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Trade-offs in a reef-building coral after six years of thermal acclimation

Anna Roik [a, b, 1, *], Marlene Wall [a, c, 1], Melina Dobelmann [d], Samuel Nietzer [d], Anna Fiesinger [c, e], Miriam Reverter [f], David Brefeld [d], Peter J. Schupp [b, d], Matthew Jackson [d], Marie Rutsch [b, d], Julia Strahl [a, b, 1, *]

[a] Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, 27570 Bremerhaven, Germany
[b] Helmholtz Institute for Functional Marine Biodiversity at the University of Oldenburg, 26129 Oldenburg, Germany
[c] GEOMAR, Helmholtz Centre for Ocean Research, Kiel, Germany
[d] Institute for Chemistry and Biology of the Marine Environment, Carl von Ossietzky University of Oldenburg, Wilhelmshaven, Germany
[e] Department of Biology, University of Konstanz, Konstanz, Germany
[f] School of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

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ABSTRACT

There is growing evidence that reef-building corals can acclimate to novel and challenging thermal conditions. However, potential trade-offs that accompany acclimation remain largely unexplored. We investigated physiological trade-offs in colonies of a globally abundant coral species (*Pocillopora acuta*) that were acclimated *ex situ* to an elevated temperature of 31 °C (i.e., 1 °C above their bleaching threshold) for six years. By comparing them to conspecifics maintained at a cooler temperature, we found that the energy storage of corals was prioritized over skeletal growth at the elevated temperature. This was associated with the formation of higher density skeletons, lower calcification rates and consequently lower skeletal extension rates, which entails ramifications for future reef-building processes, structural complexity and reef community composition. Furthermore, symbionts were physiologically compromised at 31 °C and had overall lower energy reserves, likely due to increased exploitation by their host, resulting in an overall lower stress resilience of the holobiont. Our study shows how biological trade-offs of thermal acclimation unfold, helping to refine our picture of future coral reef trajectories. Importantly, our observations in this six-year study do not align with observations of short-term studies, where elevated temperatures were often associated with the depletion of energy reserves, highlighting the importance of studying acclimation of organisms at relevant biological scales.

1. Introduction

Tropical coral reef ecosystems are facing a major crisis predominantly caused by rising ocean temperatures that lead to coral bleaching, mortality, and reef habitat erosion (Donner et al., 2005; Heron et al., 2016). Additionally, serious consequences arise for coastal communities and nations that depend on reef ecosystem services, particularly coastal protection, food provisioning, and tourist economies (Eddy et al., 2021; IPBES, 2019). Concerns about the future of coral reef ecosystems have fueled the quest for solutions. Most notably, the umbrella-term "assisted evolution" comprises several innovative ideas of human interventions that aim to help accelerate adaptation and acclimation of reef-building corals and promise to sustain tropical reef ecosystems under future climate change scenarios (van Oppen et al., 2015; Voolstra et al., 2021). Among others, two key strategies are on the rise. One is based on the adaptive (evolutionary) mechanisms of marine organisms (Howells et al., 2022; Kenkel and Matz, 2016), and the other relies on their physiological plasticity and acclimation potential (i.e., "adaptation" within a generation) (DeMerlis et al., 2022; Henley et al., 2022; Majerova et al., 2021; Martell, 2023). While many findings indicate that thermal tolerance of corals can be partially explained by genetic variation and, hence, is ingrained in genomes and heritable traits (Howells et al., 2022), some of the unexplained variation in thermal tolerance can be attributed to plasticity (Fox et al., 2019; Kenkel and Matz, 2016). It is now obvious that not only genetic variation but in large parts environmental impulses drive plasticity (Hackerott et al., 2021a). To harness this plasticity, and thus the acclimation potential of corals, "thermal preconditioning" treatments that expose coral propagules to

* Corresponding authors at: Helmholtz Institute for Functional Marine Biodiversity, University of Oldenburg, Oldenburg, Germany.
E-mail addresses: anna.roik@hifmb.de (A. Roik), julia.strahl@wwf.de (J. Strahl).
[1] Equal contribution.

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stressors have been proposed (or sub-optimal/challenging conditions). This approach aims to prime the corals for thermal stress resistance and has inspired many experimental studies in recent years (Bellantuono et al., 2012; DeMerlis et al., 2022; Henley et al., 2022).

While adaptation through trait selection is a long evolutionary process that requires several generations of organisms to act on, some corals have demonstrated remarkable plasticity, as well as the capacity to increase their stress tolerance over the course of a lifetime. This phenomenon has been mostly observed in colonies with a history of challenging thermal exposures or experience of highly variable environmental conditions like in intertidal reefs, lagoonal reefs, or areas exposed to frequent upwelling (Castillo et al., 2012; Palumbi et al., 2014a; Wall et al., 2023). Corals pre-exposed to challenging stressor conditioning are likely to perform better under new stress events compared to those without such pre-exposure, indicating that coral plasticity (in particular the thermal tolerance range) can be expanded through "environmental priming" (Hackerott et al., 2021b; Martell, 2023). Therefore, the physiological acclimation capacity within the lifetime of organisms should be considered as an increasingly important survival strategy for coral species under the environmental changes expected in the coming years.

The prospects for employing thermal preconditioning treatments to generate thermally acclimated corals are promising (Bellantuono et al., 2012; DeMerlis et al., 2022; Hackerott et al., 2021b), but trade-offs associated with gains in thermal stress resistance remain poorly understood. Higher temperatures pose physiological challenges for organisms, raising biochemical reaction rates and increasing energetic demands (Angilletta Jr et al., 2004; Hornstein et al., 2018). Organisms often shift their metabolic strategies as a compensatory response under new thermal conditions, which entails changes in metabolic enzyme activity, modifications in tissue biochemistry and ultimately resource allocation (Tattersall et al., 2012). There is evidence of such metabolic shifts in corals exposed to high temperatures. For instance, Gibbin et al. (2018) showed that although carbon and nitrogen uptake of symbiotic dinoflagellates and coral cells was altered at elevated temperature, corals remained visually healthy, likely suggesting a successful acclimation to the new thermal condition. Such shifts in metabolic strategy can however entail trade-offs that have not yet been fully explored.

