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# Host and Symbiont Physiology During Wound Regeneration in *Acropora pulchra* Under Warming Conditions

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by

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## ABSTRACT

Effects of Warming on Host and Symbiont Physiology During Wound Regeneration in the Coral *Acropora pulchra*

by

Ninah Jumamil Munk

Reef-building corals exhibit remarkable regenerative capabilities, enabling recovery from a range of physical disturbances. However, coral regeneration can incur significant energetic costs leading to tradeoffs with growth or reproduction. This physiological constraint may be exacerbated by stressful conditions, such as warming that can disrupt nutrient acquisition by algal endosymbionts (Symbiodinaceae). In this study, I investigate the role of temperature (27.9℃ & 29.5℃) and injury (abrasion & fragmentation) on energy acquisition, allocation, and utilization during regeneration. To explore these dynamics, I conducted a controlled mesocosm experiment in Moorea, French Polynesia, using a prominent reef building coral, *Acropora pulchra*. Overall, regeneration was achieved in 92% of corals 19 days post-injury, however tissue regeneration was faster in abraded corals. Interestingly, I found no significant effects of injury or temperature on growth rates of *A. pulchra.* This may be explained by a limited increase in respiration with significant increases in productivity (daily P:R) during regeneration. These results support the use of genus *Acropora* as an ideal candidate for coral restoration due to their capacity to rapidly regenerate from physical damage. Although I found

no evidence for a physiological tradeoff between growth and regeneration, these results highlight the importance of a broader investigation of physiological tradeoffs (or a lack thereof) as they apply to coral restoration efforts. As coral restoration practitioners aim to scale up production of propagated corals in land-based facilities, it is crucial to assess regenerative capacity and anticipate physiological tradeoffs for injured coral fragments under future warming conditions.

# INTRODUCTION

Reef-building corals possess an extraordinary ability to regenerate, restoring damaged tissue and skeleton following various disturbances such as predation (Rotjan and Lewis, 2008), storms (Madin and Connolly, 2006), and bleaching events (Hoegh-Guldberg et. al. 2017; Hughes et. al., 2017). This capacity for self-repair is exemplified in *Acropora* species that are known to rapidly regrow fragmented branches (Bak, 1983) as well as the "Phoenix effect" (Roff et. al., 2014), where new coral tissue regrows over dead skeletons that were previously covered in macro algae (Dias et. al., 2018). However, there can be significant energetic costs for tissue repair and skeletal regrowth, that can lead to trade-offs between regeneration and growth or reproduction (Henry & Hart, 2005; Rinkevich, 1996).

Corals primarily obtain energy through a symbiotic relationship with photosynthetic algae (Symbiodinaceae), which can provide up to 90% of their nutritional energy (Muscatine, 1990). Research on a facultatively symbiotic coral, *Astrangia poculata*, shows that the presence of algal symbionts significantly increases healing capacity, even when corals have access to additional food sources (i.e., heterotrophy). This suggests that symbiosis may play an important role in facilitating coral recovery (Burmester et al., 2017; DeFilippo et al., 2016), however, it's still unclear how environmental drivers (e.g., temperature) might constrain the healing capacity of coral symbionts.

Previous studies on how temperature influences coral regeneration reveal a complex picture, with the impacts of elevated temperature on healing and associated costs varying across species and environmental contexts. Research on *Acropora* species, known for their rapid growth, suggests that exposure to high temperatures can hinder wound recovery and

skeletal regrowth (Bonesso et al., 2017), potentially due to resource limitations and trade-offs with growth (Meesters et al., 1994; Denis et al., 2013). Conversely, in cauliflower corals of the genus *Pocillopora*, elevated temperatures, within certain limits, might actually enhance or maintain growth rates in injured corals due to trade-offs with wound healing (Lenihan and Edmunds, 2010; Rice et. al., 2019). Importantly, none of these studies assess the mechanistic underpinnings of trade-offs during regeneration which could offer critical insight into mechanisms of these variable responses. In particular, our understanding of how energy demand and energy acquisition is altered during regeneration processes is limited, but may shed light on how resources are allocated to other processes such as growth. Yet, because temperature stress can decouple the coral-algal symbiosis, rising temperatures may significantly affect the innate regenerative capacity of corals (Meesters & Bak, 1993; Bonesso et al., 2017). Given increases in the prevalence of marine heatwaves and global warming, understanding how warming impacts coral regeneration will be crucial for predicting future changes to coral reefs.

The relationship between coral regeneration and warming may also depend on the different types of injuries corals can experience. Superficial wounds (e.g., scraping by fish or mild abrasion by algae) may have different healing dynamics compared to more extensive injuries that involve removal of both tissue and skeletal structure [e.g., excavating predators, storm damage (Hall, 1997; Meesters et al., 1997)]. Wound characteristics such as the depth and size of the wound, the presence of residual tissue, and the extent of skeletal damage can all influence the healing process and interact with environmental factors like temperature (Meesters et al., 1997). For instance, deeper wounds with no remaining tissue may be more susceptible to infection and exhibit slower healing rates, especially under elevated

temperatures, as the coral's immune response is challenged and resources are diverted towards tissue repair (van de Water et al., 2015a). In contrast, superficial wounds with residual tissues left behind may be less impacted by temperature changes and heal more rapidly due to the availability of resources and the ability to regenerate from the wound margins (Lirman, 2000). Therefore, coral recovery dynamics, are likely to be dependent on the type of injury a coral is subjected (i.e., wound characteristics) and how warming interacts with the healing process over time as corals are actively regenerating.

To address these knowledge gaps and investigate how injury type and warming impact coral physiology and regeneration throughout the healing process I conducted a controlled mesocosm experiment in Moorea, French Polynesia, focusing on the branching coral *Acropora pulchra*. I subjected coral fragments to two distinct types of injuries: superficial tissue abrasions (hereafter abrasion) and skeletal fragmentation (hereafter fragmentation), simulating damage caused by different types of disturbances. I then exposed injured corals to either ambient (27.9℃) or warming (29.5℃°) seawater conditions in a fully factorial design to assess the impact of warming on coral regeneration and physiological tradeoffs. At the beginning (day 1) , middle (day 10), and end (day 19) of the experiment, I documented regeneration (healing) of tissue, corallites, and polyps and quantified various metrics of coral physiology, including respiration rate (energy demand), photosynthetic rate and efficiency (energy acquisition), and calcification (growth) rate. Overall, I had four guiding hypotheses. Firstly, I hypothesized that warming will slow regeneration by disrupting the energy input (photosynthesis) required to fuel regeneration, with fewer corals fully healed by the end of the study in warming temperatures compared to ambient. Secondly, I hypothesized that remnant tissue in abrasions will allow for more rapid healing of damaged tissue (the phoenix effect), with more abraded

corals fully healed by the middle of the study compared to fragmented corals. Thirdly, I hypothesized that injury and warming will initially raise energy demand and lower energy acquisition as coral energetics respond to acute stress, but then energy demand will lower and energy acquisition will increase over time as corals heal and acclimate to warming conditions. Finally, and building on these prior hypotheses, I hypothesized that injury and warming will decrease calcification due to shifts in coral energetics [i.e., increased energy demand (respiration) and decreased energy acquisition (photosynthesis)] with the combined effects being greater than either effect in isolation. By assessing these hypotheses with respect to injury, warming, and their interaction I aimed to gain a deeper understanding of the energetic mechanisms underpinning coral regeneration and the potential consequences of rising ocean temperatures.

## METHODS

### *Study site*

I conducted my study during the austral winter (May 28th to July 3rd, 2023) in Moorea, French Polynesia at Richard B. Gump Marine Research Station. Moorea is an ideal study system to study coral regeneration and the influence of ocean warming because it frequently experiences physical disturbance events from storms and crown of thorns sea star predation and also has regular warming related mortality events, such that these are highly relevant stressors to the system. I focused on *Acropora pulchra* due to its ecological significance as a prominent reef building coral on the fringing reef surrounding Moorea. This branching species grows in large thickets, some more than 20 meters in length, creating massive structures for

reef fish and benthic organisms (Mapstone et al., 2007; Johnson et al., 2011). Additionally, from an application perspective, branching species of the genus *Acropora* are the most commonly targeted species in coral restoration (Boström-Einarsson et al., 2020) because of their recruitment success through asexual fragmentation and fast-growing life history strategy.

To address this question I harvested branches of *A. pulchra* from six distinct thickets (i.e., physically separated by sand patches or other reef substrata) along a fringing reef on the northern shore of Moorea (17.48725° S, 149.88693° W) and transported them to flow-through seawater tables at Gump Station for further processing.

