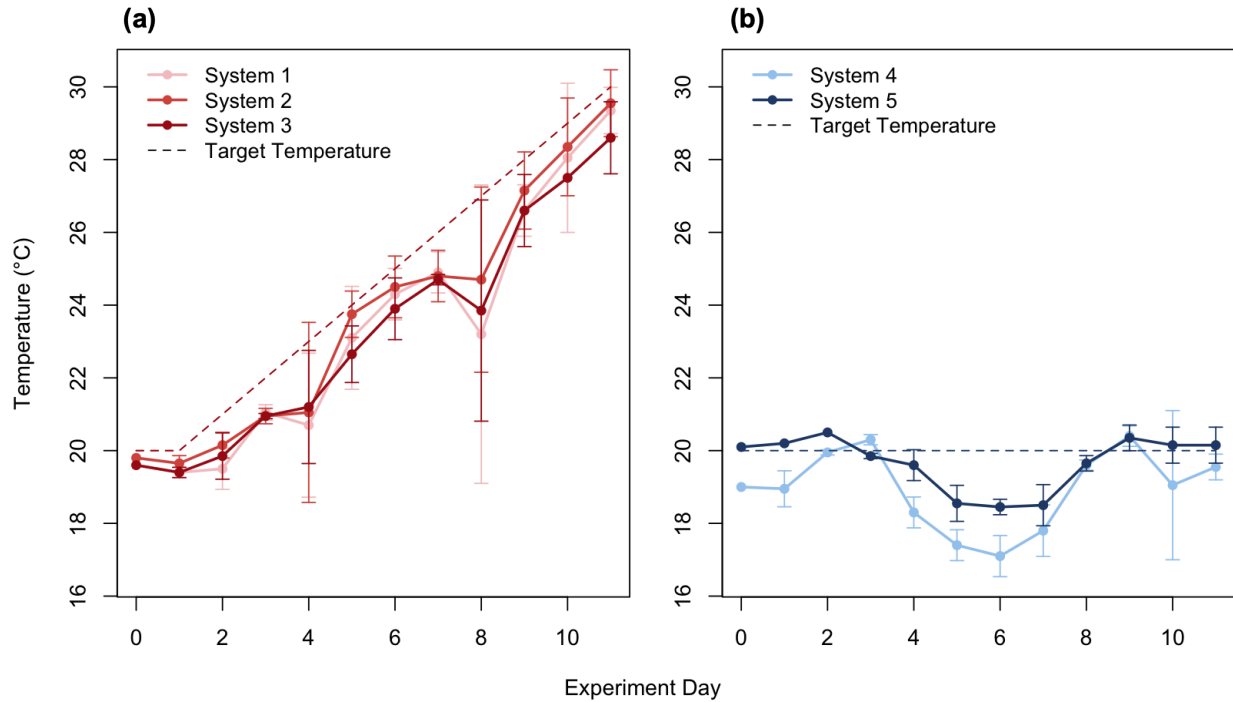


Figure 3 – System Temperatures. Mean daily temperature (°C) for (a) heat-treated systems ramped from 20°C to 30°C (+1°C daily, starting Day 2) and (b) control systems maintained at 20°C (±1°C) over the 12-day experiment. Dashed lines indicate target temperatures, and error bars represent daily standard deviations. Between Days 7 and 8, system controllers malfunctioned, causing Systems 1-4 to reach room temperature overnight.