A trade-off by definition is the outcome of the prioritization of one trait or function at the cost of another (Pörtner et al., 2006). Most commonly this relates to the allocation of resources into a specific trait, which, at a specific moment, maintains optimal performance or is important for stress mitigation (Lesser, 2013). For instance, thermal resistance in marine species is often provided at the expense of growth or reproduction as the energy investments shift towards cell protection and tissue maintenance under stress (Sokolova et al., 2012). Trade-offs related to high temperature resistance have been studied and discussed in numerous species (Karl et al., 2013; Pörtner et al., 2006; Trip et al., 2014), but remain mostly understudied in corals. To date, it has been shown that adaptive (and heritable) thermal resistance can be accompanied by trade-offs, such as declines of coral growth rates and tissue lipid content (Cornwell et al., 2021). Another noteworthy finding in the same study was that corals with a higher bleaching resistance naturally tended to host lower numbers of symbiont cells in their tissues. The lower symbiont load came at the cost of a decreased growth rate, likely a consequence of a lower photosynthetic output. In contrast, corals in a short-term (five weeks) marine heatwave experiment did not show any apparent trade-offs in fecundity or growth associated with higher heat tolerance (Lachs et al., 2023). However, it is uncertain how prolonged exposure (i.e., several months to years) to warmer conditions may change coral metabolism and whether these changes are accompanied by trade-offs.

To shed more light on potential trade-offs of successful acclimation to warmer conditions, we investigated corals over biologically relevant, year-long timescales. Corals were raised and maintained under two thermal regimes in the lab and remained there for six years (31 °C vs. 26 °C). Their parental colonies originated from a thermal regime of ~29 °C on average throughout the year, experiencing lower daily winter averages of 26 °C and diel fluctuations between 25 and 33 °C across the year. To answer the question whether trade-offs were inflicted with the acclimation process to the elevated temperature regime of 31 °C, we investigated the metabolic performance of host and symbionts, their tissue compositions (i.e., proxy for energetic condition and strategy), as well as tissue and skeletal growth rates (i.e., proxy for ecological success). We aimed to evaluate whether corals acclimated to 31 °C underwent metabolic shifts or possible trade-offs compared to those kept at the cooler temperature regime.

2. Materials and methods

2.1. Coral rearing and set-up for physiological diagnostics

Six *Pocillopora acuta* mother-colonies were collected at 1–2 m at the Luminao Reef in Guam, USA (13°27′55.25″N, 144°38′48.84″E), in July 2015 and maintained in flow-through tanks supplied with natural ambient seawater. Larvae were released and settled in August 2015 at ambient temperature conditions. Once settled, recruits were transferred and maintained at two temperatures, ambient (29 °C) and elevated (31 °C), in Guam until November 2015 (details of the coral history in Table S1, Texts S1 and S2). At the start of the experiment, the temperature of 31 °C was deliberately chosen to be 1 °C above the local bleaching threshold (Fig. S1, Raymundo et al., 2019) with the intention to exceed the stress tolerance level of corals. Recruits were then transported to the tropical seawater facilities at the Institute for Chemistry and Biology of the Marine Environment "Terramare" in Wilhelmshaven, Germany, where they were kept at the two treatment temperatures (ambient and elevated) until the assessment of physiological trade-offs in July 2021. Aquarium facilities were run with artificial seawater (Tropic Marin® Pro-Reef salt, Wartenberg, Germany). During the first year (August 2015–August 2016) survival rates were monitored and out of 828 recruits 197 recruits survived with slightly higher survival under ambient (34.8 ± 12.5 %) compared to elevated (18.3 ± 5.1 %) temperature conditions (Fig. S2). In August 2016, ambient temperature was changed to a cooler temperature of 26 °C, i.e., corresponding to the lower daily average temperature of their home reef during winter, while the elevated temperature of 31 °C was maintained (Fig. S1, Raymundo et al., 2019).

Corals from the remaining aquarium population were used for the physiological experiment in July 2021, after having been maintained for six years at the two thermal regimes. In brief, six fragments of 12 *P. acuta* colonies from each temperature regime were cemented into "plugs" using aquarium cement and a silicone plug mold (Stone Fix, Aqua Forest, Brzesko, Poland) and distributed across three experimental tanks per ambient (26 °C) and three tanks of elevated temperature (31 °C), where they remained for a 54-day period of the physiological experiment. The six fragments included one for the live physiological measurements and tissue analyses, one to two for the buoyant weight assessment, and three spare fragments. The physiological measurements were conducted towards the end of the 54-day experimental period and after a minimum of 6 weeks. During the physiological experiment, temperature was recorded hourly using HOBO Tidbit v2 temperature loggers (Onset, USA), while light intensity and fragment health (algal overgrowth and tissue paling) were assessed weekly. To ensure equal light intensity and water movement for all fragments, coral racks were rotated once a week. Corals were fed twice a week with 50 ml of a feeding solution based on clam, squid, fish and phytoplankton concentrate (Tropic Marin® Phytonic, Wartenberg, Germany). Feeding was halted three days prior to the live physiological and biochemical measurements. All technical details of the aquaria systems are provided in Text S3 of the supplements.

2.2. Live physiological measurements

To determine metabolic rates (photosynthesis and respiration), one fragment per colony was incubated under controlled conditions under light and dark conditions following the established procedures outlined in Strahl et al., 2015. We describe incubation details in the supplementary Text S4. All incubations were performed in a total of four incubation runs, one run a day over four days by alternating the temperature treatments. After the dark incubation, the incubated coral fragments were immediately snap-frozen in liquid nitrogen for further biochemical analysis and surface area determination. Raw data of net photosynthesis and dark respiration were derived as mg l^{-1} by considering the temperature and salinity during the incubations. The respective rates were calculated by linear regression of the oxygen changes using the software R (R Core Team, 2021) and a customized script including a function from the R package *rMR* v1.1.0 (Moulton, 2018). Finally, rates of net photosynthesis and dark respiration (mg O_2 cm^{-2} h^{-1}) were normalized to the tissue-covered surface area of each coral fragment.