## *Coral processing and experimental design*

Immediately after collection, coral branches were cut into fragments and transferred to partially recirculating seawater aquaria for two weeks of acclimation to tank conditions. I cut branches using a Gryphon Diamond Blade Saw to create 18 fragments (~6 cm in height) per thicket (hereafter, parental colony) producing a total of 108 *A. pulchra* fragments. Each fragment was secured to an aragonite coral plug (Ocean Wonders) with bonding glue (Bulk Reef Supply). I allowed glued fragments to cure in a flow-through seawater table for several minutes before transferring them to six identical partially recirculating seawater aquaria separated by parental colony. Each coral aquaria (20 L, N=6) exchanged filtered seawater (200 μm) with one of two sumps which were continuously supplied with new seawater from Cook's Bay, adjacent to Gump Station. Each sump contained a submersible pump to transport seawater through a three-output manifold to three of the six tanks for a flow rate between 244 to 298 L/hr. Seawater was heated in the elevated temperature sump with a Finnex TH Deluxe Titanium Heating Element controlled by a Neptune Systems A3 Apex Pro Controller. I maintained two temperature treatments representing current (ambient) and future (elevated)

temperature conditions (ambient = 27.9°C; warming = 29.5°C). Temperature loggers (HOBO Pendant MX) recorded seawater temperature every 10 minutes in tanks and sumps. After two weeks of acclimation, injury (fragmentation or abrasion) and temperature (ambient or warming) treatments were randomly assigned to each coral fragment within each parental colony. I haphazardly distributed fragments in aquaria according to their assigned temperature treatment, maintaining a fully crossed experimental design.

## *Wound regeneration*

I experimentally wounded *A. pulchra* to simulate one of two injury types: 1) abrasion and 2) fragmentation. An abrasion injury was simulated by scraping the surface area of a branch trip (1 cm in length) with a tapered micro spatula tool. A fragmentation injury was simulated by cutting off a branch tip (1 cm in length) using a Gryphon Diamond Blade Saw. I calculate the amount of tissue removed with the formula for surface area of a cylinder (CSA) disregarding one of the circular faces: $CSA = 2\pi rh + \pi r^2$. Photographs of wounds were taken with an Olympus Tough TG-6 camera at four time points (0, 1, 10, 19 days) and analyzed in ImageJ to quantify wound area and signs of healing. I documented signs of healing for a subset of *A. pulchra* (n = 24). Signs of healing included polyp, corallite, and tissue regeneration (Meesters et al., 1994). Polyp regeneration is defined as the re-emergence of tentacles, identifiable by dark pigmentation (symbionts) inside corallites within the wound site. Corallite regeneration is defined as the visual re-growth (linear extension) of radial or apical corallite structures within abrasion and fragmentation wound sites, respectively. Tissue regeneration is defined as new tissue growth within the wound site, identifiable by symbiont re-pigmentation and the restoration of *A. pulchras'* tissue pattern. Signs of healing for polyp, corallite, and

tissue regeneration were documented separately as a ‘yes’ or ‘no’ for both injury types at each timepoint.

## *Holobiont performance*

Metabolism of the coral holobiont (host, symbiont, bacteria) can be quantified by measuring respiration rate. Respiration consumes resources produced by photosynthesis and is sensitive to extrinsic factors which are energetically costly. I conducted respirometry at each timepoint of this study to examine coral holobiont respiration (light-enhanced dark respiration) (Barott et al., 2021; Innis et al., 2021) throughout regeneration from experimental wounding at two temperature regimes. Coral fragments were individually loaded into acrylic chambers (650 mL) (Australian Institute of Marine Science) filled with filtered seawater (200 μm) ensuring no air bubbles were present. Loaded chambers contained 1’’ magnetic stirrer bars and were secured onto a motorized stir plate (Australian Institute of Marine Science) and submerged in a temperature-controlled water bath (Inkbird). Seawater used to fill chambers, and the water bath were kept at 28°C and 30°C for ambient and warming temperature trials, respectively. Oxygen concentration ([O2]) and temperature were recorded within each chamber every three seconds throughout the trial with a Presens Oxygen Meter (OXY-10 SMA (G2) Regensburg, Germany) equipped with Presens Oxygen Dipping Probes (DP-PSt7) and Presens Temperature Sensors (Pt1000). Immediately following data collection for photosynthesis (see methods for *Symbiont Performance*), I measured light-enhanced dark respiration for 15 minutes in complete darkness in order to achieve a stable negative [O2] slope. Each coral fragment (N=108) was randomly assigned to one of three groups to run 12 trials across three days (four trials $day^{-1}$) for a single time point. Respiration rates were determined using repeated local linear regressions with the R package LoLinR (Olito et al.

2017) with $L_{pc}$ as the linearity metric ($L_{pc}$ = sum of the percentile-ranks of the $Z_{min}$ scores for each component metric and alpha set to 0.5 (alpha = the minimum proportion of total observations needed to fit local regressions). Respiration rates were standardized by the volume of water in the chamber (vol of chamber – vol of coral fragment) and initial geometric surface area of the coral fragment. Initial geometric surface area was obtained for each coral by measuring branch length and width with digital calipers, calculating CSA (see equation under 'Wound Regeneration') for each branch, and taking the sum of branch surface areas for each coral. $O_2$ rates measured post-injury were standardized using initial geometric surface area minus wound surface area (i.e., the area of coral tissue removed or damaged by the injury).

## *Symbiont performance*

Photosynthesis by algal symbionts (Symbiodinaceae) is the primary source of oxygen and nutritional energy for the zooxanthellate coral host to fuel metabolic processes. Like respiration, photosynthesis may be influenced by extrinsic factors and/or the capacity of light-harvesting machinery to capture and convert light energy into photosynthetic products. I examined algal symbiont performance by quantifying net photosynthetic rate and measuring photosynthetic efficiency. Net photosynthesis ($P_{Net}$) was measured during a light phase of each respirometry trial. Light intensity was controlled by an LED light (Neptune Systems Sky LED Aquarium Light) positioned ~16'' above the chambers. $P_{Net}$ was measured for 15 minutes at 100% light intensity (344 ± 69 μmol $m^{-2}$ $s^{-1}$, Apogee MQ-210X Underwater Quantum Meter). In order to achieve a stable positive [O2] slope, each coral was light acclimated (5 min at 40% and 5 min at 70% light intensity) prior to measuring photosynthesis. $P_{Net}$ rates were determined

using repeated local linear regressions with the R package LoLinR (Olito et al. 2017) as described above for respiration rate measurements. $P_{Net}$ rates were standardized for each coral fragment by the volume of water in the chamber and surface area of the coral fragment. Gross photosynthesis ($P_{Gross}$) was calculated as $P_{Net}$ plus respiration (as a positive value). I calculated daily P:R ratios (Coles and Jokiel, 1977; Krueger, 2019) from hourly rates of $P_{Gross}$ and respiration (R) for a 11h:13h day:night cycle (the length of light and dark hours in Moorea during austral winter) with the following equation:

$$\text{Daily P:R} = 11 \times P_{Gross}\, h^{-1} / 13 \times \text{Respiration}\, h^{-1}$$

Daily P:R ratios are an approximation of a daily coral metabolic budget (Odum and Odum, 1955). A ratio greater than 1 can be indicative of net autotrophy, suggesting a coral is producing more energy than it demands. A ratio of less than 1 suggests net heterotrophy, where energetic demand is surpassing production.

I also measured photosynthetic efficiency ($F_v/F_m$) of each coral throughout the study (day 0, 10, 19) with an Underwater Fluorometer Diving-PAM (Heinz Walz GmbH, Germany). Photosynthetic efficiency can be broadly defined as the capacity of light harvesting machinery to capture light energy for photosynthesis. In corals, a significant drop in $F_v/F_m$ can signal a disruption of energy transfer in photosystem II, which can be caused by abiotic stressors including elevated temperature (Warner et. al., 2010). Corals were dark acclimated before measuring photosynthetic efficiency by taking measurements 30 minutes to an hour after sunset. Three measurements were taken per coral and averaged to produce a single $F_v/F_m$ value.

### *Growth quantificatio*n

To test if wounding affected growth rate, I determined the rate of calcification (growth) during regeneration. Dry skeletal mass was derived from coral buoyant weights (Davies 1989)

using an aragonite density of 2.93 (Jokiel 1978). I quantified calcification rate by taking the difference in dry skeletal mass (final – initial) of each coral fragment and normalizing by final surface area and time (19 days) to report as mg $cm^{-2}$ $day^{-1}$. Final surface area was derived by wax-dipping dry coral skeletons to calculate surface area against a standard curve of mass difference of wax-dipped dowels with geometrically calculated surface area ($R^2 > 0.9$). Wax derived final surface areas were highly correlated with geometrically derived initial surface areas ($r = 0.8$).

