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Positive Interactions Between Corals and Damselfish Increase Coral Resistance to
Temperature Stress

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ABSTRACT

By the century's end, many tropical seas will reach temperatures exceeding most coral species' thermal tolerance on an annual basis. The persistence of corals in these regions will therefore depend on their abilities to tolerate recurrent thermal stress. Although ecologists have long recognized that positive interspecific interactions can ameliorate environmental stress to expand the realized niche of plants and animals, coral bleaching studies have largely overlooked how interactions with community members outside of the coral holobiont shape the bleaching response. Here, we subjected a common coral, *Pocillopora grandis*, to 10 days of thermal stress in aquaria with- and without the damselfish *Dascyllus flavicaudus* (yellowtail dascyllus), which commonly shelter within these corals, to examine how interactions with damselfish impacted coral thermal tolerance. Corals often benefit from nutrients excreted by animals they interact with and prior to thermal stress, corals grown with damselfish showed improved photophysiology (F_v/F_m) and developed larger endosymbiont populations. When exposed to thermal stress, corals with fish performed as well as control corals maintained at ambient temperatures without fish. In contrast, corals exposed to thermal stress without fish experienced photophysiological impairment, a more than 50% decline in endosymbiont density, and a 36% decrease in tissue protein content. By the end of the experiment, thermal stress caused average calcification rates to decrease by over 80% when damselfish were absent but increase nearly 25% when damselfish were present. Our study indicates that damselfish-derived nutrients can increase coral thermal tolerance and are consistent with the Stress Gradient Hypothesis, which predicts that positive interactions become increasingly important for structuring communities as environmental stress increases. Because warming of just a few degrees can exceed corals' temperature tolerance to trigger bleaching and mortality, positive interactions could play a critical role maintaining some coral species in warming regions until climate change is aggressively addressed.

INTRODUCTION

Positive interactions among species play key roles in structuring ecological communities (Brooker et al., 2008; Palmer, Pringle, Stier, & Holt, 2015; Renzi, He, & Silliman, 2019). Benefits of interspecific positive interactions include provisioning nutrients (Smith & Smith, 2011), protection from predators (Heil & McKey, 2003), stress amelioration (Callaway et al., 2002), and increased reproductive output and dispersal (Schupp, Jordano, & Gómez, 2010). Importantly, the outcomes of these interactions often depend on environmental context. The Stress Gradient Hypothesis predicts that the prevalence and importance of positive interactions should increase with environmental stress (Bertness & Callaway, 1994; Bruno, Stachowicz, & Bertness, 2003; He, Bertness, & Altieri, 2013). This prediction has been validated in terrestrial and marine communities, where competitors become facilitators under harsh conditions (e.g. Callaway & Walker, 1997; Crotty & Bertness, 2015), as well as in numerous symbiotic interactions where the strength and benefits of mutualisms depend on the local conditions where they occur (Bronstein, 1994; Shantz, Lemoine, & Burkepile, 2016). For example, mycorrhizal fungi can improve plant growth by providing limiting nutrients to plants (Marschner & Dell, 1994) but under extreme stress events like droughts or cold-snaps, mycorrhizal fungi's effects on gas exchange, stomatal conductance, and antioxidant enzyme activity become critical for plant survival (Augé, 2000; Duc, Csintalan, & Posta, 2018; Pedranzani et al., 2016). Thus, as global change generates stronger and more frequent stress events (Lough, Anderson, & Hughes, 2018; Pokhrel et al., 2021; Wang et al., 2019), positive interactions will become increasingly important for shaping the performance and survival of many species.

Coral reefs exist because of the mutualistic relationship between coral animals and their endosymbiotic algae from the family Symbiodiniaceae (LaJeunesse et al., 2018). These endosymbionts translocate products from photosynthesis to their coral hosts, providing most of the energy required by the coral (Muscatine, McClorskey, & Marian, 1981). In return, the

endosymbionts receive limiting nitrogen (N) and phosphorus (P), in a classic nutrient-exchange mutualism (Grover, Maguer, Allemand, & Ferrier-Pagès 2003; Godinot, Houlbreque, Grover, & Ferrier-Pagès 2011; Pernice et al., 2012). However, warming of just a few degrees can exceed corals' temperature tolerance, disrupting the symbiosis between corals and their endosymbiotic dinoflagellates and causing expulsion of the endosymbionts in a phenomenon known as "coral bleaching" (Brown, 1997). Bleached corals cannot maintain a positive energy balance through photosynthesis (Cunning, Muller, Gates, & Nisbet, 2017) and consequently often succumb to starvation and die if bleaching is prolonged (Anthony, Connolly, & Hoegh-Guldberg, 2007; van der Zande et al., 2020). Troublingly, climate change and rising ocean temperatures are making bleaching events more frequent and intense, with most tropical regions likely to experience annual coral bleaching that could extirpate thermally sensitive species by the late 21st century (UNEP, 2020; van Hooidonk et al., 2016). Accordingly, positive interactions that help corals tolerate or survive temperature stress could become critical for preserving the foundation species that maintain tropical reef communities.

In addition to the mutualism with endosymbionts, corals engage in a host of positive interactions with fishes and invertebrates that reside in and around them. These 'exosymbionts' gain shelter by residing in coral colonies and, in turn, can provide benefits to corals that include nutrient recycling, sediment removal, and protection from predators and competitors (Glynn, 1987; Meyer & Schultz, 1985; Holbrook & Schmitt, 2002; Stewart, Holbrook, Schmitt, & Brooks, 2006). For example, many planktivorous damselfishes from the family Pomacentridae gain protection from predators by sheltering in the interstitial spaces of branching corals (Holbrook & Schmitt, 2002; Schmitt & Holbrook, 2007; Pratchett, Hoey, & Willson, 2016) and excretion from these damselfish provides limiting nutrients, including ammonium (NH_4^+) and P, that can enhance coral growth (Holbrook, Brooks, Schmitt, & Stewart, 2008; Holbrook, Schmitt & Brooks, 2011). Corals that are enriched with NH_4^+ also often have increased reserves of proteins, lipids,

and carbohydrates (Ezzat, Maguer, Grover, & Ferrier-Pagès, 2015). When thermal stress occurs, corals with greater reserves of these nutritional macromolecules are more likely to survive the temporary loss of their endosymbionts (Anthony et al., 2007; Ezzat et al., 2019; Rodrigues & Grottoli, 2007). Accordingly, fish-derived nutrients could improve coral's energetic status and help them survive bleaching, greatly increasing the importance of positive interactions between damselfish and corals during thermal stress events.

In addition to potentially helping corals survive once they have bleached, there is increasing evidence that fish-derived nutrients could help corals resist bleaching in the first place. While the exact processes through which temperature-stress drives coral bleaching remain unresolved, compelling evidence is emerging that it is not always temperature *per se* that causes bleaching. Instead, limitation of resources that corals need to maintain their metabolism, scavenge reactive oxygen species (ROS), and mitigate photoinhibition may induce bleaching (Ezzat, Maguer, Grover, & Ferrier-Pagès, 2016; Morris, Voolstra, Quigley, Bourne, & Bay, 2019; Pogoreutz et al., 2017; Wooldridge, 2009). For instance, increasing productivity as temperatures rise may cause P limitation and make corals more vulnerable to ROS production and cellular damage (Rosset, Wiedenmann, Reed, & D'Angelo, 2017; Wiedenmann et al., 2013). Similarly, in lab-based studies corals supplemented with a continuous dose of 3 μM NH_4^+ during temperature-stress were able to maintain pigments necessary for photosynthesis, photoprotection, and ROS scavenging, and resist bleaching (Béraud, Gevaert, Rottier, & Ferrier-Pagès, 2013; Fernandes de Barros Marangoni, Ferrier-Pagès, Rottier, Bianchini, & Grover, 2020). Likewise, in Moorea, French Polynesia, chronic low-level nutrient enrichment improved coral thermal performance on the relatively oligotrophic fore reef habitat (Becker *et al.*, 2021). Thus, fish excretion could support bleaching resistance by providing corals with a continuous source of otherwise limiting NH_4^+ and P to enhance coral thermal tolerance.