2.3. Biochemical analysis of tissues

To determine the biochemical composition of coral host and symbiont, fragments were pre-processed following established protocols (Buerger et al., 2015). Coral tissue was removed from the skeleton using an air gun and filtered seawater. The tissue slurry of each sample was topped up to a total volume of 20 ml and homogenized for 30 s with an Ultra Turrax (IKA, USA). Separation of host and symbiont cells by centrifugation for 10 min at 4400 rpm (~1900 g) and −1 °C (Eppendorf Centrifuge 5702, Germany) followed. Subsequently, the supernatant containing host cells were aliquoted for downstream analyses. The symbiont pellet was washed and resuspended in 3.5 ml filtered seawater for downstream analyses. For biomass determination, each aliquot was filtered through a pre-combusted filter (4 h at 500 °C, Whatman GF/C, GF Healthcare Life Sciences, United Kingdom), dried for 24 h at 60 °C, and weighted (Sartorius M2P, Sartorius AG, Germany; precision: 0.001 mg). Biomass weight was calculated per surface of the coral in mg cm^{-2}. Protein concentration (Lowry et al., 1951) was determined using the DC Protein Assay Kit (Bio-Rad Laboratories Inc., Hercules, USA), a bovine serum albumin (BSA) standard, and a spectrophotometer (UV-1800, Shimadzu Corporation, Kyoto, Japan) at 750 nm. Carbohydrate concentration was measured using the phenol-sulfuric acid method for measurements with a microplate reader and a D-glucose standard (Bove, 2021). The absorbances of the samples and standards were measured in triplicates at 485 nm on a microplate reader (TriStar LB941 Multimode Reader, Berthold Technologies). The remaining tissue slurries were used to determine the total lipid concentration in triplicates (600 µl each) using the colorimetric sulfo-phospho-vanillin (SPV) method for the microplate reader at 530 nm implementing a corn oil standard (Bove and Baumann, 2021). All measured values were converted to kilojoules (kJ; protein: 23.9 kJ/g, carbohydrate: 17.5 kJ/g, lipids: 39.5 kJ/g) (Gnaiger and Bitterlich, 1984) and provided as energy reserve concentrations (both in mg and kJ) normalized to the tissue-covered surface area of the corals determined by the single wax dipping technique (Veal et al., 2010).

2.4. Measurements of skeletal traits

We determined the three skeletal growth parameters, calcification rates (mass accretion), skeletal density, and extension rates (skeletal elongation). Calcification rates were assessed by measuring 1–2 coral fragments per colony following the buoyant weight technique by taking two measurements ("start" and "end") within the period of the physiological experiment (Jokiel and Guinther, 1978; Spencer Davies, 1990). We describe the details of our buoyant weight measurement protocol in the supplementary Text S5. In brief, coral fragments were weighed while submerged in seawater using a microbalance with an underfloor weighing system (Sartorius, BP 210S). After conversion of buoyant weights to dry weights (Text S5), the mass change between the beginning and the end of the physiological assessment period was calculated and subsequently divided by the number of experimental days to calculate diurnal accretion rate.

$$\text{Dry skeletal weight (g)} = \text{weight displaced water (g)} / \text{density of water } (\text{g cm}^{-3}) * \text{skeleton density } (\text{g g}^{-3})$$

Further, values were normalized by surface area of each coral fragment (mg d^{-1} cm^{-2}). The surface area values were determined for each fragment at the end of the experiment using the wax dipping technique in a single dip (Veal et al., 2010). Skeletal densities were determined from an additional fragment per colony using the water displacement volume and the weight of the coral skeleton (Strahl et al., 2015). Details of this method are outlined in Text S6. Subsequently, linear extension rates (cm yr^1) were calculated by dividing the net calcification rates determined by buoyant weight and normalized to surface area (mg cm^{-2} yr^{-1}) by the skeletal densities (mg cm^{-3}). The calcification rates obtained from the buoyant weight technique the assessed density values (mg cm^{-3}) were used and rates were extrapolated as accretion per year (mg cm^{-2} yr^{-1}).

$$\text{Linear Extension } (\text{cm yr}^{-1}) = \text{calcification rate } (\text{mg cm}^{-2} \text{ yr}^{-1}) / \text{density}$$

Note that this procedure assumes similar calcification rates along the entire surface area of individual fragments. However, in branching species it is known that tips grow faster (up to 13.2 times faster) than the base (Rinkevich and Loya, 1984). Thus, the obtained extension rates do not represent absolute rates of the branch tip, but rather provide an estimate of how much extension rates will differ.

2.5. Statistical analyses

Statistical analyses were performed using the base R package *stats* in R (version 4.1.1). Shapiro-Wilk normality tests were used to test for normality and Levene's test to test the assumption of equal variance of data among two thermal treatments. Where the data met the assumption for parametric tests, *t*-tests were performed to determine the differences between the two thermal treatments. Non-parametric Wilcoxon-tests were performed to test the treatment-related differences, where the data did not meet the conditions for a parametric test. All boxplots were generated using *ggplot2* and assembled in Adobe Illustrator.

3. Results

3.1. Metabolic performance

Net photosynthetic rate and dark respiration rate per coral surface area (indicating the overall performance of the holobiont) were 1.5- and 1.3-fold higher at the elevated temperature, respectively (both comparisons: $p < 0.05$). However, these two metabolic rates per biomass weight (indicating the performance per tissue unit/cell unit), did not differ between the two temperatures (Fig. 1 A & B). The net photosynthetic rate had medians of 0.014 ± 0.0032 (95 % confidence interval) and 0.016 ± 0.005 mg O_2 mg^{-1} biomass and respiration rates 0.005 ± 0.0009 and 0.004 ± 0.0008 mg O_2 mg^{-1} biomass, for 31 °C and 26 °C, respectively. Fragments at 31 °C overall exhibited a slightly higher variability.

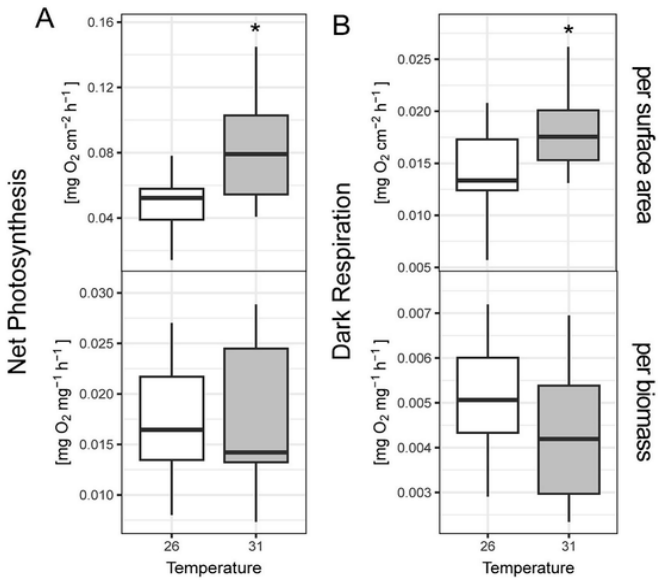

Fig. 1. Metabolic performance of thermally acclimated corals. Metabolic performance is shown as (A) net photosynthesis measured under light conditions and as (B) dark respiration per cm^2 of coral surface area (upper plot) and per mg of biomass weight (bottom plot). Thermal treatment in gray. Asterisks indicate significant group differences at significant levels: $p < 0.05$ (*). $n = 11$ to 12 per group.