## *Unexpected presence of Acropora eating flatworms*

Acropora Eating Flatworms (AEFW) were found in the experimental aquaria during day 1 of the experiment and eradicated by manual removal after visually inspecting each individual coral. To document the impact of these worms, a single person visually examined each individual coral to record 1) if there was evidence of tissue predation (i.e., bite marks) and if so 2) an estimation of percent tissue removal. To assess the impact of tissue removal by AEFW on coral growth, I included AEFW percent tissue removal as a continuous covariate in my initial growth model. Upon finding that AEFW percent tissue removal was statistically significant, I iteratively filtered the growth data, decreasing the threshold of percent removal until its effect was no longer significant in the model. For all subsequent respiration, photosynthesis, daily P:R, photosynthetic efficiency, and growth analyses, I include only corals with less than or equal to 10% damage by AEFW, N = 71. Subsequent regeneration analysis also includes only corals with less than or equal to 10% damage by AEFW, N = 14. .

## *Statistical analysis*

To assess how injury and temperature impact coral energetics, I fit linear mixed models to respiration, net photosynthesis, gross photosynthesis, daily P:R, and photosynthetic efficiency with injury (non-injured, abrasion, or fragmentation), temperature (ambient or warming), time ($1^{st}$, $10^{th}$, or $19^{th}$ day of treatment, coded categorically as beginning, middle, and end, respectively), and all two-way interactions and a three way interaction between injury, temperature, and time as fixed effects using the lme4 package in R (Bates et al. 2015). Parental colony was included as a random effect, with individual coral nested within parental colony to allow random intercepts for each coral individual. To determine how injury and temperature impact coral growth, I also fit a linear mixed model to calcification rate with injury (non-injured, abrasion, or fragmentation) and temperature (ambient or warming), and a two-way interaction between injury and warming as fixed effects and parental colony as a random effect. Pairwise comparisons were made on fixed effects to determine significant differences between groups with estimated marginal means or least-squares means using the emmeans package (Lenth 2023). In cases where there was not a significant three-way interaction of injury, temperature and time, pairwise comparisons were made across significant two-way interactions (e.g., if temperature*time is significant I looked at differences between temperature-time combinations pooled across injury types). To determine how injury and temperature influence regeneration, I conducted 1) Kaplan Meier survival curves and 2) Cox Proportional Hazards mixed models. I treat signs of healing (polyp, corallite, and tissue regeneration) as discrete response variables. Each variable was analyzed separately with injury (abrasion or fragmentation) , temperature (ambient or warming), and the interaction between injury and temperature as fixed effects and parental colony as a random effect. All data analyses were conducted in R statistical environment (Version 4.3.2) using R Studio (Version

2023.03.1+446). All data and code used for this study are available on GitHub (https://github.com/ninahmunk/Acropora_Regeneration-main).

## RESULTS

### *Experimental aquaria maintained ambient and warming seawater temperature regimes.*

I effectively maintained distinct temperature regimes in the experimental aquaria, with average temperatures of 27.9 ± 0.7486°C and 29.5 ± 0.3508°C for ambient and warming regimes, respectively. Daily average temperatures ranged from 27.12 to 28.31°C and 28.74 to 29.70°C for ambient and warming regimes, respectively (Fig. A1). Averaged over the duration of the experiment (19 days), the warming regime was 1.65°C ± 0 .33 higher than the ambient regime.

### *Tissue regeneration is faster in abraded corals.*

On average, the amount of surface area (i.e., live tissue) removed due to fragmentation was 1.07 ± 0.04 $cm^{-2}$, with a resulting wound area of only 0.22 ± 0.02 $cm^{-2}$. For abrasions, the amount of live tissue removed is equivalent to the resulting wound area and was on average 0.95 ± 0.03 $cm^{-2}$. Regardless of injury type, 92% (13/14) of *A. pulchra* fragments displayed at least two out of three signs of healing (polyp, corallite, and/or tissue regeneration) by the end of the experiment (Fig. 1; Table 1). However, abrased corals were more likely to have regenerated new tissue in the wound site than fragmentation (cox survival analysis; Fig. 2C; Table 2). I did not detect statistically significant effects of injury, temperature, or the

interactions of injury and temperature on polyp or corallite regeneration by the end of the experiment (Table 2).

### *Warming increases daily productivity.*

Warming positively influenced coral daily productivity, with daily P:R reaching a peak during the middle of regeneration (Fig. 3C), with a statistically significant interaction between temperature and time (Table 3). Surprisingly, injury did not substantially influence P:R, with neither injury nor injury interactions of temperature and/or time proving significant in the mixed effects model (Table 3). Pairwise comparisons reveal that warming significantly increased daily P:R from the beginning to the middle of regeneration ($p < 0.0001$) and significantly decreased P:R from the middle to the end ($p = 0.03$) (Fig. 3C). Furthermore, coral daily P:R in warming conditions was significantly higher during the middle ($p < 0.001$) and end of regeneration ($p = 0.01$) compared to ambient (Fig. 3C).

The only detectable effect of injury on metabolism (i.e., photosynthesis or respiration) was on net photosynthesis ($P_{Net}$), which had a statistically significant three-way interaction between injury, temperature, and time on net photosynthesis (Table 3), which was driven primarily by significantly higher $P_{Net}$ in abraded corals (but not fragmented or uninjured corals) at the end of regeneration in warming conditions compared to ambient (pairwise comparisons, $p < 0.03$, Fig. 4).

I found statistically significant effects of temperature ($p < 0.01$) and time ($p = 0.017$) on gross photosynthesis ($P_{gross}$) and no significant effects of injury or significant interactions of temperature and/or time with injury (Table 3). Pairwise comparisons reveal significantly

higher $P_{gross}$ in warming conditions compared to ambient ($p < 0.01$) (Fig. 3C) and significantly higher $P_{gross}$ at the end of regeneration compared to the middle of regeneration ($p = 0.02$) (Fig. 3B).

Warming did not influence a distinct pattern on respiration, with no differences in respiration rates between temperature treatments at any timepoint during regeneration (Figure 3A). However, I detected a statistically significant interaction between temperature and time on respiration and no significant effects of injury or significant interactions of temperature and/or time with injury (Table 3). Pairwise comparisons reveal that respiration rates significantly lowered from the beginning to the middle of regeneration in warming conditions ($p < 0.0001$) but not ambient conditions. In both warming ($p < 0.001$) and ambient conditions ($p < 0.0001$) respiration rates significantly increased from the middle to the end of regeneration. Prior to the start of the experiment, there were no significant differences in daily P:R, $P_{Net}$, $P_{gross}$, or respiration across all treatment groups.

## *Warming eventually reduces photosynthetic efficiency*

Warming negatively influenced *A. pulchra* photosynthetic efficiency ($F_v/F_m$), significantly reducing $F_v/F_m$ by the end of the study (Fig. 5). I detected a significant interaction between temperature and time on $F_v/F_m$ and no significant effects of injury or significant interactions of temperature and/or time with injury (Table 4). Pairwise comparisons reveal that $F_v/F_m$ in warming conditions was significantly lowered from the middle to the end of regeneration ($p < 0.01$) and significantly lower than $F_v/F_m$ in ambient conditions ($p < 0.01$). In warming conditions, average end point $F_vF_m$ values are lowest in uninjured corals, 0.9% lower than fragmented corals and 1.3% lower than abraded corals. Pooled across injury status,

warming reduced $F_v/F_m$ by 3% from pre-experiment measurements to endpoint measurements compared to only 0.5% at ambient temperature. Prior to the start of the experiment (pre-treatment), $F_v/F_m$ happened to be significantly higher in corals which were assigned to the fragmentation + warming group, however, by the middle timepoint $F_v/F_m$ was lowered and there were no significant differences between treatments.

### *Injury and temperature had no effect on coral calcification.*

I did not observe significant effects of injury, temperature, or the interaction between injury and temperature on *A. pulchra* calcification rates (Fig. 6; Table A1). Calcification rates of *A. pulchra* fragments (N = 71) ranged from 0.59 to 2.59 mg $cm^{-2}$ $day^{-1}$ with an average rate of 1.62 ± 0.05 mg $cm^{-2}$ $day^{-1}$.