Despite the well-documented potential for fish-derived nutrients to affect coral thermal tolerance, only a single study to date has examined whether fish presence influences coral bleaching (Chase, Pratchett, Frank, & Hoogenboom, 2018). This study found that *Seriatopora hystrix* colonies harboring damselfish maintained higher symbiont densities than colonies without damselfish during a natural bleaching event. However, when this study took place, the 2016 bleaching event was one of the most severe on record and by the end of the study, all the colonies studied had bleached regardless of fish occupancy and >90% died. Accordingly, while damselfish appear unable to increase *S. hystrix* survival during extreme marine heatwaves, it remains unclear how other coral species may respond or whether fishes influence coral performance, survival, or recovery under the more moderate bleaching conditions that are expected to occur annually in the near future.

We tested whether positive interactions between damselfish and corals can alleviate the deleterious impacts of thermal stress on corals. We kept branches of antler coral, *Pocillopora grandis*, (formerly *P. eydouxi*; Hoeksema & Cairns, 2021) in aquaria with and without the damselfish *Dascyllus flavicaudus* (yellowtail dascyllus) that often shelters within these corals on the reef. We tracked changes in the physiological status of corals through two weeks of acclimation at ambient water temperatures (27.5°C) with or without fish, followed by ten days of temperature stress at 30.5°C, and ten days of recovery at 27.5°C. Our study addresses three basic questions. First, how do damselfish-derived nutrient subsidies impact coral physiology? Second, how do these nutrient subsidies influence the response of corals to thermal stress? And third, how do they impact coral recovery following thermal stress? We hypothesized that when damselfish were present, corals would benefit from fish-derived nutrients and maintain photophysiological function during thermal stress for longer than corals kept without fish. As a result, we predicted that corals that harbored damselfish would experience a slower decline in symbiont densities during thermal stress and avoid the need to catabolize tissue to meet their

energetic requirements, resulting in higher reserves of protein in corals associated with fishes. Finally, we predicted that after thermal stress subsided, association with damselfish and their nutrient subsidies would significantly accelerate the recovery of symbiont populations and coral energy reserves, resulting in greater survival and a more rapid recovery of growth rates in corals associated with damselfish.

METHODS

Coral Collection and Experimental Setup

In August of 2016, we identified six mature *P. grandis* colonies (minimum diameter = 20 cm) at 10 m depth on the north shore fore reef of Moorea, French Polynesia (17° 30' S, 149° 50' W) that were separated by at least 10 m and did not house any resident damselfish. From each parent colony, we collected thirteen, 10 cm long branch fragments. These individual fragments were secured to nylon line and transported to 5 m depth, where they were suspended ~20 cm above the substrate for ten days to recover and acclimate to higher light levels. After ten days of recovery in the field, we brought the fragments to shore in coolers filled with seawater. On shore we immediately utilized one fragment from each parent colony for initial physiological measurements (see below). The remaining 12 fragments from each parent colony were split into two groups of six and hung in twelve, 75 l experimental aquaria, with each aquarium containing six fragments from a single parent (Figure 1).

Each aquarium was equipped with a 416 lph submersible pump to circulate water and provided with continuous flow of ambient seawater from the reef at ~8 lph. In half of the tanks, we added two yellowtail dascyllus captured from the reef by divers with hand nets (mean weight \pm SE = 22.3 \pm 4 g per individual). We placed a small PVC structure at one end of every aquarium to provide refuge for the fish and control for any effects of structure in tanks without

fish. Fragments of *P. grandis* were suspended near the surface on the opposite end of each aquarium to prevent the fish from sheltering among the corals, thereby minimizing potential differences in waterflow and mass transfer associated with fish movement that may impact bleaching resistance, thereby helping to isolate the effect of nutrients. Every morning, afternoon, and evening throughout the experiment, flow-through seawater to the tanks was stopped for 30 minutes and 1.5 g of dry flake-food (TetraMarine Saltwater Flakes, Tetra US, Blacksburg VA, USA) was added to every tank, regardless of fish occupancy. After 15 minutes, we siphoned any remaining food from the tanks and water flow was resumed.

The coral fragments were maintained at 27.5°C for two weeks with or without damselfish present. After two weeks of acclimation, we increased the temperature in half of the aquaria over 24 hours to a final temperature of 30.5°C, which is roughly a full degree above bleaching thresholds in Moorea (Pratchett, McCowan, Maynard, & Heron, 2013). This design created 3 aquaria maintained under each of four treatment combinations: 1) 27.5°C – Fish, 2) 27.5°C + Fish, 3) 30.5°C – Fish, and 4) 30.5°C + Fish. Coral fragments were maintained at either 27.5°C or 30.5°C for 10 days, after which we lowered the temperature in the heated aquaria back to 27.5°C and monitored coral recovery for an additional 10 days (Figure 1). Water temperatures were recorded every ten minutes in each aquarium throughout the experiment with Apex temperature probes (Neptune Systems, Morgan Hill CA, USA; Figure S1). All aquaria were covered with shade cloth and maintained outdoors under natural sunlight during the day, providing a peak midday light intensity of $\sim 650 \mu\text{M m}^{-2} \text{s}^{-1}$ in the aquaria as measured with a LiCor LI-192 light sensor (Li-Cor Biosciences, Lincoln NE, USA), which is similar to peak midday irradiance recorded underwater at the collection site (Carpenter, 2019). Each night the experimental array was tented with a large plastic tarp to prevent freshwater inundation from rain.

Seawater Nutrient Measurements

To determine how the yellowtail dascyllus impacted nutrient levels in our experimental aquaria we measured NH_4^+ , nitrate (NO_3^-), and soluble reactive phosphorus (SRP) in every aquarium approximately weekly throughout the experiment (See Supplemental Materials for details). We also measured baseline excretion rates from ten yellowtail dascyllus that were captured from the reef following methodology outlined by Schaus et al. (1997) as modified by White et al. (2009). Briefly, fish were captured by divers using hand nets, brought back to the lab, and held in aquaria for 24 hours without feeding. After 24 h, each fish was weighed to the nearest 0.1 g and placed in a sterile ziplock bag filled with 1 l of filtered seawater that had been passed through a 0.7 μm glass fiber filter. Ten bags containing fish, along with 2 control bags filled with only filtered seawater were placed in a large water bath maintained at ambient temperature in flow-through seawater for a 30-minute incubation. At the start and end of the incubations, water samples were collected from each bag to measure NH_4^+ and SRP, which are the primary forms of N and P excreted by fishes. Excretion rates were calculated based on the difference in nutrient concentration before and after incubations, using the empty control bags to account for background changes in nutrient levels. Because fishes could also benefit corals by providing particulate organic matter (POM) that corals could feed on, in weeks two and four we quantified POM in each of the aquaria by filtering 2 l of water through individually weighed, pre-combusted 0.7 μm glass fiber filters. We then dried the filters to a constant weight at 60°C and reweighed each to measure total particulate matter. After weighing, we combusted the filters in a muffle furnace at 500°C for four hours to burn off organic matter and reweighed them, using the difference in mass as a proxy for POM.

Coral Physiological Measurements

To assess how fishes influenced coral physiology and thermal tolerance, we measured the dark-adapted quantum yield, symbiont density, and tissue protein content of fragments throughout the experiment. Measurements were taken on Day 1 when the corals were brought

to shore, prior to acclimation with damselfish, and on Day 14 after two weeks of acclimation with or without damselfish present. Temperatures were then increased in half of the tanks over 24 hours to 30.5°C, and subsequent measurements made on Days 17, 20, and 24, corresponding to 3, 6, and 10 days of temperature stress, respectively. After completing our measurements on Day 24, we lowered the temperatures in the heated aquaria back to 27.5°C over 24 hours and collected final measurements on Day 34, after 10 days of recovery.