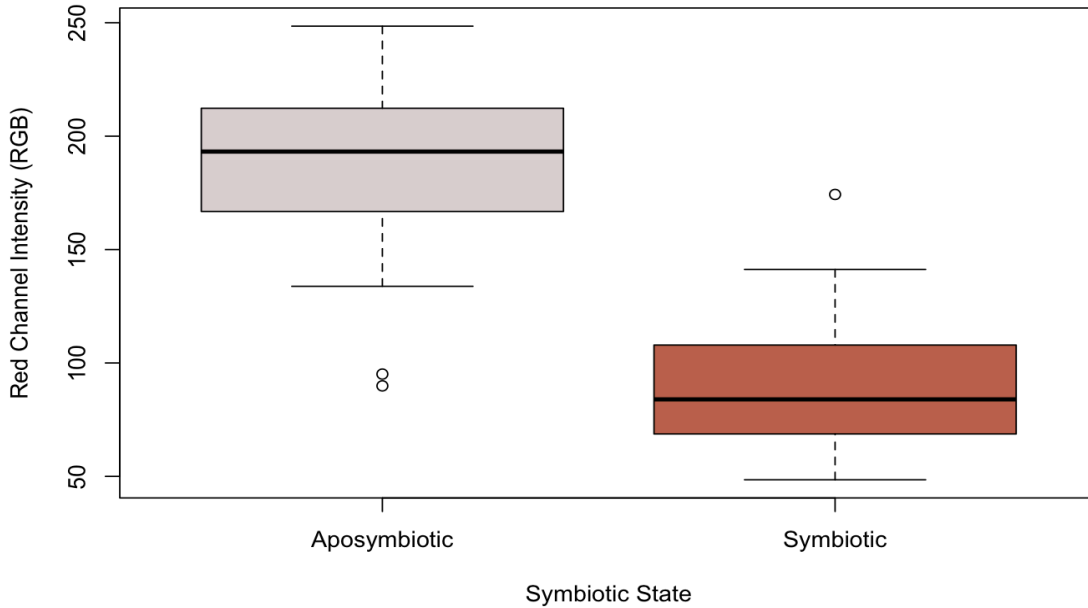


Figure 4 – Color Analysis. Mean red channel intensity (RGB) of *Astrangia poculata* nubbins in aposymbiotic (grey, n = 42) and symbiotic (brown, n = 42) states. Boxplots show median, interquartile range, and minimum–maximum range. Average red intensity was calculated per nubbin across 10 points of interest using MATLAB.