## DISCUSSION

I aimed to better understand the balance between energy acquisition, allocation, and utilization during coral regeneration to address how warming oceans influence coral recovery from injury. I hypothesized that 1) warming would slow regeneration by further enforcing energy limitation and disrupting the function of photosynthetic symbionts, 2) abraded corals would heal faster than fragmented corals due to residual tissues within abrasion wounds, 3) injury and warming wound raise energy demand and lower energy input in the beginning of regeneration as corals respond to acute stress, but then would lower energy demand and increase energy input over time as corals heal and acclimate to warming, and 4) that injury, warming, and their interaction would decrease calcification rates by diverting energy towards regeneration and increasing metabolic costs. My findings largely do not support these hypotheses and highlight the resilience of *Acropora pulchra* to both injury and warming. All

corals survived (N = 71) and calcification rates were unaffected by injury and warming, but tissue regeneration was faster in abrasion injuries compared to fragmentation. I observed no immediate effects of injury or warming on coral energetics. However, by the end of the experiment, there were detectable effects of injury and warming on coral holobiont physiology and these effects partially differed in direction from those anticipated.

## *Mechanisms of coral regeneration under warming conditions*

Observed effects of warming on *A. pulchra* physiology post-injury are driven by several potential mechanisms. Warmer temperatures can stimulate physiological activity, including photosynthesis and respiration in heat treated corals, resulting in changes in energetic expenditure and acquisition. Extreme temperatures (3 and 5 ℃ above thermal optimum) and injury by abrasion have been shown to significantly reduce photosynthesis and increase respiration in *A. cervicornis* (Paradis et. al., 2019). Here, I do not observe reductions in photosynthesis or increases in respiration due to warming or injury, potentially because my treatments did not initiate an immediate stress response. Less extreme warming conditions can initially increase photosynthesis, but eventually result in a bleaching response with time (Rädecker et. al., 2020). Rädecker et. al., 2020 observed 27% higher photosynthesis in heat treated corals after 10 days, but after 21 days they observed a 78% and 67% decline in algal symbiont densities and chlorophyll a content (i.e., bleaching), respectively. Here I observe depressed respiration during the middle of regeneration followed by recovery at the end (Fig. 3A). This metabolic recovery coincides with enhanced productivity (Figure. 3B & 3C), which was likely essential for fueling the rapid regeneration observed in both fragmented and abraded corals. This suggests that injured *A. pulchra* can effectively allocate energy towards

regeneration even under warming conditions and that small increases in temperature below tolerance thresholds may actually enhance energy acquisition. In the facultatively symbiotic coral, *Astrangia poculata,* diminished healing capacity was attributed to symbiont loss rather than wound stress, underscoring the responsibility of algal symbionts in providing energy for wound regeneration (DeFilippo et al., 2016). However, prolonged exposure to thermal stress can be detrimental to the coral-algal symbiosis by disrupting the electron transport chain (Oakley et al., 2014), building up oxidative stress, and limiting resources for photosynthesis (Buxton et al., 2009), which will eventually impair algal symbiont photosynthetic capabilities. Here, I observe reduced photosynthetic efficiency due to warming conditions (Figure 5), indicating potential stress on the photosynthetic machinery of algal symbionts (Warner et al., 1999) which could have longer-term negative implications for energy acquisition (Maxwell & Johnson, 2000; Warner et al., 1996). The interplay between enhanced physiological activity and photoinhibitory stress, highlights the complex responses of corals to warming, emphasizing the need for further research into the cellular and molecular processes involved.

*Acropora pulchra* exhibited a robust capacity for regeneration under warming conditions, without compromising growth rates. This aligns with previous studies on *Acropora*, which are known for their rapid regeneration abilities (Bak, 1983) but differs from studies that have shown impaired growth at warmer temperature (Bonesso et al., 2016; Anderson et al., 2019). The results of this study also contrast with results on other coral species, such as *Pocillopora spp.* or *Porites spp.*, where elevated temperatures can either enhance or hinder growth depending on the context (Edmunds and Lenihan, 2009; Lenihan and Edmunds, 2010). These highly variable results, both here and in the literature, highlight the complex relationship between coral metabolism and temperature, which likely varies enormously across

taxa and is highly sensitive to both the temperature relative to species specific thermal tolerance (i.e., positive before thresholds of damage and negative beyond these thresholds) and timescale (positive in the short-term but negative after multiple weeks of exposure).

The concept of the "phoenix effect", where residual tissues within abrasion wounds facilitate regeneration, is another key mechanism in the regeneration process (Roff et al., 2014). Here I observe faster regeneration of tissue in abraded corals compared to those which were fragmented. These remnant tissues reduce the demand for resources from the wound perimeter, allowing for more efficient energy allocation towards healing. It's possible that rapid tissue regeneration in abrasion wounds played a role in the high net photosynthetic rates of abraded corals (Figure 3). At warmer temperatures, certain strains of Symbiodiniaceae can have enhanced population growth (Karim et al., 2015), which could have contributed to higher photosynthetic rates and faster tissue regeneration. Future research should focus on the mechanisms underlying these species-specific responses to injury and thermal stress, including the role of algal symbiont dynamics.

## *High regenerative capacity underscores coral resilience*

The implications of these findings for coral resilience are significant. The remarkable regenerative capacity of *Acropora pulchra* under warming conditions, surpassed hypothesized predictions of resilience to injury. This demonstration of greater resilience to injury and warming may be attributed to several factors, including rapid growth rates, efficient metabolic recovery, and productive symbiosis. Additionally, the small wound sizes in these experiments likely facilitated faster regeneration, as they had low surface area to perimeter ratios, which are more manageable for the coral to heal (Bak and Steward-Van es, 1980; Meesters et al.,

1997; Lirman et al., 2000). These components may be critical for the survival of coral reefs in the face of climate change, as it allows corals to recover from physical disturbances more rapidly. Poor regenerative capacity can have detrimental implications for overall fitness with respect to colony size, competition for space (Highsmith, 1982), and disease susceptibility (Bak and Criens 1981; van de Water et al., 2015a), which can ultimately lead to partial (Meesters et al., 1997) or full colony mortality (Meesters and Bak, 1993). The ability of *A. pulchra* to maintain high regenerative capacity and growth rates under warming temperatures suggests that certain coral species possess inherent biological traits that enhance their adaptability to changing environmental conditions (Pratchett et al., 2013). High predation rates on *Acropora* in the Indo-Pacific (Rotjan and Lewis, 2008) may have driven an adaptive response for high regenerative capacity to various injury types.

My study highlights the potential for leveraging the regenerative capacities of branching corals like *Acropora pulchra* in restoration efforts. Moreover, the resilience of *A. pulchra* I document here underscores the importance of considering the physiological processes underpinning coral regeneration when developing restoration strategies. Monitoring and optimizing environmental conditions, such as temperature, is critical in supporting coral regeneration and growth. As climate change continues to increase ocean temperatures and the prevalence of marine heatwaves (Oliver et. al., 2013), it is essential to understand how these factors interact with coral regeneration. Overall, this knowledge can inform the selection of coral species and genotypes for restoration projects, ensuring that the chosen corals possess the necessary traits to withstand thermal stress (Caruso et. al., 2021) and recover from injuries (Baums et al., 2019). Integrating these physiological insights into restoration practices will be

useful for developing effect strategies to restore and preserve coral reefs in a rapidly changing climate.