At each sampling time point we haphazardly selected one fragment from each tank for sampling. We used PAM fluorometry to measure the maximum dark-adapted quantum yield of PSII (F_v/F_m) after 30 minutes of dark acclimation (see Supplemental Materials for detailed fluorometry methodology). After taking fluorescence measurements, we removed the tissue from each fragment with a waterpik and centrifuged the resulting tissue slurry at 5,000xG for 5 minutes to separate the coral tissue and Symbiodineaceae. Symbiont pellets were resuspended in 1 ml filtered seawater while the coral tissue was rapidly frozen by submersing the sample tubes in -80°C acetone for 5 minutes, followed by storage at -80°C for protein analysis. Symbiont density of each fragment was calculated from eight replicate counts on a Neubauer hemocytometer and normalized to the fragments skeletal surface area, as determined by wax dipping (Stimson and Kinzie, 1991). Additionally, DNA was extracted from symbiont samples collected at the initial and final timepoints using a Qiagen DNeasy Powersoil kit (Qiagen) following manufacturers guidelines and sequenced for ITS2 profiling through the SymPortal framework (Hume et al., 2019; See Supplemental Material for detailed methods). To determine protein content of coral tissue, we lyophilized the frozen coral tissue at -80°C to a constant weight. Next, the freeze-dried tissue was homogenized and diluted in 0.5 ml of PBS buffer, vortexed for 20 min, and immersed in a sonicating water bath for an additional 20 min. The solution was then filtered through a 0.2 µm filter and the resulting supernatant analyzed on a Millipore Direct Detect infrared spectrometer against a bovine serum albumin standard (EMD

Millipore, Billerica MA, USA). Finally, we measured differences in coral calcification rates, as determined by changes in buoyant weight (Davies 1989), for the fragments collected on the final day of thermal stress and after the 10 day recovery period. To minimize handling stress, no measurements of buoyant weight were taken when fragments were brought to shore so growth rates were not available for the acclimation phase. We chose calcification as a proxy for coral performance as it is an energetically expensive process that is tightly coupled to Symbiodiniaceae's ability to provide photosynthate to the coral host (Gattuso et al., 1999). Furthermore, calcification is a critical determinant of a coral's ability to occupy space, reinforce its skeleton, and produce reef habitat (Kuffner et al. 2018), making it a relevant metric for the resumption of important ecosystem functions on coral reefs following bleaching. Detailed methodology for our physiological sampling is described in the Supplemental Materials section.

Analyses

Differences in NH_4^+ , NO_3^- , SRP, and the total N:P and NH_4^+ :P ratios between the treatments were assessed via mixed effects models that included temperature and fish presence as fixed effects and random effects for aquarium ID and measurement date. In all five models, nutrient concentration was log transformed to normalize the distribution of the residuals. Even after transformation the residual variance between treatments in our NO_3^- , SRP analyses was significantly higher when fishes were present. Therefore, while the differences between values were large (see Results), significance at the $\alpha = 0.05$ level should be interpreted with caution.

To determine how damselfish influenced coral physiology prior to thermal tolerance, we used analysis of covariance (ANCOVA) to test for differences in F_v/F_m , Symbiodiniaceae density (hereafter symbiont density), and tissue protein content in coral fragments after the acclimation period. Each ANCOVA included fish presence as a fixed factor and measurements of the respective response metric taken from each of the parent colonies on Day 1 as a covariate to

account for differences between initial condition. When significant differences were detected, we used Tukey's HSD post hoc tests to test for differences between treatments.

To analyze the effects of damselfish on corals during thermal stress, we used planned contrasts to examine changes in each metric within treatments through time and between treatments on the final day of thermal stress. To do so, we used mixed-effects models that included yield, symbiont density, or protein content as the response variable and temperature, damselfish presence, and day as fixed factors. Aquarium ID and parent colony (i.e., the putative genotype) were included as random effects to account for covariance within aquaria and genetically conserved responses to thermal stress. We used pairwise comparisons with Benjamini-Hochberg corrections for false-discovery rates to test for differences from initial measurements taken immediately prior to initiating thermal stress (Day 14) versus subsequent time points within each treatment, and between treatments on the final day of thermal stress (Day 24).

To assess coral recovery after thermal stress we compared each physiological parameter between Days 14 and 34, under the assumption that parameters which had recovered would not significantly differ between the end of acclimation and recovery. Initial attempts to use multifactorial analyses to assess recovery led to over-parameterization of several models. Therefore, we instead used Welch's paired t-tests to compare post-acclimation and post-recovery measurements of F_v/F_m , symbiont density, and protein content within each treatment.

Finally, at the end of both the thermal stress and recovery periods, we used mixed-effects models similar to those previously described to determine how temperature stress impacted coral growth rates during and after thermal stress in the presence and absence of damselfish. These models used the change in fragment buoyant weight corrected for surface

area as a proxy for growth. Fish presence and temperature treatment were used as interacting fixed-effects and parent colony was again included as a random effect.

All analyses were conducted in R v4.01 (R CoreTeam, 2021). Mixed-effects models were conducted using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) and planned contrasts were conducted with the emmeans package (Lenth, 2021). Reported values are given as means \pm 1 SE unless otherwise noted.

RESULTS

Seawater Nutrients

On average, yellowtail dascyllus excretion produced $1.15 \pm 0.07 \mu\text{M NH}_4^+ \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ and $0.05 \pm 0.01 \mu\text{M P} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. As a result, damselfish significantly increased nitrogen and phosphorus availability throughout the experiment, but temperature had no effect on nutrient levels. Differences in N availability were driven by changes in NH_4^+ , which averaged $2.20 \pm 0.42 \mu\text{M}$ (mean \pm SE) in aquaria when damselfish were present, versus $0.05 \pm 0.02 \mu\text{M}$ when damselfish were absent ($\chi^2_{(1)} = 61.28$, $p < 0.001$; Figure 2A). In contrast, NO_3^- concentrations did not differ between damselfish or temperature treatments (Figure 2B). Phosphorus levels were over twice as high when fishes were present (0.29 ± 0.04) versus absent (0.12 ± 0.01 ; $\chi^2_{(1)} = 17.28$, $p < 0.001$) with a marginally significant effect of temperature ($\chi^2_{(1)} = 2.94$; $p = 0.09$) and no interaction between the two (Figure 2C). As a result, the average N:P ratios did not statistically differ between treatments (Figure 2D). However, the ratio of $\text{NH}_4^+:\text{P}$ was ~20-fold higher when damselfish were present ($\chi^2_{(1)} = 64.06$, $p < 0.001$; Figure 2E). Particulate organic matter ranged from 4.9 to 15.7 mg l^{-1} but did not differ between temperature or damselfish treatments (Figure S2).

Effects of Fish Presence on Coral Physiology

We found that damselfish significantly influenced coral physiology before, during, and after thermal stress (Figures 3A, 4A, & 5A). Prior to thermal stress, the average F_v/F_m in coral fragments acclimated with damselfish was 0.70 ± 0.01 versus 0.64 ± 0.01 in corals held without damselfish ($F_{(1,9)} = 27.75$, $p < 0.001$; Figure 3B). Symbiont density followed a similar pattern, increasing nearly 20% when corals were acclimated with damselfish ($F_{(1,9)} = 15$, $p = 0.004$; Figure 4B). Analysis of the Symbiodiniaceae community composition based on next-generation sequencing of the ITS2 region indicated that all of the corals associated with symbionts from the genus *Cladocopium* and ITS2 type profiles were dominated by variants of type C42, recently identified as an ITS2 variant of *C. latusorum* (Turnham et al., 2021; Figures S2 & S3). Coral tissue protein content also trended upward from 503.3 ± 16.9 mg·g⁻¹ dry weight when damselfish were absent to 584.8 ± 37.8 mg·g⁻¹ when damselfish were present, however this change was not statistically significant ($F_{(1,9)} = 3.45$; $p = 0.09$; Figure 5B).

The presence of fish also impacted coral physiology during temperature stress. For F_v/F_m , there was a significant interaction between temperature, fish presence, and time ($\chi^2_{(3)} = 11.65$, $p = 0.009$). Corals kept at ambient temperatures maintained a constant F_v/F_m throughout the thermal stress period, with the average quantum yield slightly higher when damselfish were present (0.68 ± 0.004) versus absent (0.65 ± 0.006). In heated aquaria, F_v/F_m declined with the onset of thermal stress but the severity of decline was dependent on fish presence. When damselfish were present F_v/F_m declined initially by ~4.6% ($p = 0.009$ and 0.003 for Day 14 vs. Day 17 and Day 14 vs. Day 20 respectively) but recovered to pre-stress levels by the tenth day of thermal stress (Day 14 vs. Day 24 $p = 0.19$; Figure 3A). In contrast, when damselfish were absent the decline in F_v/F_m in heated aquaria was over 2X greater than when they were present and F_v/F_m remained significantly below pre-stress levels throughout the thermal stress period (Day 14 vs. Day 24 $p < 0.001$). As a result, on the final day of thermal stress F_v/F_m in heated aquaria without damselfish was significantly lower than all other treatments (Figure 3C).