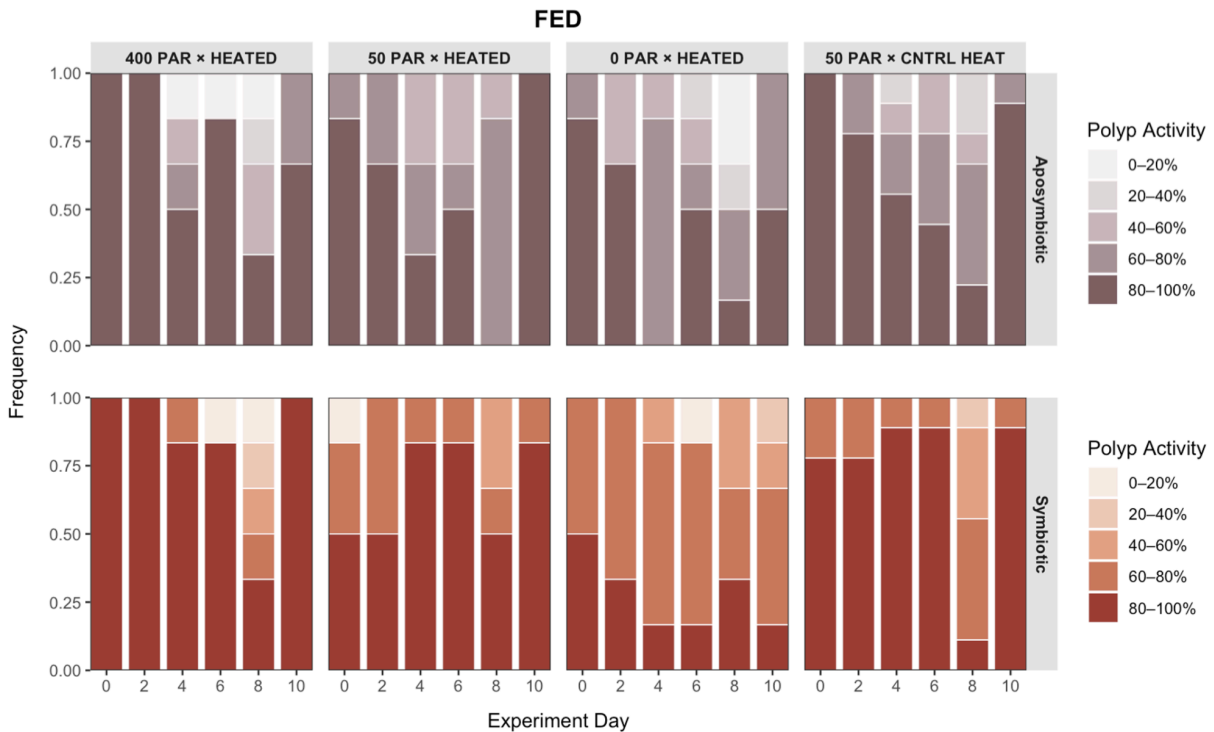


Figure 5 – Feeding Behavior (Fed). Frequency of polyp activity, quantified as the proportion of extended tentacles, across the experimental period for fed aposymbiotic (grey) and symbiotic (brown) *Astrangia poculata* nubbins. Activity was qualitatively assessed 30 minutes post-feeding and categorized in 20% intervals (legend). Panels are organized by combined light (400, 50, 0 PAR) and temperature treatments (heated or control). All fed tanks received a prepared *Artemia* solution (tracer-labeled or unlabeled; see Fig. 2).