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## FIGURES AND TABLES

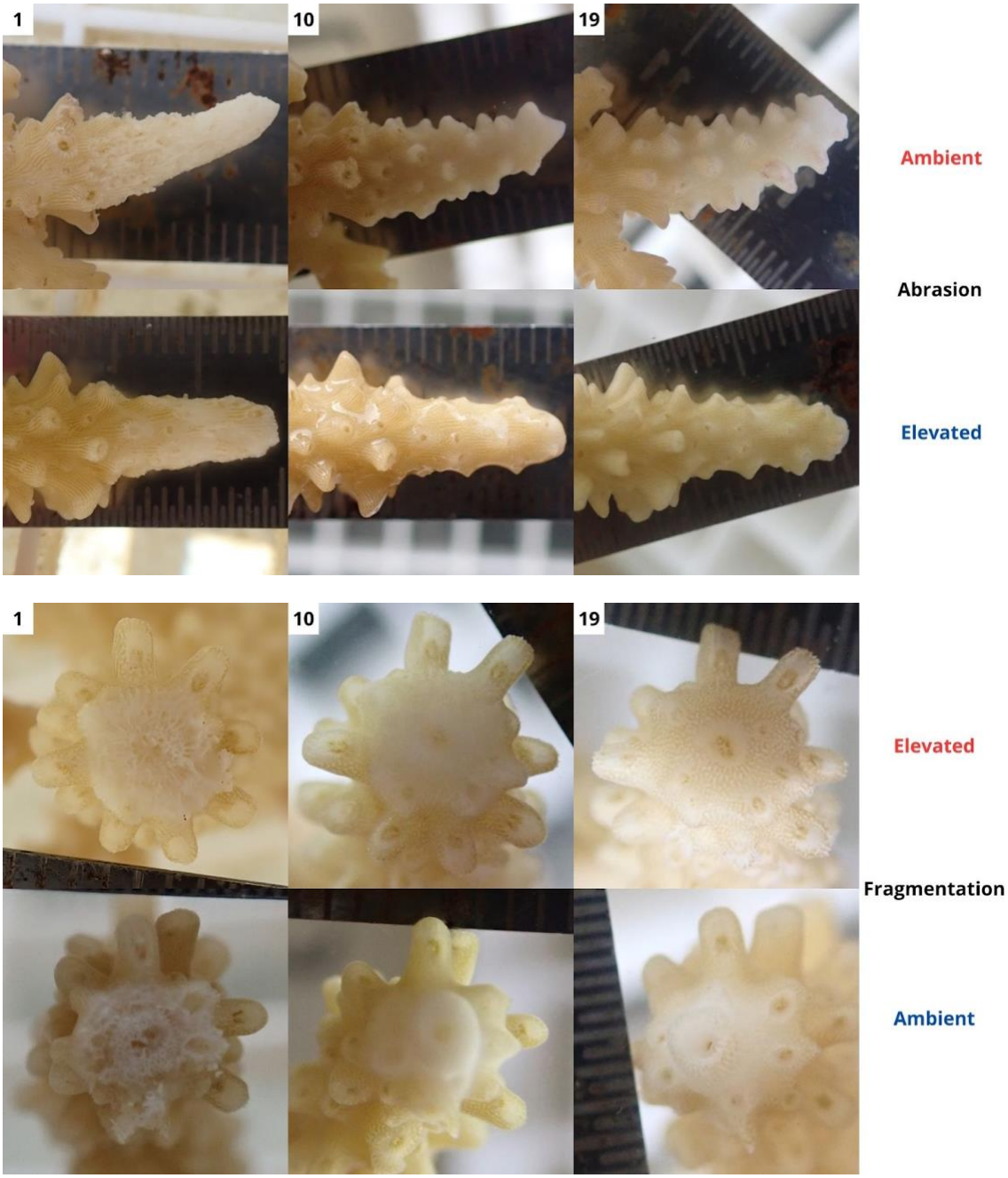


Figure 1. Photograph time series of wound regeneration in *A. pulchra* from abrasion and fragmentation injury at ambient and warming temperature. From left to right, photographs show stages of wound regeneration at the beginning (day 1), middle (day 10), and end (day 19) of the experiment.

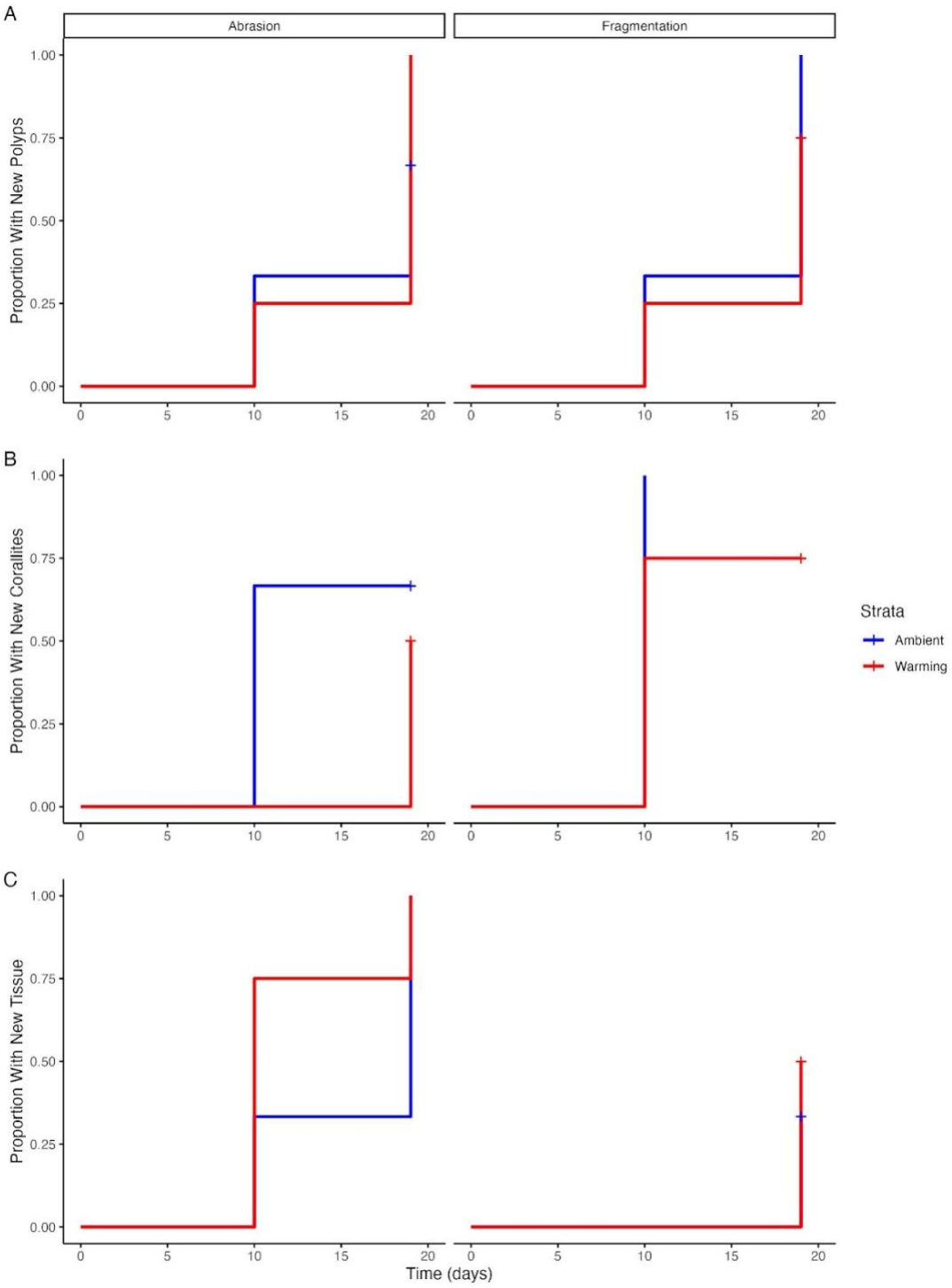


Figure 2. Kaplan Meier survival curves displaying the proportion of corals with regenerated A) polyps, B) corallites, and C) tissue for abrasion and fragmentation wounds in ambient (blue) and warming (red) conditions. Instead of survival, curves represent probability of regeneration with the event being the presence of new polyp(s), corallite(s), or tissue.

Table 1. Results from three Kaplan–Meier survival curves for tissue regeneration, polyp regeneration, and corallite regeneration from fragmentation and abrasion injuries at ambient (27.9 ℃) and warming (29.5 ℃) temperature conditions. The events in this survival analysis are tissue, polyp, or corallite regeneration. Intervals by which no individuals had reached regeneration (e.g., 100% survival) are not shown in the table. SE is standard error, and CI is confidence interval. In any treatment where all individuals have healed, an 'NA' is present for SE and 95% CI at that given time interval.

| Event | Treatment | Time | # not regenerated | # regenerated | Proportion not regenerated | SE | lower 95% CI | upper 95% CI |
|---|---|---|---|---|---|---|---|---|
| Tissue Regeneration | Fragmentation | | | | | | | |
| | Ambient | 19 | 3 | 1 | 0.667 | 0.272 | 0.3 | 1 |
| | Warming | 19 | 4 | 2 | 0.5 | 0.25 | 0.188 | 1 |
| | Abrasion | | | | | | | |
| | Ambient | 10 | 3 | 1 | 0.667 | 0.272 | 0.3 | 1 |
| | Ambient | 19 | 2 | 2 | 0 | NA | NA | NA |
| | Warming | 10 | 4 | 3 | 0.25 | 0.217 | 0.0458 | 1 |
| | Warming | 19 | 1 | 1 | 0 | NA | NA | NA |
| Polyp Regeneration | Fragmentation | | | | | | | |
| | Ambient | 10 | 3 | 1 | 0.667 | 0.272 | 0.3 | 1 |
| | Ambient | 19 | 2 | 2 | 0 | NA | NA | NA |
| | Warming | 10 | 4 | 1 | 0.75 | 0.217 | 0.4259 | 1 |
| | Warming | 19 | 3 | 2 | 0.25 | 0.217 | 0.0458 | 1 |
| | Abrasion | | | | | | | |
| | Ambient | 10 | 3 | 1 | 0.667 | 0.272 | 0.2995 | 1 |
| | Ambient | 19 | 2 | 1 | 0.333 | 0.272 | 0.0673 | 1 |
| | Warming | 10 | 4 | 1 | 0.75 | 0.217 | 0.426 | 1 |
| | Warming | 19 | 3 | 3 | 0 | NA | NA | NA |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Corallite Regeneration | Fragmentation | | | | | | | |
| | Ambient | 10 | 3 | 3 | 0 | NA | NA | NA |
| | Warming | 10 | 4 | 3 | 0.25 | 0.2165 | 0.0458 | 1 |
| | Abrasion | | | | | | | |
| | Ambient | 10 | 3 | 2 | 0.3333 | 0.2722 | 0.673 | 1 |
| | Warming | 19 | 4 | 2 | 0.5 | 0.25 | 0.188 | 1 |