We also observed significant interactive effects of damselfish and temperature ($\chi^2_{(1)} = 7.49$, $p = 0.006$), damselfish and time ($\chi^2_{(3)} = 10.33$, $p = 0.02$), and temperature and time ($\chi^2_{(3)} = 8.03$, $p = 0.05$) on symbiont density throughout the thermal stress period. Here, average symbiont density was higher when damselfish were present ($\sim 650,000 \pm 16,000$ cells cm^{-2}) versus absent ($\sim 415,000 \pm 29,000$ cells cm^{-2}). This pattern was driven almost entirely by the decline in symbiont density in corals in heated aquaria kept without damselfish. In these heated aquaria, average symbiont densities showed a marginally significant decline of 30% over the first 3 days of thermal stress (Day 14 vs. Day 17; $p = 0.06$), and a significant decline of more than 50% by the 6th day of temperature stress (Day 14 vs. Day 20; $p < 0.001$) that remained throughout the thermal stress period (Day 14 vs. Day 24 $p < 0.001$). In contrast, pairwise comparisons indicated that symbiont densities were stable through time in all other treatments (Figure 4B). As a result, on the final day of thermal stress symbiont densities were significantly lower in heated aquaria without damselfish than in the other treatments (Figure 4C).

Protein content followed similar qualitative patterns as quantum yield and Symbiodiniaceae density (Figure 5A), with significant effects of damselfish ($\chi^2_{(1)} = 4.39$, $p = 0.04$), temperature ($\chi^2_{(1)} = 3.91$, $p = 0.05$), and time ($\chi^2_{(3)} = 12.64$, $p < 0.01$), and a marginally significant interaction between damselfish presence and temperature ($\chi^2_{(1)} = 3.53$, $p = 0.06$). Without the interaction term, the model indicated that coral protein content was on average $\sim 100 \text{ mg}\cdot\text{g}^{-1}$ dry tissue weight higher when damselfish were present but $60 \text{ mg}\cdot\text{g}^{-1}$ lower in thermally stressed corals. However, the marginally significant interaction term suggests that these responses were not additive and planned contrasts between treatments on Day 24 indicated that at the end of the thermal stress period, protein content was significantly lower in corals exposed to thermal stress without fish present than in those exposed to thermal stress with damselfish ($p = 0.03$) or kept at ambient temperatures both with and without damselfish ($p = 0.03$ and $p = 0.05$ respectively; Figure 5C).

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Ten days after thermal stress had ended, we found mixed evidence that the bleached corals from heated aquaria without damselfish had begun to recover. Dark-adapted quantum yield increased by ~3% over the recovery period and did not differ from measurements taken within the same treatment on Day 14 before thermal stress began (Welch's $t = 2.58$, $p = 0.097$; Figure 3D). However, symbiont density remained significantly lower than pre-stress levels (Day 14 vs. Day 34 Welch's $t = 5.43$, $p = 0.009$; Figure 4D) while protein content remained marginally lower (Day 14 vs. Day 34 Welch's $t = 2.73$, $p = 0.064$; Figure 5D). For all other treatments, there were no signs of bleaching and no differences in any measured physiological metrics between the end of the acclimation and recovery periods.

Effect of Fish Presence on Coral Growth

At the end of the thermal stress period we found significant differences in the growth rates of coral fragments between the treatments ($\chi^2_{(1)} = 4.33$, $p = 0.04$). Corals in both the 30.5 and 27.5°C treatments that were kept with damselfish grew on average 17.7 ± 4.21 and 18.6 ± 5.2 $\text{mg}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$ respectively, or 6- to 8-times faster than fragments that were subjected to thermal stress without fish present (Figure 6A). Similarly, corals maintained at ambient temperatures without fish grew nearly 12 $\text{mg}\cdot\text{day}^{-1}$ faster than the thermally stressed corals without fish, although this trend was not statistically significant (post hoc $p = 0.07$). By the end of the recovery period the difference in coral growth rates between treatments was even greater ($\chi^2_{(1)} = 4.6$, $p = 0.03$, Figure 6B). In the heated treatment without damselfish, one of the coral fragments developed a small dead spot at the top of the branch and the other fragments remained extremely pale. Coral growth in this treatment ceased, with average change in mass of -0.26 ± 2.48 $\text{mg}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$ that suggested that at least one fragment was experiencing skeletal dissolution over the recovery period. During the recovery period, fragments kept at ambient temperatures without damselfish continued to grow at an average rate of 10.63 ± 2.12 $\text{mg}\cdot\text{cm}^{-2}\cdot\text{day}^{-1}$, but due to high variability differences in growth rates were only marginally

significant between temperature treatments when damselfish were absent (post hoc $p = 0.06$). In contrast, both ambient and heated treatments with damselfish continued to grow significantly faster than corals from the heated treatment without fish (post hoc $p = 0.003$ and 0.002 respectively).

DISCUSSION

Here, we found that the positive interaction between damselfish and coral helped corals resist thermal stress. After only two weeks in the presence of damselfish, corals increased their photophysiological function and symbiont density and were able to maintain their symbiont populations, protein reserves, and growth rates through a subsequent ten-day period of temperature stress. In contrast, corals exposed to the same 3°C temperature increase without damselfish present experienced physiological impairment, began to bleach, and stopped growing. Thus, our study demonstrates that positive interactions between corals and damselfish can help corals tolerate heat-stress by delaying or preventing the onset of photo-physiological impairment and the breakdown of the coral-algal symbiosis.

Energy reserves are a critical determinant of corals' ability to survive and recover from bleaching (Anthony, Hoogenboom, Maynard, Grottoli, & Middlebrook, 2009; Rodrigues & Grottoli, 2007). We sought to understand whether corals in association with damselfish would be better equipped to survive bleaching and recover afterwards due to their greater energy reserves but were unable to fully explore bleaching and recovery because corals housed with damselfish did not bleach during our experiment. Instead, damselfish presence increased bleaching resistance and buffered associated corals from the negative effects of thermal stress. In contrast, without damselfish *P. grandis* experienced photoinhibition, symbiont loss, and a decline in tissue protein content. This decline in protein was likely driven by the inability of the corals to meet their energetic requirements through photosynthesis or feeding, necessitating catabolism of tissue to maintain metabolic function, which in turn can exacerbate bleaching

(Rädecker et al., 2021). Coral fragments that were kept with damselfish continued to meet their metabolic requirements, as evidenced by their stable protein content and positive rates of calcification throughout the experiment. Consequently, even if these colonies had eventually bleached under prolonged temperature stress, the delayed onset of tissue catabolism would likely allow them to survive longer than fragments exposed to similar stress without damselfish present, thereby increasing their chances of surviving until temperatures cooled.

Bleaching typically occurs after weeks of accumulated thermal stress (Kayanne, 2017), but we observed tissue paling and significant declines in symbiont density and protein content over just 10 days of temperature stress. The rapid response that we observed was likely due to the rate at which we heated aquaria for the thermal stress treatment (3°C over 24 hours). While corals in lagoons, tidepools, and other inshore environments can experience similar, or even more severe temperature fluctuations (Putnam & Edmunds, 2011), the fore reef in Moorea is unlikely to experience such rapid warming (Washburn, 2021). As a result, *P. grandis* from the fore reef may be poorly adapted to cope with rapid increases in temperature. However, acute heat stress assays that involve heating corals 3, 6, or even 9°C in just 3 hours have been shown to accurately predict thermal tolerance of corals as well as classic, long-term bleaching experiments (Voolstra et al. 2020). Thus, while the accelerated warming rate could have contributed to the rapid decline in coral performance that we observed when damselfish were absent, our results are still likely representative of true differences in thermal tolerance.

Mechanisms of Bleaching Resistance

Damselfish could improve bleaching resistance through several, non-exclusive mechanisms. First, damselfish sheltering in corals increase water flow and mass-transfer rates within the interstitial spaces of their host colonies (Garcia-Herrera, Ferse, Kunzmann, & Genin, 2017), which could alleviate bleaching by improving heat transfer (Stocking et al., 2018) or nutrient uptake (see below). However, our experimental fragments were suspended individually

in the water column, away from damselfish shelters, and turbulent flow was enhanced in all aquaria via submersible aquarium pumps, making it unlikely that differences in water motion contributed to the observed increase in thermal tolerance. Heterotrophic feeding on particulate organic matter (POM) could also have helped corals resist and survive bleaching by providing both an alternate energy source for bleached corals or a source of micronutrients like iron and zinc (e.g., Geesey, Alexander, Bray, & Miller 1984) that contribute to coral thermal tolerance (Ferrier-Pagès, Sauzéat, & Balter, 2018; Reich, Rodriguez, LaJeunesse, & Ho, 2020). Damselfish could therefore enhance coral thermal tolerance via egestion of POM that corals consume. While potentially important, this mechanism is also unlikely to explain the differences in thermal tolerance in our study since we found no differences in POM between aquaria with and without damselfish (Figure S2), although it is possible that additional POM was rapidly consumed by corals and our measurements missed the flux of this material. Accordingly, excretion of dissolved inorganic nutrients by damselfish remains the most important mechanism influencing the improved thermal tolerance in our study.