3.2. Skeletal growth and biomass accretion

Corals living at 31 °C calcified at a significantly slower pace (1.8-fold lower calcification rate, $p < 0.01$) compared to corals living at 26 °C (Fig. 2 A). At the same time, these corals formed skeletons of higher densities at 31 °C (2.12 g cm^{-3} ± 0.07), exceeding the densities measured in the ambient temperature group (1.58 g cm^{-3} ± 0.12) by 1.4-fold (Fig. 2 B, $p < 0.001$). Living under the elevated temperature also resulted in a 2.5-fold lower extension rate compared to corals living under the cooler ambient temperature ($p < 0.001$, Fig. 2 C). Overall biomass was significantly elevated in the coral holobionts at 31 °C (Fig. 2 D, $p < 0.01$) as a result of significantly increased biomass in host (1.9-fold) and symbiont (1.5-fold) (Fig. 2 E–F, $p = 0.006$, $p = 0.009$, respectively).

3.3. Energy storage

The total energy content of the holobiont was significantly higher in corals under the elevated temperature (1.8-fold increase, $p < 0.001$) when normalized to coral surface area (Fig. 3 A). This difference was driven by the significantly increased lipid content in these corals (2.6-fold increase, $p < 0.001$ and $p < 0.001$, Fig. 3 B). Carbohydrates and proteins remained at similar levels in both treatments (Fig. 3 C–D). The protein concentrations measured were slightly lower in corals at 31 °C compared to corals at 26 °C (0.9-fold decrease, $p < 0.05$, when normalized to mg, Fig. 3 D). The strongly increased lipid level determined at holobiont level at 31 °C was stemming from the host, which overall had significantly higher total energy content per surface area (median 59.0 J cm^{-2} ± 10.53) under the elevated temperature (2.0-fold higher, $p < 0.001$, Fig. 3 E) and significantly higher lipid content (median 45.7 J cm^{-2} ± 9.40 and 3.0-fold increase compared to 26 °C, $p < 0.001$, Fig. 3 F). Furthermore, carbohydrate content per surface area was higher in host tissues under 31 °C (median 1.35 J cm^{-2} ± 0.23, 1.2-fold elevated, $p < 0.05$, Fig. 3 G), but protein content was at similar levels in both treatments (median 11.1 J cm^{-2} *vs.* 10.7 J cm^{-2}, *n.s.*, Fig. 3 H). Symbiont energy content played a proportionally smaller role in the total holobiont energy budget with values ~10–25 J cm^{-2} and ~5–13 J mg^{-1}, compared to (*vs.* host values ranging at ~20–80 J cm^{-2} and ~15–45 J mg^{-1}. In comparison to the host and holobiont, symbiont energy content overall varied at a smaller scale between the thermal conditions of 26 °C and 31 °C, but the total energy content per biomass unit was significantly decreased under 31 °C (0.7-fold decrease, $p < 0.01$, when normalized to mg of biomass, Fig. 3 I), which is in contrast to what we have found at the holobiont and host level. This decline was driven by significant declines per unit of biomass revealed for all three parameters, lipids (0.7-fold, $p < 0.05$, Fig. 3 J), carbohydrates (0.7-fold, $p < 0.05$, Fig. 3 K), and proteins (0.5-fold, $p < 0.01$, Fig. L). When calculated by surface area, all three symbiont parameters including symbiont total energy reserves appear homogeneous between the two thermal conditions (total median 16.2 J cm^{-2} ± 2.99 at 31 °C, 15.3 J cm^{-2} ± 3.10 at 26 °C, *n.s.*).

4. Discussion

Our study reports first insights into the metabolic shifts and trade-offs in pocilloporid corals that acclimated to elevated temperatures, relative to their reef of origin. The investigated corals appeared visually healthy and thriving during the six years they were exposed to the experimental thermal conditions. The 31 °C-acclimated corals operated at increased metabolic rates, while prioritizing energy investment into lipid storage and biomass accumulation over skeletal growth. These acclimated corals hosted symbionts that appeared compromised (i.e., lower energy content) in comparison to the corals kept at the cooler temperature of 26 °C. We discuss the observed trade-offs at the elevated temperature, their consequences for this globally abundant and ecologically relevant coral species, and the potential long-term consequences for the coral reef ecosystems.

4.1. Increase of energetic production and higher energy reserve investment under the elevated temperature

Our data highlight that long-term exposure of corals to an elevated temperature can result in a remarkably strong channeling of resources into tissue growth and accumulation of energy reserves, while neglecting growth of the coral skeleton. It is a common notion that marine invertebrates can maximize their fitness under challenging environmental circumstances through prioritizing one trait over another. They undergo physiological shifts that change their relative energy allocation strategy (Pörtner et al., 2006; Sokolova et al., 2012). In our study, we must assume that energy expenditure for biomass under the elevated temperature was significantly increased at the expense of skeletal growth, since tissue growth is more energy consuming than skeletal accretion (Kenneth R. N. Anthony et al., 2002). Our corals with their enhanced productivity at 31 °C were able to cover the increased costs of enhanced biomass production, but this might have led to a deficit in meeting energy requirements for calcification. In other previous studies, however, under challenging environmental conditions other than elevated temperature, skeletal growth was typically prioritized over biomass. In particular under light deprivation which slows photosynthetic rates, the coral *Montipora digitata* shifted its relative energy investment from tissue growth to reproduction and skeletal growth in response to declining resource availability (Leuzinger et al., 2012). Similarly, under severe energy limitation caused by shading, this coral maintained skeletal growth even at the expense of reproduction. In other cases, biomass accumulation was reported to increase under more light availability in *P. acuta*, while calcification rates remained stable (Wall et al., 2017). However, across a diversity of coral species including Pocilloporidae, tissue biomass has been typically negatively correlated with skeletal growth and often, the slow-growing coral species would maintain more biomass per surface area (Precoda et al., 2020). This aligns with the observation in our corals, where *P. acuta* shifted