Table 2. Results from three cox proportional hazard models for tissue regeneration, polyp regeneration, and corallite regeneration from fragmentation and abrasion injuries at ambient (27.9 ℃) and warming (29.5 ℃) temperature with parental colony as a random effect. The interaction term is absent from the model for corallite regeneration due to rapid healing creating insufficient data and is indicated by NAs. Significance is indicated by a hazards ratio (HR) less than 1, confidence interval (CI) not overlapping 1, and a p-value < 0.05.

| Event | Characteristic | HR | 95% CI | p |
|---|---|---|---|---|
| Tissue Regeneration | Fragmentation | - | - | |
| | Abrasion | 17 | 1.34, 216 | **0.029** |
| | Ambient | - | - | |
| | Warming | 1.55 | 0.13, 17.8 | 0.7 |
| | Abrasion × Warming | 0.92 | 0.05, 17.4 | >0.9 |
| Polyp Regeneration | Fragmentation | - | - | |
| | Abrasion | 0.47 | 0.08,2.89 | 0.4 |
| | Ambient | - | - | |
| | Warming | 0.54 | 0.11,2.70 | 0.4 |
| | Abrasion × Warming | 3.6 | 0.33,38.9 | 0.3 |
| | Fragmentation | - | - | |

| | | | | |
|---|---|---|---|---|
| Corallite Regeneration | Abrasion | 0.33 | 0.09, 1.25 | 0.1 |
| | Ambient | - | - | |
| | Warming | 0.43 | 0.12, 1.55 | 0.2 |
| | Abrasion $\times$ Warming | NA | NA | NA |

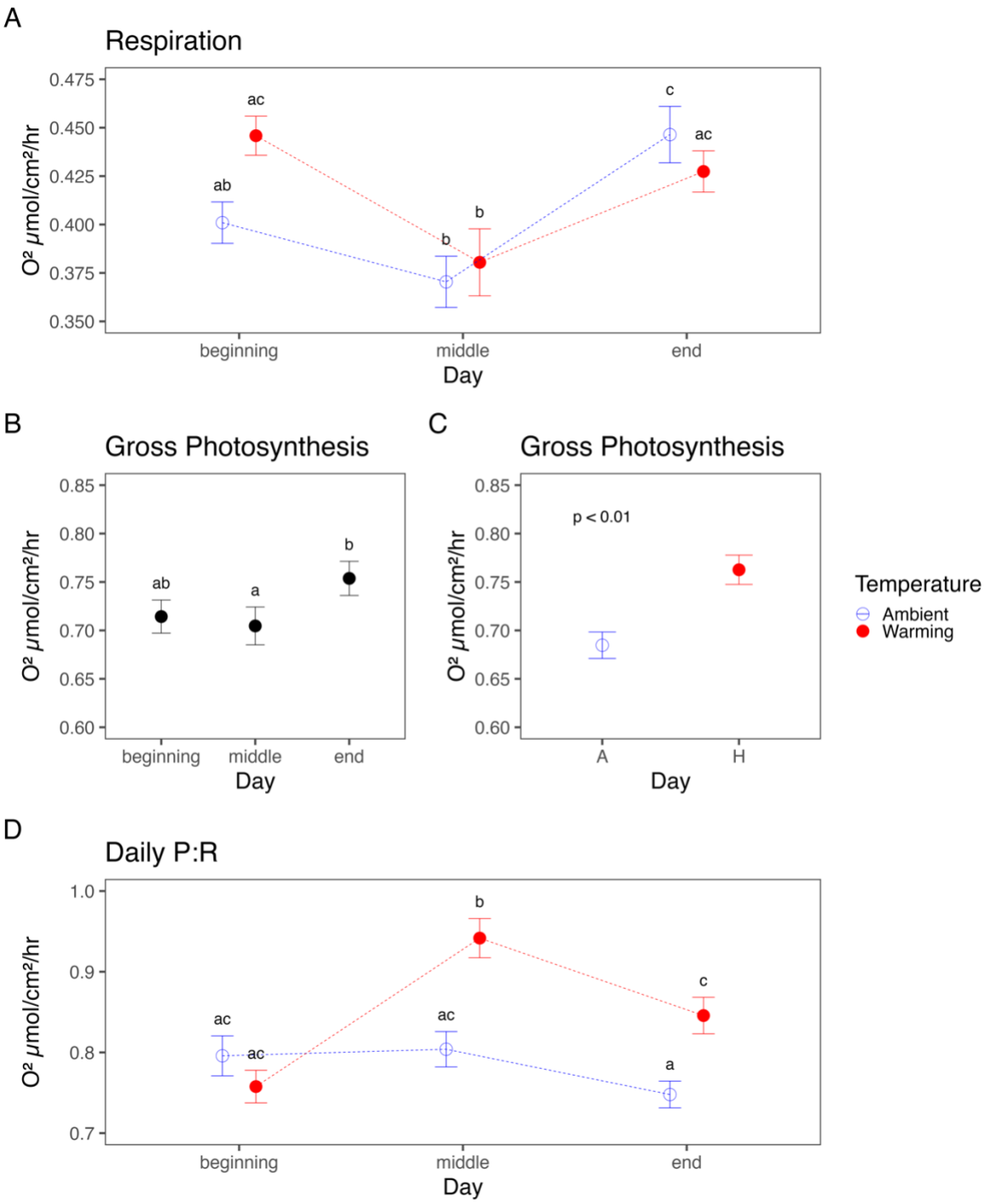


Figure 3. Average A) respiration rates, B/C) gross photosynthesis rates, and D) daily P:R from respirometry trials during the beginning (day 1), middle (day 10), and end (day 19) of regeneration. Average rates in plots A & D are subset by ambient (blue, open circles) and warming (red, closed circles) temperatures pooled across injury type because there was no significant effect or interactive effects of injury with temperature or time. Average rates in plot

B are pooled across injury type and temperature and in plot C pooled across injury type and time because there were significant main effects of temperature and time and no significant effect or interactive effects of injury with temperature or time. Bars around circles are standard errors. Letters show statistically significant differences based on estimated marginal means from linear mixed effects models with injury, temperature, time (all categorical), and all their interactions.