We found that yellowtail dascyllus produced both NH_4^+ and P at levels known to influence coral bleaching (e.g., Weidenmann et al., 2013, Beraud et al. 2013, Marangoni et al. 2020; Han et al., 2022), but discerning the relative role that these nutrients played in our study is challenging. If greater P availability had driven the increase in thermal tolerance, we would expect to have seen lower P levels and higher N:P ratios in heated treatments when damselfish were absent. Indeed, while SRP levels were ~40% lower in these heated treatments than in control aquaria (Figure 2C), likely due to increased uptake of P by coral under thermal stress (Godinot, Houlbreque, Grover, & Ferrier-Pagès 2011; Ezzat et al., 2016), there was no evidence that SRP ever became limiting. Although we did not measure dissolved organic phosphorus (DOP), which can be an additional pool of P for corals (Ferrier-Pagès et al. 2016), DOP requires costly upregulation of phosphatase enzymes that typically occurs only when P is

limiting (Jackson et al. 1989; Annis and Cook 2002; Weidenmann et al. 2013). Increased phosphatase production is unlikely in our experiment as SRP levels remained relatively high even without damselfish and average N:P ratios were similar across all treatments (Figure 2D), suggesting that P was never limiting. Instead, the low levels of NH_4^+ when damselfish were absent suggest that NH_4^+ was limiting, and that supplemental NH_4^+ from damselfish excretion likely conferred greater thermal tolerance to corals.

Ammonium is the preferred source of N for dinoflagellates like Symbiodineaceae and even at low concentrations, NH_4^+ can suppress NO_3^- uptake (Grover, Maguer, Allemand, & Ferrier-Pagès 2003). However, when NH_4^+ is limiting, Symbiodineaceae utilize NO_3^- as an alternate N source. The utilization of NO_3^- requires an energetically expensive reduction that results in lower rates of photosynthesis, reduced carbon translocation, and lower calcification rates in corals (Dagenais-Bellefeuille & Morse, 2013; Ezzat et al., 2015; Shantz & Burkepile, 2014). Furthermore, increased NO_3^- utilization can cause imbalances in coral redox status, resulting in increased levels of oxidative stress (de Barrow Marangoni et al. 2020) and, in field studies, increased bleaching susceptibility (Burkepile et al., 2020). In our study, low NH_4^+ availability when damselfish were absent likely caused symbionts to utilize NO_3^- that was abundant in the incoming seawater (Figure 2), thereby increasing oxidative stress and reducing energy transfer to the host. At ambient temperatures, this reduction in energy transfer would manifest as lower coral calcification rates and energy reserves, explaining the trend towards lower protein content and slower growth rates at the end of the acclimation period when damselfish were absent (Figures 5 & 6). As temperatures increase however, reduced carbon production and energy transfer could impair the host and symbiont's abilities to mitigate oxidative stress and repair the cellular damage that leads to coral bleaching, potentially explaining the greater thermal sensitivity. For example, energy-limited corals may have a reduced ability to upregulate resource-intensive protective mechanisms, like increasing

production of heat shock proteins, fluorescent proteins, and antioxidants, (Bollati et al., 2020; Downs et al., 2002; Fang et al., 1997). Energy limitation can also inhibit processes that prevent limitation of other resources hypothesized to drive bleaching like phosphatase activity to facilitate DOP hydrolysis and prevent P limitation (Wiedenmann et al., 2013) or carbon concentrating mechanisms to prevent CO₂ limitation (Wooldridge, 2009). Thus, supplemental NH₄⁺ from fishes may benefit corals by reducing their dependence on potentially harmful NO₃⁻ that is becoming abundant around developed coastlines (Carlson et al., 2019; Zhao et al. 2021).

Positive Interactions on Changing Coral Reefs

Decades ago, ecologists recognized the importance of biotic interactions that can alleviate environmental stress to expand the realized niche occupied by different species. Today, as climate change alters environments, these positive interactions could become increasingly important for maintaining the persistence of species as conditions change (Bulleri et al., 2018). Yet on coral reefs, only a handful of studies have looked beyond the coral – symbiont relationship to examine how positive interactions could influence coral thermal tolerance. This omission is striking given that >800 invertebrate species associate with corals and scores more cryptobenthic fishes live within and around colonies (Ainsworth et al., 2020). Numerous examples demonstrate that these coral-associates can have positive effects on their host corals (e.g., Meyer & Schultz 1985; Stewart et al., 2006; Holbrook et al., 2008, 2011; Shantz et al., 2015; Chase et al., 2020a). However, outside of a few notable examples, we know very little about the ecology or impacts of interactions between corals and these close associates during thermal stress events.

Planktivorous damselfishes in particular associate with numerous coral species, often in great abundance (Pratchett et al. 2016). For instance, on the northern Great Barrier Reef between ~50-100% of *P. damicornis*, *Stylophora pistillata*, *Echinopora lamellosa*, and *Acropora valenciennesi* colonies surveyed around Lizard Island housed damselfishes (Pratchett et al.,

2012). Similarly, Holbrook et al. (2008) found that ~75% of the *Pocillopora* spp. colonies they surveyed in Moorea harbored resident fishes, with roughly 1/3rd housing over 20 individuals at any given time. Based on the excretion rates measured here and in other studies of planktivorous Pomacentrids (e.g., Cantrell et al., 2015; Algeier 2021), the nutrient contributions of these fishes directly around corals are similar to the range of nutrient concentrations known to improve coral thermal tolerance (Beraud et al. 2013, Marangoni et al. 2020; Han et al., 2022). However, to date only one other study has examined how fishes influence coral thermal tolerance (Chase et al., 2018). Here, the authors found that during the 2016 global bleaching event wild colonies of *Seriotopora hystrix* on the Great Barrier Reef retained higher symbiont densities and protein content when they housed whitetail dascyllus (*Dascyllus aruanus*). Unlike our study, when Chase et al. (2018) experimentally mimicked the 2016-17 bleaching event on the GBR by exposing *Pocillopora damicornis* corals in the lab to 15 days of temperature-stress at 7.5 to 8°C above ambient conditions, all their experimental corals bleached, regardless of fish presence. This level of warming represents a far more severe bleaching event than the ten-day, 3°C increase we simulated and suggests that while positive interactions with fish may help corals resist moderate thermal stress, they will be insufficient to protect corals from longer, more severe marine heatwaves.

Our differing results highlight the numerous factors that may be relevant when assessing positive interactions on reefs. Species-specific differences in coral and Symbiodineaceae thermal tolerance (e.g., Voolstra et al., 2021), nutrient requirements of symbionts (McIlroy, Wong, & Baker, 2020), and interaction strength between coral – fish pairings (Chase, Pratchett, & Hoogenboom, 2020b) mean that the benefits provided by fishes and realized by corals may be species dependent. For instance, differences in coral branching morphology, or the “openness” of colonies, could influence the residence time and flushing rates of fish-derived nutrients from the interstitial spaces of corals and thus mediate the effects of nutrients on coral

physiology (Holbrook et al. 2008). The broader environmental context in which fish-coral interactions occur must be also considered. For example, the benefits conferred by mutualists that provision nutrients often depend on the availability of these nutrients in the environment (Shantz et al., 2016). Accordingly, when NH_4^+ or P are abundant on a reef, local delivery of these nutrients by fishes may have little to no effect on corals. Similarly, corals that meet large portions of their nutritional requirements through heterotrophy may be less likely to benefit from fish-derived nutrients, although fishes have been found to improve the growth of multiple coral species that encompass a range of heterotrophic capabilities on the reef when feeding still occurs (e.g., Meyer & Schultz 1985; Lieberman et al., 1995; Holbrook et al., 2008; Shantz et al., 2015). One possible explanation is that fish-derived POM could be an important food source for corals. Our study occurred when there was no active bleaching in Moorea, so we were unable to explore these additional factors but future field studies are warranted to understanding of how environmental context shapes the importance of fish-derived nutrients for corals.