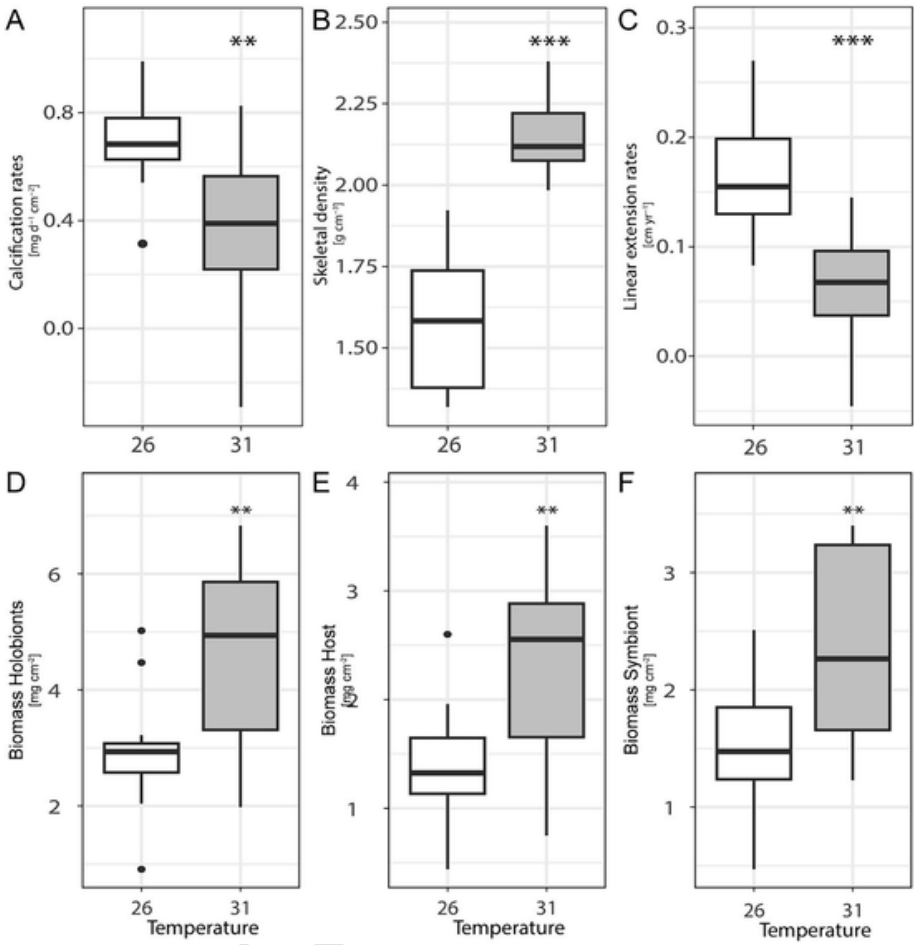

Fig. 2. Growth traits of thermally acclimated corals. Skeletal growth parameters are presented as (A) calcification rates (as skeletal mass accretion per day and surface area), (B) skeletal density and (C) linear extension rates. Biomass accumulation is shown (D) in total for the coral holobiont, and also specifically for the (E) host and (F) the symbionts. Extension rates were calculated assuming similar calcification rates along the entire surface area of individual fragments. Thermal treatment in gray. Asterisks indicate significant differences at significant levels: $p < 0.05$ (*), $p < 0.01$ (**) and $p < 0.001$ (***); n = 11 to 12 per group.

from fast colony growth to slow growing under elevated temperature, at the same time increasing their biomass strongly as a possible acclimation strategy. In summary, under resource constraints (e.g., light- or nutrient-deficient conditions) skeletal growth is maintained and preferred over biomass accumulation. On the other hand, a productivity boost (e.g., increased photosynthesis and/or algal symbiont density) associated with increasing temperatures tends to promote the investment into biomass and lipid accumulation at the expense of skeletal growth (Anthony et al., 2002; Tanaka et al., 2007), as was demonstrated in this study.

4.2. Benefits of the investment shift into biomass and energy reserves

We observed that the biomass composition of corals differed between the two thermal regimes. The 2.6-fold increase in tissue lipids of corals living at elevated temperature shows that they prioritized energy investment in lipid storage. This trait of acclimation observed in our six-year long study does not align with observations from short-term studies, where elevated temperatures caused depletion of tissue lipids in corals (Bove et al., 2022; Schoepf et al., 2013). In these short-term bleaching experiments, depletion of host tissue lipids has been interpreted as a stress-response driven by a shift in symbiont cellular pathways (gluconeogenesis, i.e., glucose production via lipid and amino acid breakdown), and consequent change in the quality of translocated products (i.e., decrease in fatty acids and complex molecules) (Hillyer et al., 2017; Pei et al., 2022). This highlights the importance of studying acclimation of organisms over their relevant biological scales, where successful acclimation mechanisms, which can include trade-offs, can be distinguished from stress-responses.

By increasing their tissue energy content, corals in our experiment have likely gained the benefit of preparedness for future unfavorable conditions, as high lipid stores have been previously linked to better coral health, lower mortality and higher recovery rates following stressful conditions (Anthony et al., 2009, 2002; Grottoli et al., 2014). For example, lipid compounds are utilized during the onset of bleaching (Grottoli et al., 2004; Rodrigues et al., 2008) and, thus, a high energy content can enable corals to withstand bleaching conditions for a longer period of time. Investments into tissue accumulation and energy content can also be beneficial by enabling rapid tissue repair after events of stress and tissue damage (Henry and Hart, 2005; Traylor-Knowles, 2016). It is a common notion that rising environmental temperatures accelerate biochemical and metabolic reactions in marine ectotherms (Angilletta Jr et al., 2004). In corals this is often accompanied by increasing investment into cell protection and tissue maintenance (to avoid cell damage), while colony growth is reduced. Previous studies have shown enhanced investment into higher antioxidant activity and increased biomass content in *Montipora capitata* after repeated thermal stress (Wall et al., 2021, 2018). Such progressive upregulation of constitutive antioxidant activity (e.g., superoxide dismutase and catalase levels) typically helps to protect tissue biomass (Lesser and Stochaj, 1990)