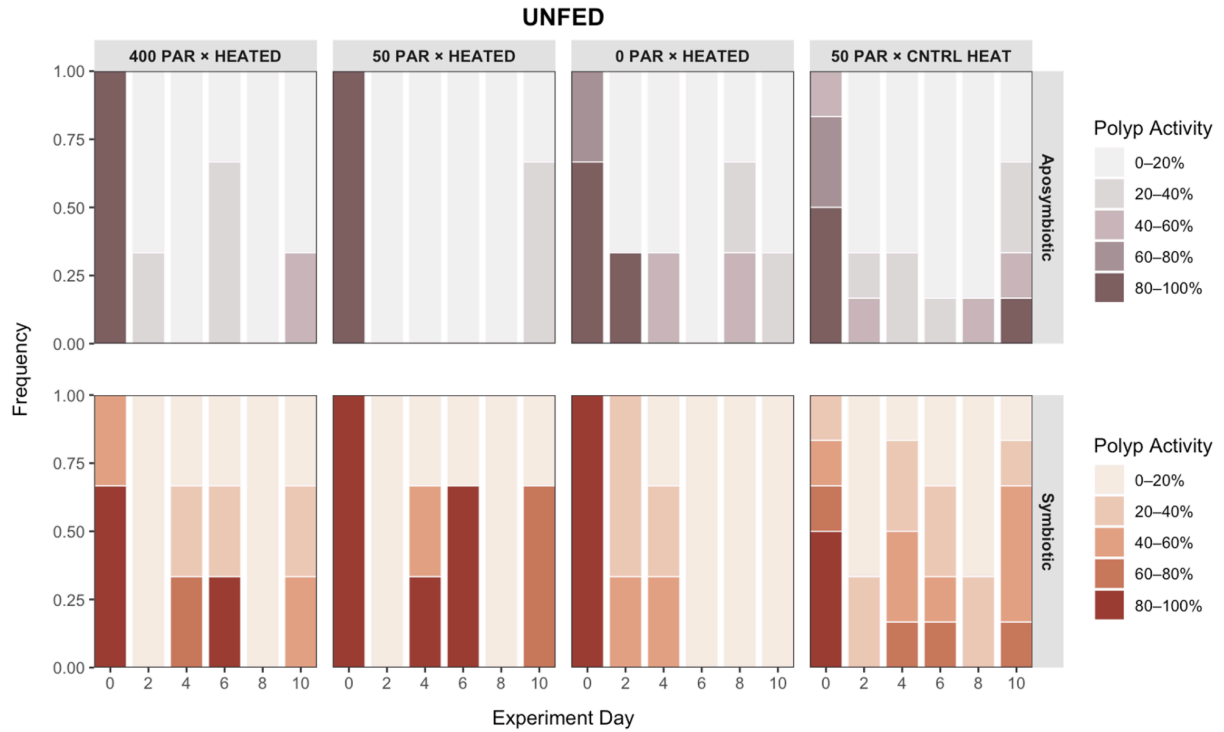


Figure 6 – Feeding Behavior (Unfed). Frequency of polyp activity, quantified as the proportion of extended tentacles, across the experimental period for unfed aposymbiotic (grey) and symbiotic (brown) *Astrangia poculata* nubbins. Activity was qualitatively assessed 30 minutes post-feeding of fed tanks and categorized in 20% intervals (legend). Panels are organized by combined light (400, 50, 0 PAR) and temperature treatments (heated or control). Unfed tanks are identified in Fig. 2.

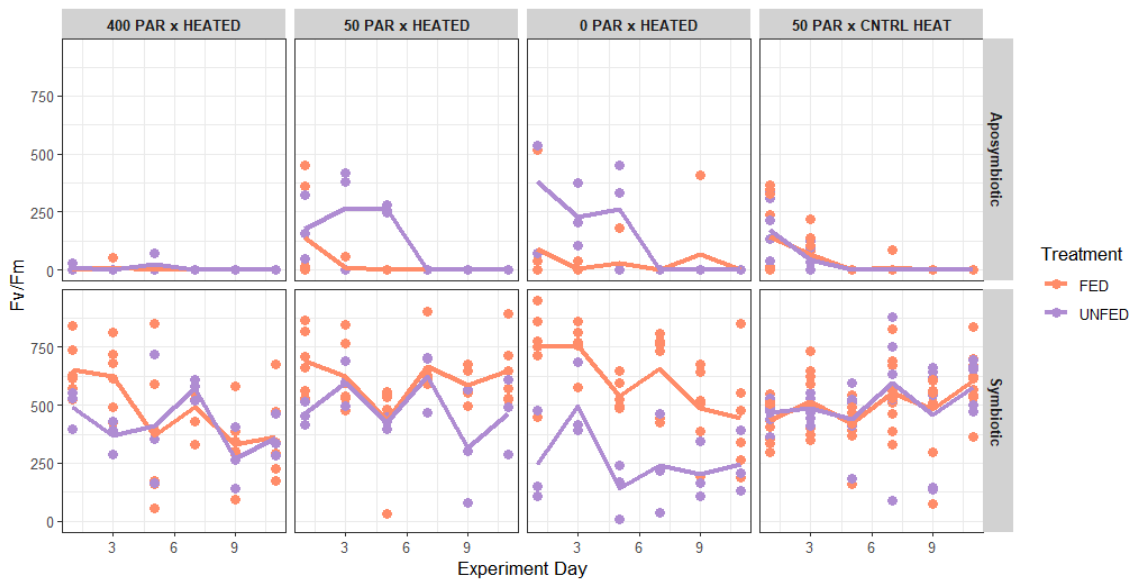


Figure 7 – Photosynthetic Efficiency (PAM). Photosynthetic efficiency (Fv/Fm) of *Astrangia poculata* nubbins across the experimental period, separated by symbiotic state (aposymbiotic top, symbiotic bottom; n = 42 each). Measurements were taken on Days 1, 3, 5, 7, 9, and 11 using a JUNIOR-PAM fluorometer (Walz). Panels are organized by combined light (400, 50, 0 PAR) and temperature treatments (heated or control). Lines depict changes in mean Fv/Fm over time, and colors denote feeding treatment (fed = orange; unfed = purple).

Discussion

The purpose of this study was to evaluate how combined thermal and light stressors influence the symbiotic state of the facultative coral *Astrangia poculata*, with a particular emphasis on trophic strategy responses across varying light intensities. We first hypothesized that nutrient dynamics between the symbiont and host influence the coral's strategy in regulating symbiont populations, and that heterotrophic feeding buffers coral responses to environmental stressors like heat and light challenges. We tested these hypotheses by quantifying feeding behavior (with polyp extension as a proxy) and measuring the photosynthetic efficiency of algal symbionts present. Our results indicate that the various combinations of heat and light treatments elicited distinct responses between aposymbiotic and symbiotic corals under fed and unfed conditions, with interactive effects of symbiotic state, trophic strategy, and external stressors.