Even if greenhouse gas emissions are substantially reduced, most corals will experience temperatures beyond their thermal limits on an annual basis (UNEP 2020). Accordingly, efforts to identify positive interactions that can be managed to increase coral survival during marine heatwaves may become as important for preserving reefs as identifying local stressors that compound coral mortality during and after bleaching (Anthony et al., 2015; Donovan et al., 2021). Some commercially harvested fish species play critical roles in nutrient cycling on reefs (e.g., Layman, Allgeier, Rosemond, Dahlgren, & Yeager, 2011; Shantz et al., 2015) and protecting important sources of fish-derived nutrients could be one such approach. Another area that remains particularly understudied is the impact of coral-associated animals on the coral microbiome. The consortia of microbes found within the coral microbiome may play a large role in coral health, nutrient cycling, and thermal tolerance (Rädecker, Pogoreutz, Voolstra, Wiedenmann, & Wild, 2015; Reshef, Koren, Loya, Zilber-Rosenberg, & Rosenberg, 2006;

Santoro et al., 2021) but almost nothing is known about how fish or other coral associates influence the physiology and resilience of corals through their impacts on the microbiome. Eventually the growing severity and duration of thermal stress events will likely overwhelm the ability of positive interactions to ameliorate their negative effects, highlighting the need to reduce emissions for reefs to persist in their current form and distribution. Until then, a greater understanding of facilitation on reefs may allow positive interactions to be better managed or manipulated and buy time for the world's coral reefs.

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DATA AVAILABILITY

Data for this manuscript are publicly available through Dryad at

<https://doi.org/10.5061/dryad.XYZ>. Raw sequencing data are archived in NCBI under SRA PRJNA864826.

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Figure Legends

Figure 1: Diagram depicting experimental design. Corals were collected and acclimated in a common garden offshore for 10 days before being moved to shore to acclimate with or without damselfish for an additional 14 days. On Day 14, temperatures were increased in half of experimental tanks for 10 days followed by 10 days of recovery at ambient temperatures.

Figure 2: Concentrations of **(A)** ammonium (NH_4^+), **(B)** nitrate (NO_3^-), **(C)** soluble reactive phosphorus (SRP), and ratios of **(D)** N:P, and **(E)** NH_4^+ :P in heated (red) and ambient temperature (blue) aquaria when damselfish were present (left panels, triangles) and absent (right panels, circles). Error bars show ± 1 SE.

Figure 3: **(A)** Average maximum dark-adapted quantum yield of photosystem II (F_v/F_m) measured throughout the experiment. Asterisks denote significant differences within treatments between time points from pairwise comparisons corrected for false discovery rates. **(B)** Mean F_v/F_m at the end of the acclimation period. P-value from global ANCOVA. **(C)** Change in F_v/F_m calculated between the end of laboratory acclimation and the end of the thermal stress period. Lowercase letters indicate significant differences between treatments based on pairwise comparisons corrected for false-discovery rates **(D)** Change in F_v/F_m calculated between the

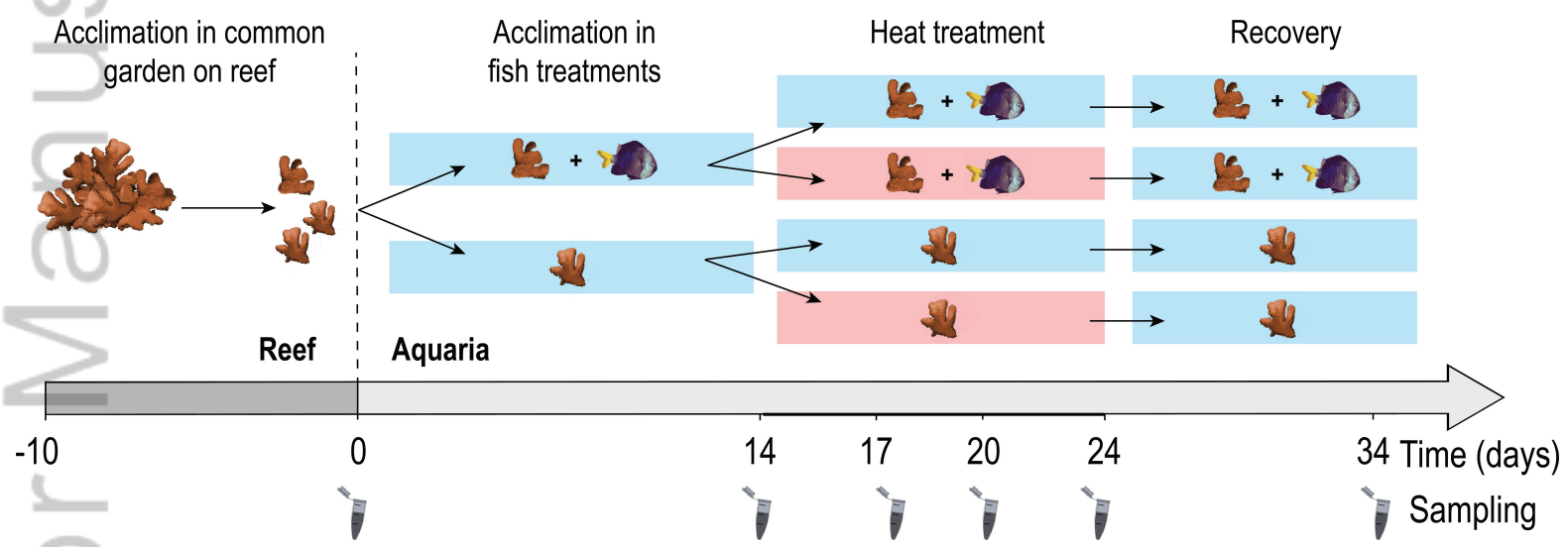
end of laboratory acclimation and the end of the recovery period. No within-treatment differences in F_v/F_m were detected between the end of acclimation versus recovery period. In all panels ambient temperature treatments are shown in blue, heated treatments in red. Triangles indicate fragments maintained with damselfish, circles indicate fragments kept without damselfish. Error bars show ± 1 SE.

Figure 4: **(A)** Average Symbiodiniaceae density measured throughout the experiment. Asterisks denote significant differences within treatments between time points from pairwise comparisons corrected for false discovery rates. **(B)** Mean Symbiodiniaceae density at the end of the acclimation period. P-value from global ANCOVA. **(C)** Change in symbiont density calculated between the end of acclimation and the end of the thermal stress period. Lowercase letters indicate significant differences between treatments based on pairwise comparisons corrected for false-discovery rates **(D)** Change in symbiont density calculated between the end of acclimation and the end of the recovery period. Asterisks mark treatments in which symbiont density remained significantly lower at the end of the recovery period than at the end of the acclimation period. In all panels ambient temperature treatments are shown in blue, heated treatments in red. Triangles indicate fragments maintained with damselfish, circles indicate fragments kept without damselfish. Error bars show ± 1 SE.

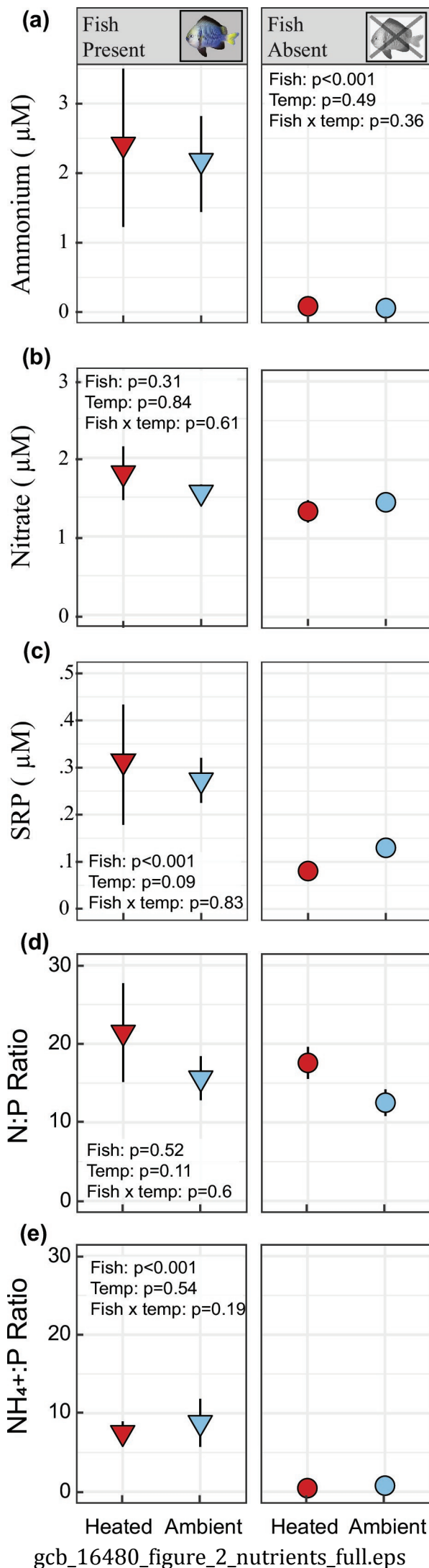
Figure 5: **(A)** Mean tissue protein content measured throughout the experiment. Asterisks denote significant differences within treatments between time points from pairwise comparisons corrected for false discovery rates. **(B)** Mean tissue protein content at the end of the laboratory acclimation period. P-value from global ANCOVA. **(C)** Change in tissue protein content calculated between the end of acclimation and the end of the thermal stress period. Lowercase letters indicate significant differences between treatments based on pairwise comparisons corrected for false-discovery rates **(D)** Change in tissue protein content calculated between the