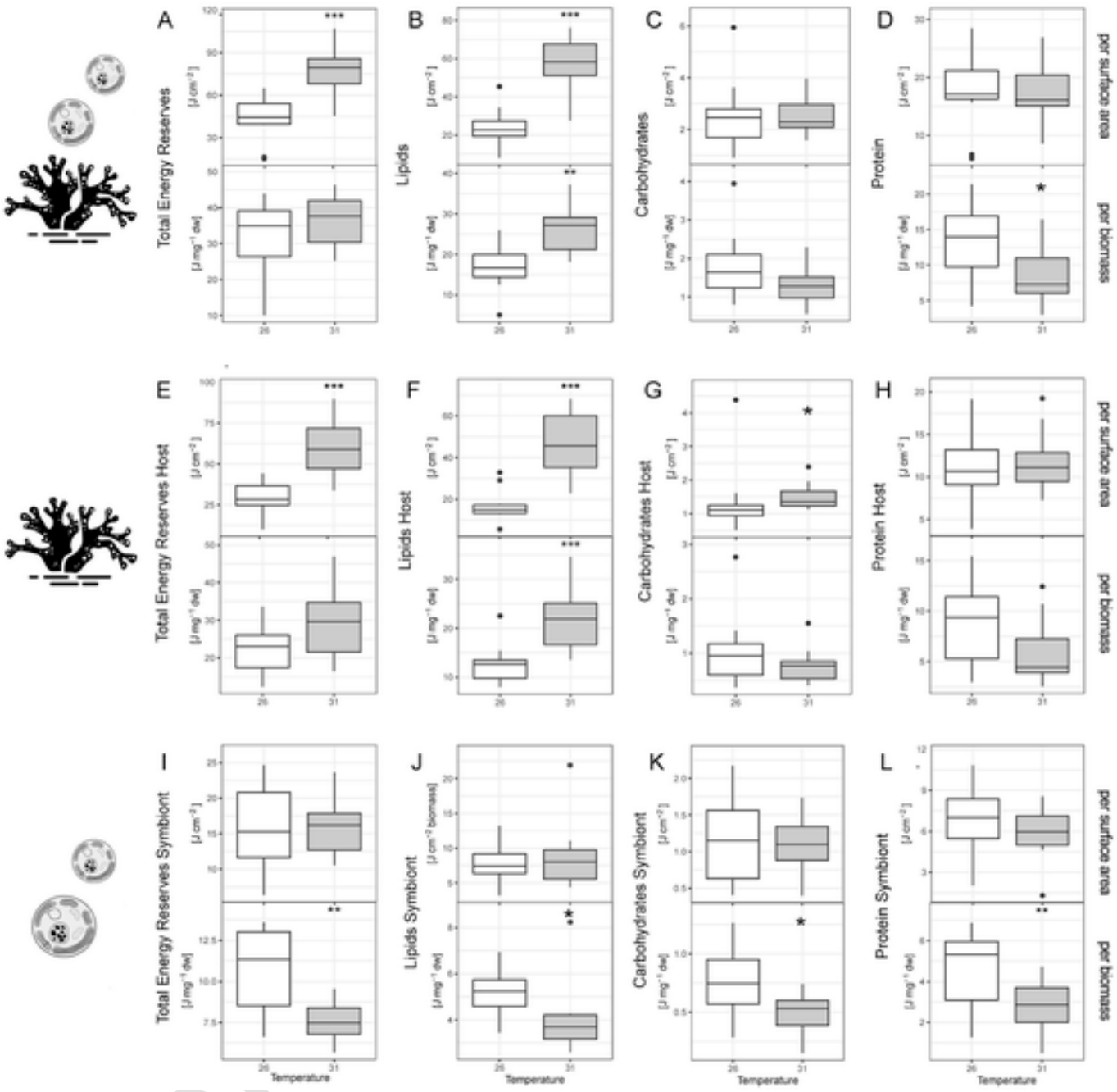

Fig. 3. Tissue energy content of thermally acclimated corals. The total energy reserves and content of lipids, carbohydrates and proteins in coral tissues are shown for (A–D) the holobiont and also for (E–H) hosts and (I–L) symbionts, individually. All variables are shown per cm^2 of coral surface area (upper plot) and per mg of biomass weight (bottom plot). Thermal treatment in gray. Asterisks indicate significant group differences at significant levels: $p < 0.05$ (*). n = 11 to 12 per group.

and can increase the odds of overall survival under thermal stress. The question of whether the accumulation of energy reserves including antioxidant front-loading will be indeed beneficial to corals when facing stress events, remains unanswered.

4.3. Reduced skeletal growth and consequences

Considering that the energy supply is typically sufficiently high to cover all physiologically relevant processes in marine ectotherms under the moderate thermal conditions (Leuzinger et al., 2012; Sokolova et al., 2012), the reduction in calcification at the elevated temperature in this experiment is an indicator that corals were operating beyond their thermal optimum for skeletal growth. The observed response of skeletal growth was in agreement with the thermal optimum ranging between 27.5 and 29.5 °C that is known for a range of coral taxa from the Great Barrier Reef (GBR) or the Caribbean (Álvarez-Noriega et al., 2023; Silbiger et al., 2019). For *P. verrucosa* from the GBR, for instance, optimal calcification temperature was 29.5 °C and severe declines in calcification capacity have been recorded beyond this optimum, with up to ~30 % declines already at 31 °C (Álvarez-Noriega et al., 2023). A similar situation can be assumed for the corals in the present study, where calcification rates at 31 °C were 40 % lower compared to the ambient temperature conditions. Since our corals' home reef, Luminao, is a fringing reef that can experience midday temperature peaks above

~31 °C during the hottest months of the year, the new constant exposure temperature of 31 °C in our experiment was expected to exceed their natural thermal optimum. In a recent study, exposure of *P. damicornis* corals to 31 °C clearly exceeded the growth optimum as indicated by the reduced growth rates which was accompanied with the impairment to control their calcifying fluid (Guillermic et al., 2021). Such a scenario may also account for the observed lowered calcification rates in our study.