Photosynthetic Efficiency (PAM)

Photosynthetic efficiency (Fv/Fm) was generally higher in symbiotic coral samples across all treatments, as expected. In the control tank (control temperature and 50 PAR), aposymbiotic and symbiotic samples exhibited consistent Fv/Fm values regardless of feeding. Aposymbiotic samples initially had a rather low Fv/Fm on Day 1, confirming, along with the overlap in distribution in color analysis (Aichelman et al., 2019), the presence of a minimum amount of algal symbionts (Fig. 4; Fig. 7). Fv/Fm decreased to zero on Day 5 and remained there for the remainder of the experimental period. Control symbiotic samples, however, generally increased across the experimental period (Fig. 7). This sets the baseline to compare with for future analysis.

For the heated systems under control light treatment (50 PAR), fed and unfed aposymbiotic samples diverged in photosynthetic efficiency initially. Fed aposymbiotic corals in this treatment mirrored the photosynthetic activity of the control-treated aposymbiotic corals, while the unfed corals had an initial increase in Fv/Fm, but then, the treatments equalized at zero on Day 7. The dark (0 PAR) heated system demonstrated a clear downward trend of Fv/Fm for both the symbiotic and aposymbiotic corals (Fig. 7). The unfed aposymbiotic samples decreased in Fv/Fm over time, while the fed consistently remained closer to 0, mirroring results of the 50 PAR heated tanks as well as the control temperature tank (Fig. 7). This result supports our hypothesis that nutrient dynamics between the symbiont likely shapes the coral host's strategy for regulating its symbiont population. As aforementioned, low light levels inhibit symbiont photosynthesis, reducing autotrophic input (Lindsay et al., 2025) and likely driving the algae symbionts to turn to parasitism (Baker et al., 2018; Wiedenmann et al., 2023). Unable to acquire energy from the little amount of algal symbionts it might have had (Fig. 4), coupled with no heterotrophic inputs, unfed aposymbiotic corals' decrease in photosynthetic activity was likely the host corals exhibiting continuous dysbiosis (Lindsay et al., 2025). This was likely stress-induced symbiont loss due to the heat and lack of nutrients (Martinez et al., 2022); however, prior studies have hypothesized that dysbiosis from a lack of food source could be due to the coral seeking to eat their algal symbionts for energy (Wiedenmann et al., 2023). Additionally, the similarity in Fv/Fm values of fed, aposymbiotic corals in control and dark conditions, as well as both temperature conditions (Fig. 7), suggests that fed aposymbiotic corals react the same in normal conditions as they would in heated and low light. This further supports our hypothesis that nutrient dynamics

between the symbiont likely shape the coral host's strategy for regulating its symbiont population, because, except for high light conditions, fed aposymbiotic corals had very similar photosynthetic outputs to all other treatments. This finding also expands on previous research, which confirmed that heat and light stress generate distinctive pathomorphological responses, acting on symbionts through different mechanisms (Downs et al., 2013), showing that this might also be possible in temperate corals as well.

The fed symbiotic samples in the heated tanks under 50 PAR light exceeded their unfed counterparts, particularly in the beginning and the end, despite having rather similar patterns of fluctuation throughout the experimental period (Fig. 7). These results align with prior studies (Wutchik et al., 2024), which suggested that early in the heat stress response, host symbiotic corals have to dedicate energy to controlling symbiont proliferation. Unfed corals do not have an alternative food source to mitigate this energy loss, where the fed corals do, supporting our hypothesis that heterotrophy acts as a buffer to heat and light challenges. A similar pattern can be seen across the other heated tanks, most notably the 0 PAR heated tank, where the fed symbiotic corals are constantly much higher than the unfed symbiotic corals (Fig. 7). In this tank, the lack of light is limiting the symbiont's ability to photosynthesize, which would usually lead to dysbiosis or a downregulation of symbiote production (Lindsay et al., 2025), however, the continuously high photosynthetic activity (higher than the control symbiotic corals) suggests that with the not only are the symbiotes able to either to keep multiplying due to the added energy source from heterotrophy, or lack of light either does not have the effect assumed or heterotrophic activity from the coral animal may act as an even more complex buffer than assumed.