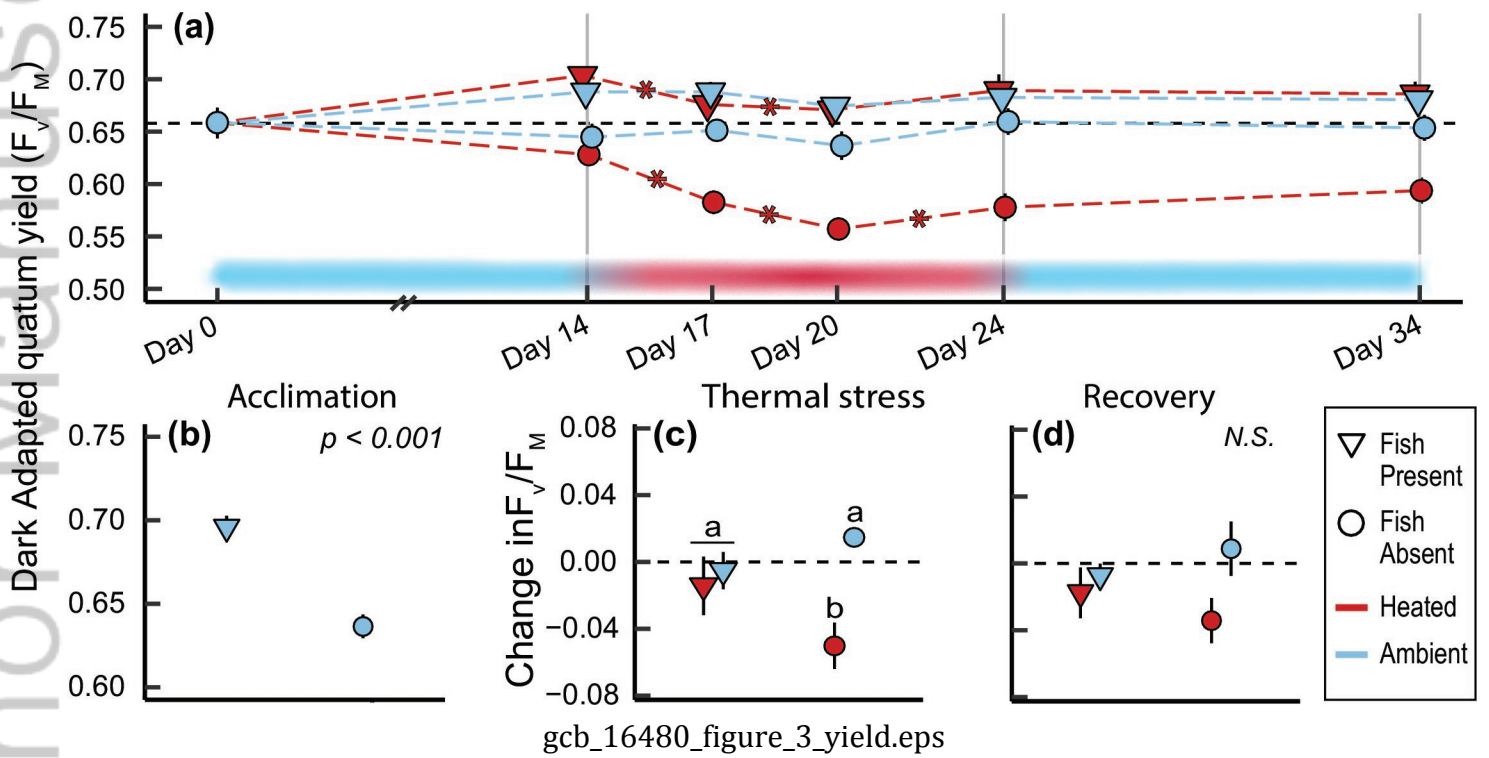
end of acclimation and the end of the recovery period. No within-treatment differences in protein content were detected between the end of acclimation versus recovery period. In all panels ambient temperature treatments are shown in blue, heated treatments in red. Triangles indicate fragments maintained with damselfish, circles indicate fragments kept without damselfish. Error bars show ± 1 SE.

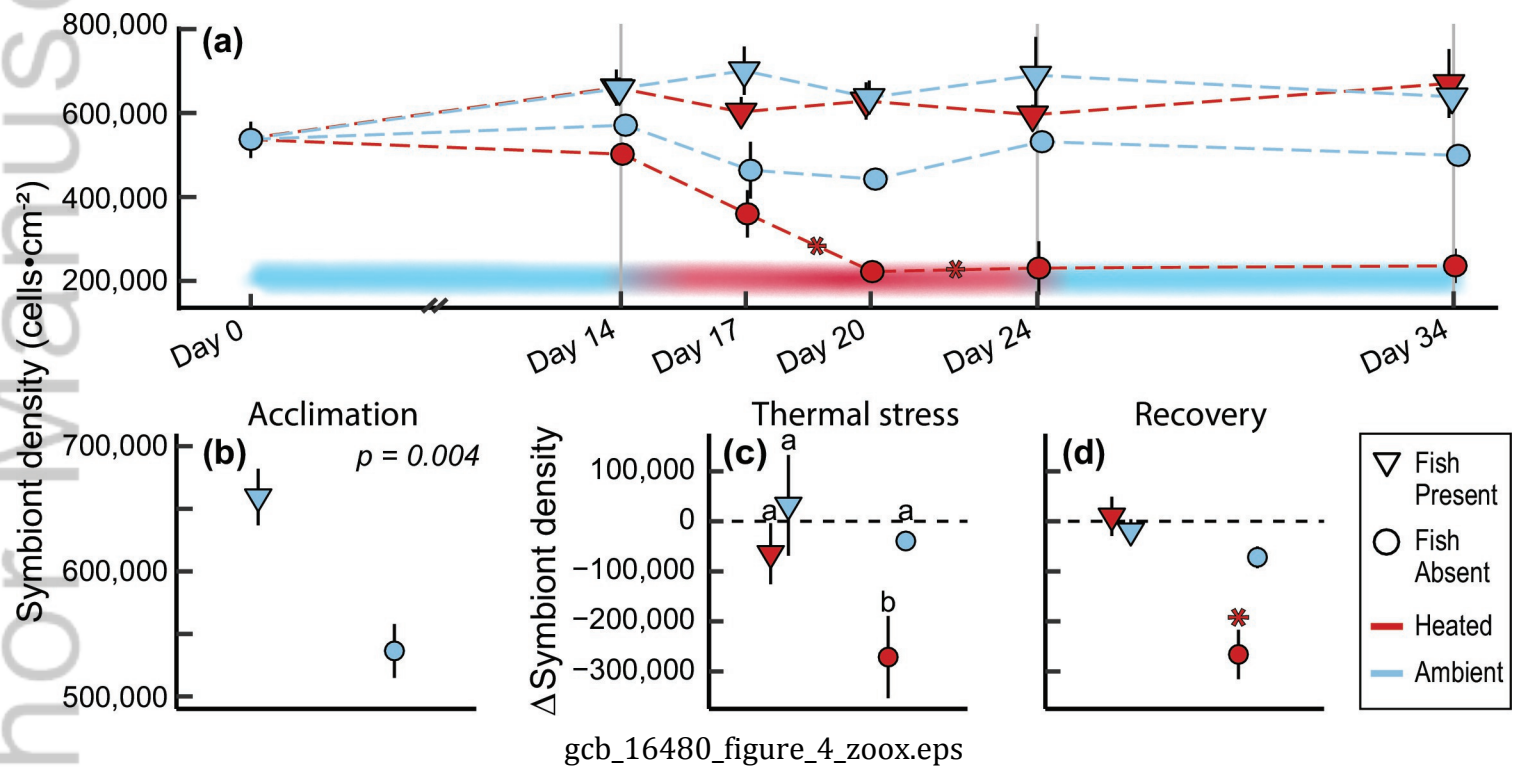
Figure 6: Mean growth rates of coral fragments maintained with and without damselfish after **(A)** ten days of thermal stress and **(B)** ten days of recovery. Letters indicate significant differences from post-hoc comparisons after FDR corrections. Triangles indicate fragments maintained with damselfish, circles indicate fragments kept without damselfish. Error bars show ± 1 SE.