Our findings revealed that higher temperatures induced changes in skeletal properties. Specifically, our pocilloporid corals at 31 °C developed denser skeletons, which provide stability and more skeletal robustness. Dense skeletons are best known from slow-growing coral species (Precoda et al., 2020). Also, it is more common that colonies tend to form higher-density skeletons when they inhabit challenging environments like high energy habitats such as the reef crest, where wave and current impact is high and triggers the increased skeletal density (Madin et al., 2008; Smith et al., 2007). The trait of high-density skeletons is undoubtedly beneficial in environments under physical forcing. While it has been observed that coral species reduce their skeletal density under the influence of higher than usual temperatures (e.g., corals reduced their skeletal robustness in inshore reefs), the only exception has been *P.* cf *damicornis* (McWilliam et al., 2022). This aligns with our finding and suggests that pocilloporid skeletons become of higher density under elevated thermal conditions. This also demonstrates that such growth tendencies, and consequently trade-offs, are likely species-specific. Corals with high-density skeletons must calcify faster in order to keep up with the skeletal linear extensions achieved by corals with lower-density skeletons. Hence, the investment into a dense skeleton comes at the cost of reduced linear extension at a similar growth rate, resulting in slower colony expansion (Precoda et al., 2020). In our study, high density together with the lower calcification rates of corals at 31 °C, resulted in skeletal extension rates substantially lower compared to their 26 °C counterparts. Therefore, developing high density skeletons, especially in combination with lower calcification rates, needs to be considered as a significant trade-off with ramifications not only at holobiont scale, but also far-reaching ecological consequences for reef growth dynamics and maintenance of the three-dimensional reef structure.

4.4. Changes of energy translocation in the host-symbiont relationships: a benefit to the host at the expense of the symbionts?

Unlike calcification rates, the photosynthetic performance of symbionts was not constrained under elevated temperature. In contrast, photosynthesis was boosted in the 31 °C-acclimated corals. This aligns with the results from short-term coral performance assays conducted in the Caribbean (Silbiger et al., 2019) and underscores that optima for photosynthetic productivity were not constrained at the elevated temperature tested. However, the boost of symbiont productivity due to enhanced photosynthesis and higher symbiont biomass, which is suspected to increase overall energy levels for the holobiont, only benefited the host, not the symbionts themselves, as the energy content of the symbionts in our study remained the same as in the control treatment. Instead, host tissues had increased strongly in biomass and energy content, suggesting that the transfer of energy from symbiont to host under elevated temperatures must have been increased, either by optimizing or enforcing translocation of photosynthates. It has been previously established in a pocilloporid coral that a 'sub-lethal' thermal exposure had a significant impact on nutrient cycling and metabolism, entailing modifications of the energetic exchange of the two partners in symbiosis (Gibbin et al., 2018).

The detailed examination of the host and symbiont fraction allowed to further obtain a glimpse into the complex dynamics of possible symbiont-host interactions that accompanied the thermal acclimation. Symbionts at 31 °C were diagnosed with lower protein, carbohydrate, and lipid levels per symbiont biomass. Interestingly, these values, in relation to coral surface area, have remained similar under both temperatures. This shows that symbiont biomass per host biomass did not change, despite boosted energy production and once again highlights the strong investment and resource channeling into the energy storage of the host. These nuanced findings further indicate that symbionts likely underwent cell-morphological changes influenced by the elevated temperature. The capacity of morphological restructuring has been reported from symbionts that were classified as stress "resistant" compared to other more "sensitive" species/strains, which did not feature such morphological plasticity (Hoadley et al., 2015). Resistant symbionts demonstrated morphogenesis (enlargement) of chloroplasts at elevated temperature, as well as an increase in cell volume, chlorophyll fluorescence, and pigment content (Gong et al., 2020; Hoadley et al., 2016). As such, these symbionts may have increased and optimized their photosynthetic output under the elevated thermal conditions that contributed to boosting the metabolic rates in both holobiont partners. This morphological plasticity coupled with increased energy content (both in proteins and lipids), observed in these previous studies, can be interpreted as a beneficial trait of the symbionts, which can help enhance holobiont stress resistance under challenging thermal conditions. In contrast, our findings show a 'skinny', but productive symbiont paired with a well-nourished host, highly enriched in tissue lipids, which also can be an indication of a changed nutrient cycling between two partners (Gibbin et al., 2018) and of enhanced translocation of symbiont resources (Rädecker et al., 2021).

While most studies to date have investigated the transition period between the stable and the unstable symbiotic state during thermal stress (aka. coral bleaching), our study provides new valuable insights into the symbiont-host trait dynamics in a stable symbiosis that has acclimated to an elevated temperature of 31 °C. We do not fully understand yet, whether this 31 °C-acclimated symbiotic state will also prove beneficial during an acute thermal stress event. We can hypothesize two contrasting scenarios, 1) that the increased investment into host tissues could increase stress resistance and could help the coral to deal with future stressors (Grottoli et al., 2004), or, 2) that the enhanced translocation of symbiont resources to the host might bring the holobiont closer to a dysbiotic state (Rädecker et al., 2021) and, thus, will increase its susceptibility to stressors. This remains to be determined in a future study, but overall, our current findings have already shed light on the physiological and metabolic shifts that allow coral holobionts to acclimate successfully under warmer temperatures.

4.5. Underlying mechanisms of the observed physiological shifts (aka. trade-offs) under the elevated temperature

The successful acclimation of *P. acuta* to the elevated temperature could be the result of physiological plasticity, genetic selection and adaptation, or a combination of both (Fox et al., 2019; Palumbi et al., 2014b; Torda et al., 2017). We suspect that the thermal history of the parental colonies in the reef, as well as the early exposure of the offspring to elevated temperatures, have contributed to the acclimation success of corals in our experiment. Since exposure to thermal variability is a good predictor of high stress tolerance and remarkable plasticity in corals (Bay and Palumbi, 2017; Hackerott et al., 2021b; Wall et al., 2023), the thermal history of the parents from the Luminao reef flat, which has a large thermal range, could be one explanation why the offspring was able to acclimate to the new elevated temperature of 31 °C. Furthermore, corals in this study have "learned" to thrive under the new elevated temperature since the very first exposure at juvenile stage, as no signs of distress were noted during the six years of cultivation. This early exposure during their recruitment might have additionally facilitated the success of acclimation, as developmental exposure to challenging conditions have been shown to influence plasticity in various organisms (Bowler and Terblanche, 2008). However, it will be

worthwhile to further explore the underlying genetic make-up of the offspring, since allele shifts were often associated with enhanced thermal tolerance of *ex situ* bred corals (Dixon et al., 2015; Howells et al., 2021). The possibility remains in our study that selection of recruits took place after settlement, as a higher number of recruits survived under 29 °C compared to 31 °C (Supplementary Fig. S2). Larval selection process has been characterized in other studies showing that heat-selected coral larvae were significantly enriched in heat-shock proteins, had improved energy production, oxidative stress and immune responses (Dixon et al., 2015; Howells et al., 2021). Evolutionary processes cannot yet be fully ruled out as a driver for the observed physiological differences reported between the corals raised at the two thermal regimes.