In the heated system at high light (400 PAR), aposymbiotic samples were consistently at 0 Fv/Fm, regardless of the feeding (Fig. 7). This challenges prior research that found that unfed aposymbiotic corals tend to increase in photosynthetic efficiency, without an alternative food source available (Tivey et al., 2020). A similar disagreement can be seen in symbiotic samples as they remained very consistent, except for an initial divergence (Fig. 7). Based on prior research, an increase in photosynthetic efficiency in unfed symbiotic samples was expected. Yet, *A. poculata* did not appear to alter its trophic strategy to be more heterotrophic, which is out of line with the expected symbiont management through cell-cycle regulation (Gorman et al., 2022).

All of the symbiotic corals in the heated treatments were associated with a decline in photosynthetic activity, while the control temperature tank saw a relative increase, as expected (Fig. 7); however, the aforementioned discrepancy between fed and unfed samples supports our second hypothesis that heterotrophic feeding likely buffers *A. poculata* stress responses to heat and light challenges. Past research, like Meunier et al., (2022), has found that through heterotrophy, corals survive over unfed counterparts that have to rely exclusively on autotrophy, and confirming this in our study shows that this remains true with the addition of the light stress. This serves to expand understanding of coral resilience to multi-stressors, including heat, when they can adapt to or adopt heterotrophy, giving hope for the future of coral reefs.

It is important to note that none of these discrepancies between heat, light, or feeding treatments were statistically significant, but the differences between symbiotic states were. It is possible that the two experimental weeks were not long enough for the environmental factors to cause a

significant effect, but it is definite that *A. poculuata*'s symbiotic state is a determining factor in its stress responses.

Feeding Behavior

Unfed corals exhibited significantly less polyp activity than fed corals across treatments, confirming that feeding condition (fed or unfed) predominantly influenced polyp extension and supporting our hypothesis that heterotrophic input influences feeding behavior under stress (Figs. 5 & 6). Control aposymbiotic and symbiotic corals showed activity throughout the experimental period, though minimal at times. Sporadic polyp activity was observed in unfed aposymbiotic corals in the 0 PAR and 400 PAR heated treatments, although activity in both declined substantially after Day 0 (Fig. 6). This indicates that while they were under stress, they did not experience complete mortality, nor was it high enough stress for them to stay retracted continuously. Comparatively, unfed aposymbiotic corals maintained under control light (50 PAR) and heat conditions also exhibited little to no activity for most of the experimental period, with the exception of the final day (Fig. 6). Thus, these corals were likely experiencing a stronger stress response (limitation in energetic dynamics) than the other treatments. These observations contrast the expectation that high heat alone represents the strongest stress response and show the importance of heterotrophy in supporting energy balance (Aichelman et al., 2016) and mitigating stress responses (Rivera et al., 2023). For unfed symbiotic corals, a similar sporadic pattern following Day 0 was observed for those in the 50 PAR and 400 PAR heated treatments. However, symbiotic corals maintained in 0 PAR heated conditions showed no polyp activity after Day 4, suggesting a higher stress response (Fig. 6). This is in line with prior research that found that symbiotic corals usually have a more noticeable stress response to low light than high light (Alvarez et al., 2022).

The fed corals, on the other hand, exhibited high amounts of polyp activity in comparison throughout the experimental period. There was a consistent dip in activity in corals across all treatments on Day 8, likely aligning with an equipment malfunction the night prior (Fig. 5). It is important to note that just like their unfed counterparts, symbiotic corals in the 0 PAR heated treatments had the lowest polyp activity and consequently the highest stress response (Fig. 5). Once again confirming that symbiotic corals usually have a higher stress response to low light than high light. There was also notably more polyp activity in the high light corals compared to the dark conditions in both control systems (Fig. 5). This would suggest that in fed corals, the interaction between high light and heat caused minimal polyp stress responses in both aposymbiotic and symbiotic corals, and may even be preferred compared to control conditions. The same cannot be said about the unfed corals (Fig. 6), once more supporting our hypothesis that heterotrophy can buffer the response to the interaction of light and heat.