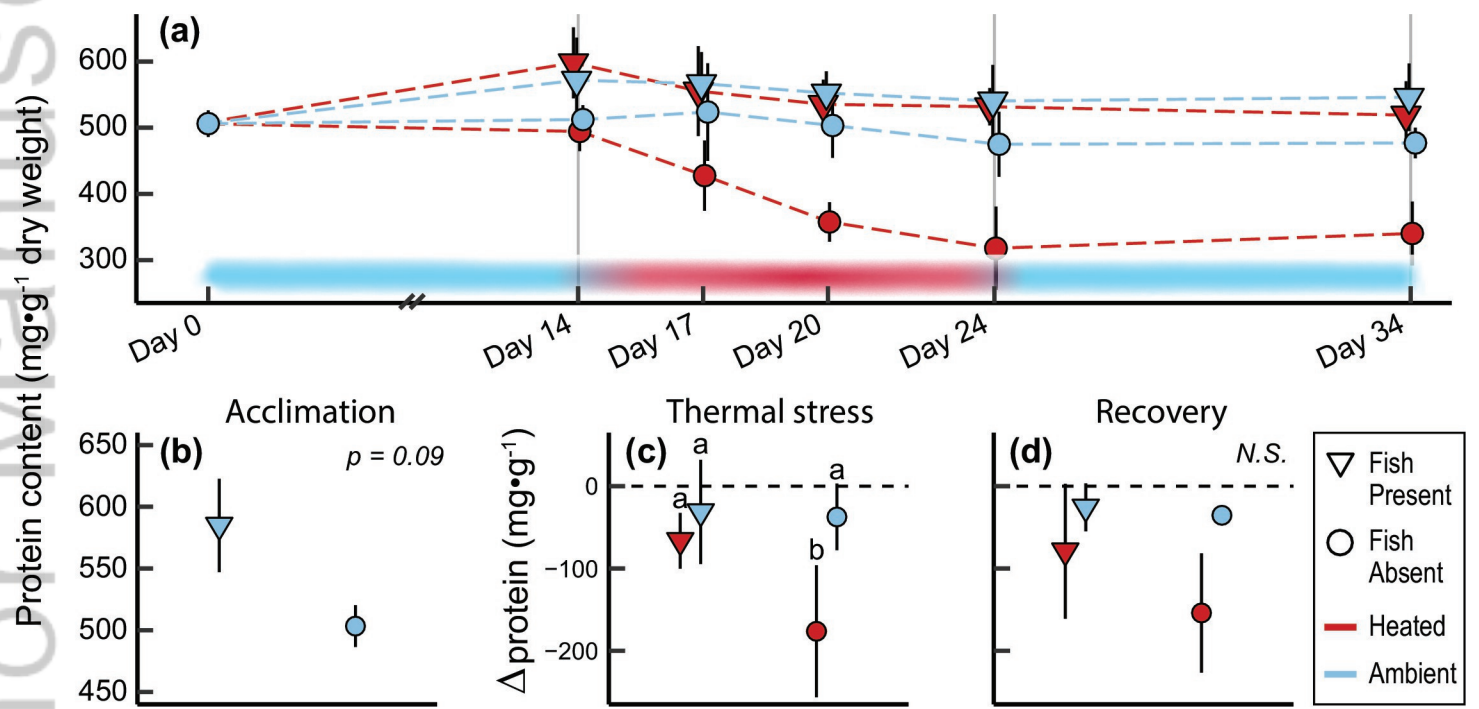


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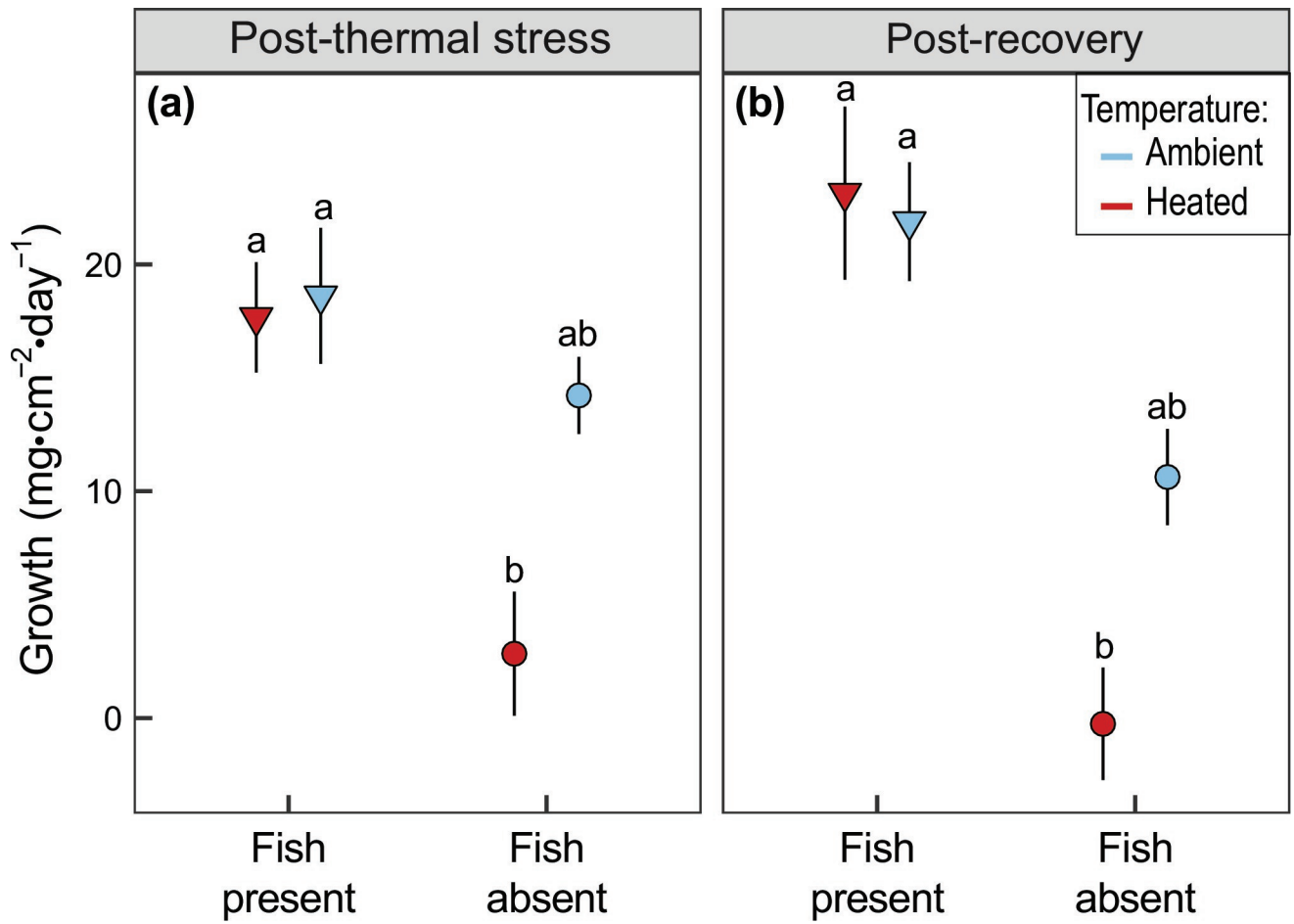








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