4.6. Ecological implications and considerations for active reef restoration

The increasing severity and frequency of deteriorating coral bleaching events (Donner et al., 2005; Heron et al., 2016) have been driving the development of proactive measures that aim to protect corals from thermal stress (van Oppen et al., 2015). Some anticipated approaches consider selection of thermally tolerant coral specimens for reef restoration (Humanes et al., 2021; Morikawa and Palumbi, 2019), while others intend to use thermal preconditioning treatments aiming to improve thermal tolerance of nursery corals (DeMerlis et al., 2022; Henley et al., 2022; Wall et al., 2023). Our findings have demonstrated that the desired trait of higher thermal tolerance can come at the cost of skeletal growth, at least for the coral *P. acuta* (from Guam). Further trade-offs beyond the decline of colony growth are possible. It will be crucial to investigate reproduction, as it determines coral population fitness with critical repercussions for the persistence of reef communities and the recovery of populations following severe heat stress events (Fisch et al., 2019; Johnston et al., 2020).

The far-reaching ecological consequences of trade-offs have not been considered nor assessed yet. For instance, a reduction in skeletal growth is expected to limit the growth capacity of an entire reef structure, which is a critical ecological feature ensuring that a reef will be able to maintain a positive carbonate budget (Roik et al., 2018, 2015) and keep pace with future sea-level rise (Perry et al., 2018), hence provide coastal protection and retain its ecosystem services into the future (Eddy et al., 2021; IPBES, 2019). Furthermore, with reduced colony growth rates corals may show less resilience and poor recovery from the pressures of other stressors, such as, i.e., increased forcing and frequency of storms and ocean acidification which increases with ocean warming (Madin et al., 2014; Mollica et al., 2018). On the other hand, corals that are able to produce a skeleton of higher density, such as observed in the heat-acclimated *P. acuta* in this study, may be able to buffer some of the negative effects of ocean acidification, which has been demonstrated to reduce coral skeletal density (Mollica et al., 2018). Consequences of trade-offs can be complex and whether adaptation/acclimation to one stressor (e.g., a higher temperature) may also increase the resistance to other stressors (e.g., ocean acidification, eutrophication, disease), is a question that has so far received little attention. Some restoration projects have already started integrating the assessment of trade-offs in their monitoring programs. For instance, coral nurseries in Florida reported a potential trade-off between disease resistance (a desired trait) and reproductive output of their nursery corals (Koch et al., 2022). Overall, studies exploring trade-offs of coral thermal tolerance show that an efficient strategy to create new intervention protocols should focus on a set of multiple desired traits for coral restoration recruits (Caruso et al., 2021; Edmunds and Putnam, 2020). Wright et al. (Wright et al., 2019) provided the first indication that certain coral traits could be advantageous against multiple stressors. However, it is noteworthy that the traits underpinning stressor tolerance were not identified and the experiment only lasted 10-days. A careful consideration, assessment, and cost-benefit evaluation of each new method and of the full suite of potential ecological consequences, which may arise from the respective method, will be vital to the development of efficient new interventions.

5. Conclusion

We have set out to determine whether increases in thermal resistance come at a physiological cost for the coral *P. acuta*, a ubiquitous Indo-Pacific coral species. Investigations of corals that acclimated to two distinct thermal conditions (a cooler ambient and an elevated temperature) identified two key trade-offs. After six years at the elevated temperature, corals allocated more resources towards soft tissue growth and lipid storage, while maintaining slower yet denser skeleton growth. The trade-off between energy storage and skeletal growth, likely involved the exploitation of symbionts, demonstrating how corals must balance physiological and metabolic mechanisms in order to acclimate to higher temperatures. On the one hand, the coral hosts at the elevated temperature appeared well-prepared to withstand future stressors due to their energy reserves. On the other hand, their symbionts were unable to accumulate substantial energy stores, potentially rendering them more vulnerable. Our results demonstrate how a “gain” in thermal tolerance could limit the calcification and reef-building capacity of corals, while enhancing the coral host's resilience to stressors. More long-term assessments of trade-offs in other coral species will be needed to determine if our observations are specific to *P. acuta* or might be more widespread. Our results challenge the observations of short-term studies where elevated temperatures depleted tissue lipids in corals, emphasizing the significance of studying acclimation over relevant biological scales. Long-term studies like ours will help to obtain a more comprehensive picture of the future coral reef trajectory and help to more accurately assess the potential of anticipated interventions that aim at increasing coral thermal tolerance.

CRediT authorship contribution statement

Anna Roik: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marlene Wall:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis. **Melina Dobelmann:** Visualization, Investigation, Formal analysis. **Samuel Nietzer:** Supervision, Resources, Methodology. **Anna Fiesinger:** Methodology, Formal analysis, Data curation. **Miriam Reverter:** Writing – review & editing. **David Brefeld:** Methodology, Investigation. **Peter J. Schupp:** Resources, Funding acquisition. **Matthew Jackson:** Supervision, Investigation. **Marie Rutsch:** Investigation. **Julia Strahl:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data and code underlying this study were submitted to pangaea.de: https://doi.pangaea.de/10.1594/PANGAEA.963327 and https://doi.pangaea.de/10.1594/PANGAEA.963328.

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Permissions

Research was conducted under the permit of the DEPARTMENT OF AGRICULTURE DIVISION OF AQUATIC AND WILDLIFE RESOURCES (DAWR) and MPA APPLICATION SPECIAL REQUEST (Section 63123 of Title 5, Guam Code Annotated GCA) to PJS. Corals were collected under the Special License for The Collection of Coral, issued to UOGML by DAWR under section 63123 of Title 5, GCA, and exported under permission of CITES issued by the US Fish and Wildlife Service (export # 15US62023B/9).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.174589.

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