Based on the results of the ANOVA tests, feeding condition had the strongest significance on polyp activity, while light and heat treatments had a minor influence. Tukey HSD post-hoc tests indicated that the most significant difference in activity occurred between unfed aposymbiotic corals in control conditions and fed symbiotic corals under heated treatments. Despite constant exposure to heat stress, the combination of heterotrophic and autotrophic energy sources likely allowed fed symbiotic corals to maintain coral health than unfed controls, illustrating a buffer to behavioral stress responses under external stress (Lindsay et al., 2025).

Experimental Limitations

Coral nubbin size could not be fully standardized within the scope of this study, likely resulting in variation in the number of polyps per fragment, potentially affecting differences in feeding capacity and energetic demand. Future studies could record and incorporate polyp number per nubbin for subsequent analyses, along with an initial qualitative health score to compare with final conditions. Although nubbins were categorized by symbiotic state (aposymbiotic or symbiotic), symbiont density can fluctuate temporally and spatially, notably among neighboring polyps (Dimond & Carrington, 2008; Sharp et al., 2017). Some nubbins may have exhibited mixed symbiotic states in this study, potentially influencing trophic strategy. To address this limitation, red channel intensity values obtained through pre-experimental color analysis were used to distinguish symbiotic state of each nubbin, with higher values indicating increased symbiont presence (Fig. 4). Repeating this analysis following the experimental period would allow for comparison with initial states and improve understanding of symbiotic shifts over the course of the experiment.

Technological issues also affected temperature stability in several of the experimental systems. An overnight malfunction of aquarium system controllers between Days 7 and 8 resulted in the temporary loss of heat regulation in Systems 1-4, likely lasting a few hours. This was reflected in temperature variability, as evidenced by maximum standard deviation values on Day 8, though target temperature conditions were promptly restored by the following morning (Fig. 3). *A. poculata* is known to be relatively tolerant of thermal change (Trumbauer et al., 2021; Brennan et al., 2018) and this therefore unlikely had a lasting physiological affect on the corals. This event may have contributed, however, to the reduced polyp activity observed during feeding on Day 8 (Figs. 5-6).

Future Work and Broader Implications

Work conducted beyond the experimental period will focus on tracer-fed individuals (Fig. 2), which received $^{13}\text{C}/^{15}\text{N}$ -labeled *Artemia salina*. This will allow for assessment of nutrient assimilation and exchange between the coral host and its symbionts and may serve as indicators of shifts in trophic strategy (Solomon et al., 2025). The behavioral responses, such as polyp activity, observed in this study can then be linked to underlying nutritional dynamics. Additionally, the duration of the experimental period may also represent a limitation. Further research could capture long-term responses, including acclimation or delayed shifts in trophic strategy.

The findings of this study contribute to a growing understanding of coral thermal tolerance by emphasizing the importance of trophic strategy alongside symbiotic state. While bleaching status is often considered a primary indicator of coral health, our findings suggest that coral responses to environmental stress are more dynamic and behaviorally involved, adjusting as stressors fluctuate. Heterotrophic feeding under low-light or thermally variable conditions may be an underappreciated aspect of resilience. Corals may rely on energy acquisition through a shift to heterotrophy when environmental stressors limit symbiont productivity, such as photosynthesis.

Conservation strategies can also shift, as efforts that focus solely on single-stressor response may overlook trophic connectivity. By demonstrating that trophic strategy is closely tied to coral

stress responses, supported by stable isotope analysis, this study supports a more integrative approach for assessing coral resilience. Understanding how corals balance symbiosis and trophic strategy under compound strategies is vital for realistic and informed predictions of reef persistence in an increasingly variable ocean.

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