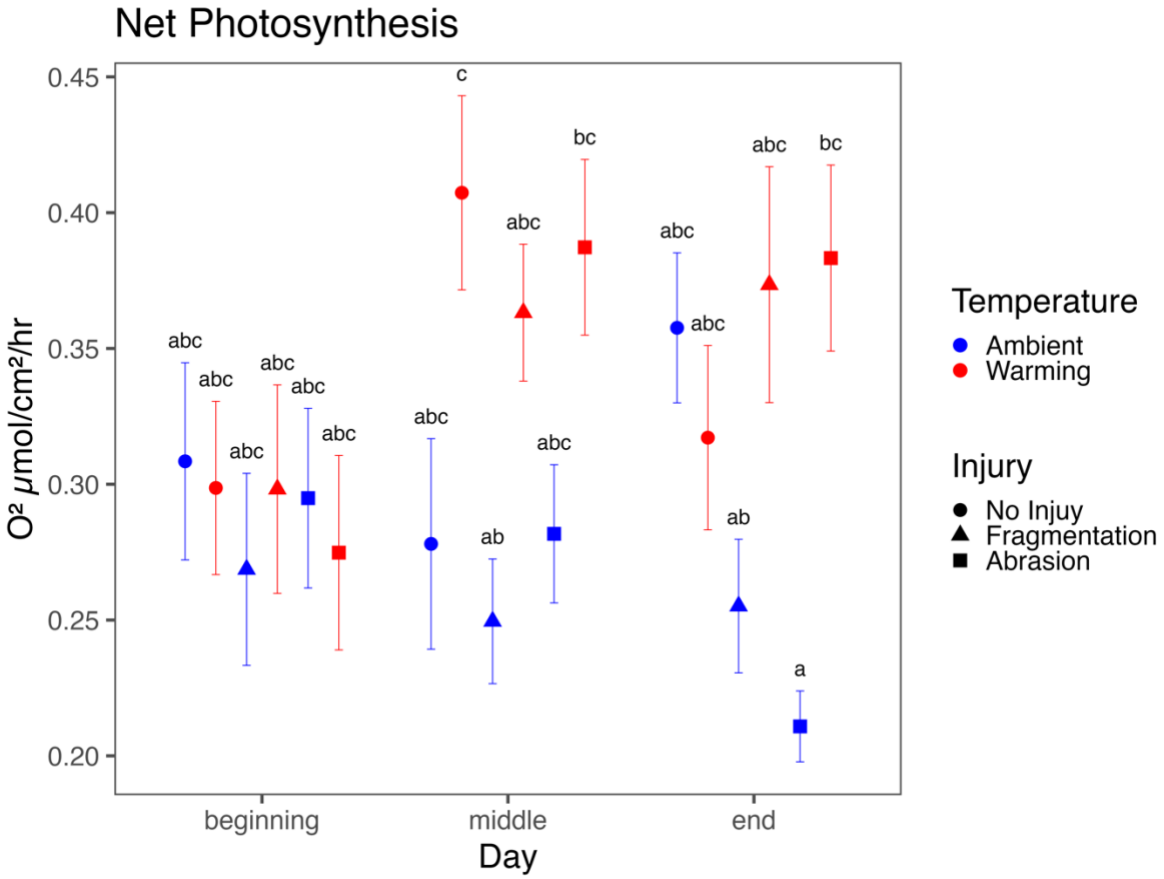


Figure 4. Average rates of net photosynthesis from respirometry trials during the beginning (day 1), middle (day 10), and end (day 19) of regeneration. Average rates are subset by ambient (blue) and warming (red) temperatures and injuries: no injury (circle), fragmentation (triangle), abrasion (square). Bars around circles are standard errors. Letters show statistically significant differences based on estimated marginal means from linear mixed effects models with injury, temperature, time (all categorical), and all their interactions.

Table 3. ANOVA tables of four linear mixed effects models for net photosynthesis, respiration, gross photosynthesis, and daily P:R using Satterthwaite's approximation for degrees of freedom. The models had individual and parental colony as random effects and

fixed effects of temperature (ambient and warming), injury (no injury, fragmentation, or abrasion), and time (beginning (day 1), middle (day 10), and end (day 19)). Effects of temperature, injury, and time were fixed and fully crossed.

| Variable | Effect | SS | Mean SS | d*f* | DenDF | *F* | *p* |
|---|---|---|---|---|---|---|---|
| Net Photosynthesis | Injury | 0.027 | 0.013 | 2 | 61.281 | 1.311 | 0.277 |
| | Temperature | 0.160 | 0.160 | 1 | 61.266 | 15.632 | **<0.001** |
| | Time | 0.051 | 0.026 | 2 | 130.000 | 2.516 | 0.085 |
| | Injury × Temperature | 0.025 | 0.012 | 2 | 61.323 | 1.210 | 0.305 |
| | Injury × Time | 0.013 | 0.003 | 4 | 130.000 | 0.325 | 0.861 |
| | Temperature × Time | 0.127 | 0.064 | 2 | 130.000 | 6.228 | **<0.01** |
| | Injury × Temperature × Time | 0.114 | 0.028 | 4 | 130.000 | 2.784 | **0.029** |
| Respiration | Injury | 0.003 | 0.002 | 2 | 61.334 | 0.708 | 0.497 |
| | Temperature | 0.001 | 0.001 | 1 | 61.322 | 0.501 | 0.482 |
| | Time | 0.149 | 0.075 | 2 | 130.001 | 31.889 | **<0.0001** |
| | Injury × Temperature | 0.004 | 0.004 | 2 | 0.004 | 0.811 | 0.449 |
| | Injury × Time | 0.006 | 0.002 | 4 | 130.001 | 0.645 | 0.631 |
| | Temperature × Time | 0.037 | 0.018 | 2 | 130.001 | 7.809 | **<0.001** |
| | Injury × Temperature × Time | 0.003 | 0.001 | 4 | 130.001 | 0.361 | 0.836 |
| Gross Photosynthesis | Injury | 0.037 | 0.018 | 2 | 61.246 | 1.574 | 0.215 |
| | Temperature | 0.112 | 0.112 | 1 | 61.238 | 9.620 | **<0.01** |
| | Time | 0.098 | 0.049 | 2 | 130.000 | 4.230 | **0.017** |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Injury × Temperature | 0.021 | 0.011 | 2 | 61.265 | 0.916 | 0.405 |
| | Injury × Time | 0.029 | 0.007 | 4 | 130.000 | 0.620 | 0.649 |
| | Temperature × Time | 0.063 | 0.031 | 2 | 130.000 | 2.693 | 0.071 |
| | Injury × Temperature × Time | 0.092 | 0.023 | 4 | 130.000 | 1.973 | 0.102 |
| Daily P:R | Injury | 0.012 | 0.006 | 2 | 61.291 | 0.389 | 0.680 |
| | Temperature | 0.177 | 0.177 | 1 | 61.267 | 11.484 | **<0.01** |
| | Time | 0.362 | 0.181 | 2 | 130.000 | 11.750 | **<0.0001** |
| | Injury × Temperature | 0.032 | 0.016 | 2 | 61.492 | 1.034 | 0.362 |
| | Injury × Time | 0.006 | 0.001 | 4 | 130.000 | 0.092 | 0.985 |
| | Temperature × Time | 0.303 | 0.152 | 2 | 130.000 | 9.839 | **<0.001** |
| | Injury × Temperature × Time | 0.120 | 0.030 | 4 | 130.000 | 1.949 | 0.106 |

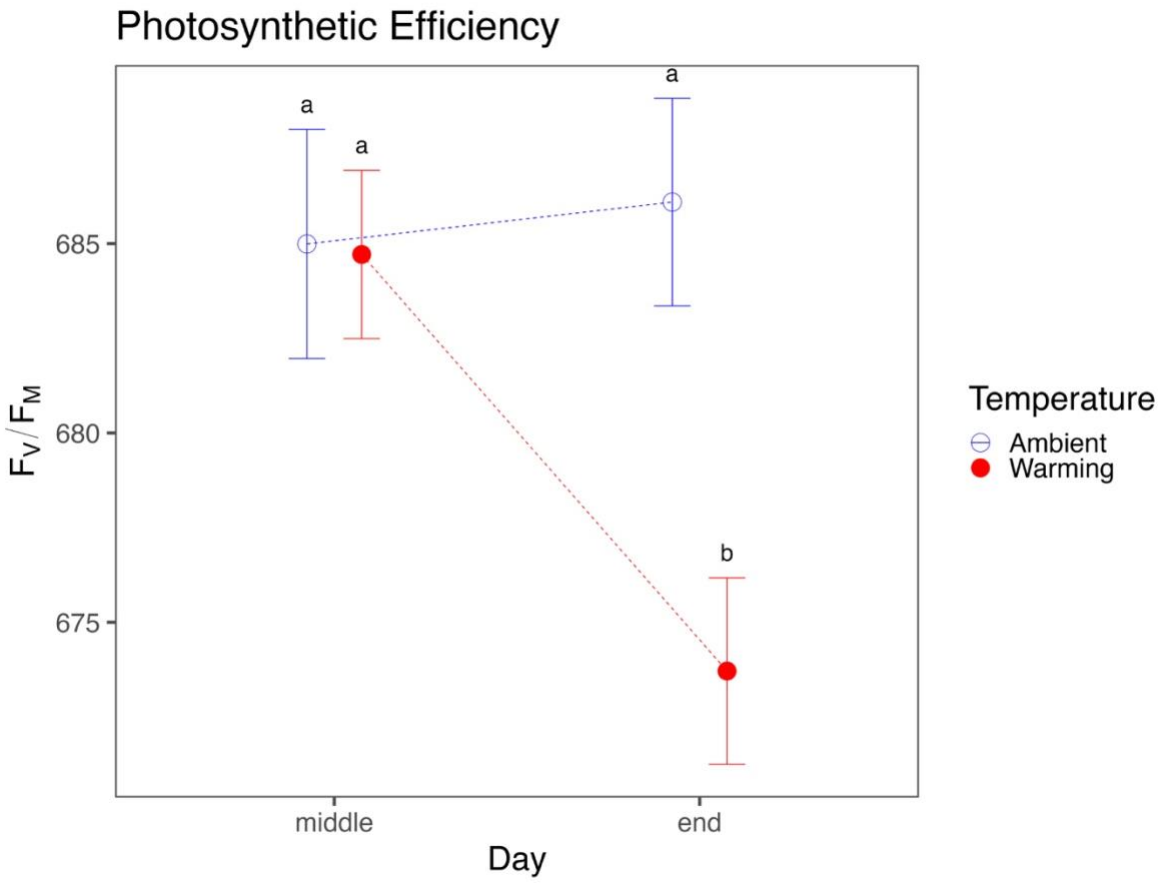


Figure 5. Average photosynthetic efficiency ($F_v/F_m$) at middle and end of regeneration. Average $F_v/F_m$ values are subset by ambient (blue, open circles) and warming (red, closed circles) temperatures, pooled across injury type because there was no significant effect or interactive effects of injury with temperature or time. Bars around circles are standard errors. Letters show statistically significant differences based on estimated marginal means from linear mixed effects models with injury, temperature, time (all categorical), and all their interactions.

Table 4. ANOVA tables of a linear mixed effects model for photosynthetic efficiency using Satterthwaite's approximation for degrees of freedom. The model had parental colony as a random effect and fixed effects of temperature (ambient and warming), injury (no injury, fragmentation, or abrasion), and time (beginning (day 1), middle (day 10), and end (day 19)). Effects of temperature, injury, and time were fixed and fully crossed.

| Variable | Effect | SS | Mean SS | d*f* | DenDF | *F* | *p* |
|---|---|---|---|---|---|---|---|
| Photosynthetic Efficiency | W | 54.75 | 27.37 | 2 | 61.78 | 0.143 | 0.867 |
| | T | 1056.67 | 1056.67 | 1 | 61.757 | 5.506 | **0.022** |
| | I | 905.91 | 905.91 | 1 | 65 | 4.72 | **0.033** |
| | W × T | 1094.68 | 547.34 | 2 | 61.869 | 2.852 | 0.065 |
| | W × I | 212.69 | 106.34 | 2 | 65 | 0.554 | 0.577 |
| | T × I | 1257.11 | 1257.11 | 1 | 65 | 6.55 | **0.013** |
| | W × T × I | 273.02 | 136.51 | 2 | 65 | 0.711 | 0.495 |

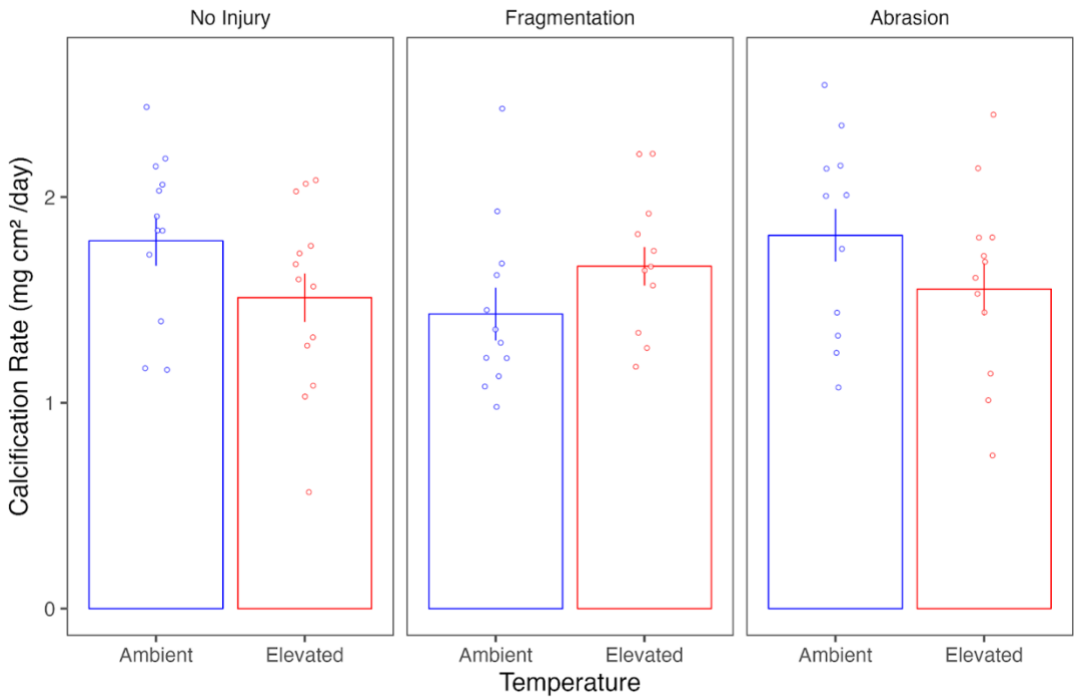


Figure 6. Average coral calcification rates (mg $cm^{-2}$ $day^{-1}$) at ambient (blue) and elevated (red) temperatures for uninjured, fragmented, and abraded corals. Bars represent standard errors.

# APPENDIX

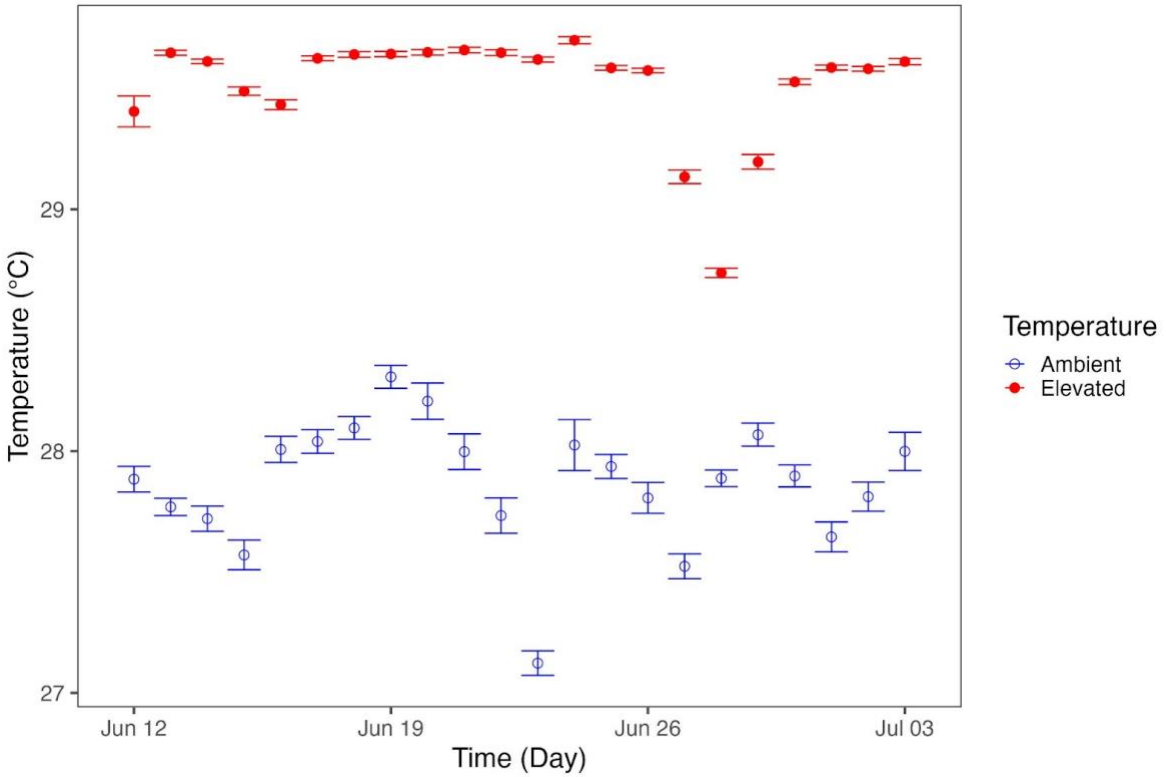


Figure A1. Temperature of experimental aquaria throughout the study period. Points are daily mean temperatures for ambient (blue, open circles) and elevated (red, closed circles) temperature treatments. Bars around points are standard errors.

Table A1. ANOVA table of a linear mixed effects model for calcification rate using Satterthwaite's approximation for degrees of freedom. The model had parental colony as a random effect and fixed effects of temperature (ambient and warming) and injury (no injury, fragmentation, or abrasion). Effects of temperature and injury were fixed and fully crossed.

| Variable | Effects | SS | Mean SS | d*f* | DenDF | *F* | *P* |
|---|---|---|---|---|---|---|---|
| Calcification Rate | W | 0.225 | 0.112 | 2 | 62.183 | 0.661 | 0.52 |
| | T | 0.187 | 0.187 | 1 | 62.184 | 1.096 | 0.299 |
| | W × T | 0.943 | 0.943 | 2 | 62.461 | 2.77 | 0.07 |