Science of the Total Environment 996 (2025) 180234

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

# Thermally resistant coral *Stylophora pistillata* survives but does not thrive under chronic elevated baseline temperature

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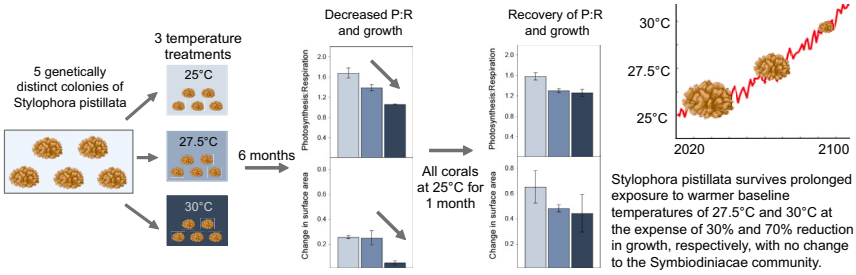
## HIGHLIGHTS

- *Stylophora pistillata* is tolerant of elevated baseline temperatures for six months.
- Shift in resource allocation away from growth to maintain physiological function
- Bleaching resistant corals may be tolerant of chronically elevated temperatures.
- Corals recover growth after only one month at current baseline temperatures.
- Implications for future coral reef net accretion and future survival

## GRAPHICAL ABSTRACT




## ARTICLE INFO

*Keywords:*
Coral reefs
Ocean warming
Climate change
Heat stress
Heat resistance
*Stylophora pistillata*

## ABSTRACT

Coral reefs are threatened worldwide from unprecedented increases in ocean temperatures, resulting in corals gradually living closer to their maximum thermal threshold. With ocean temperatures expected to warm up to 3 °C by 2100, understanding the effects of chronic elevated baseline temperature is important in determining the thermal physiological limits of corals and developing realistic restoration strategies to ensure the future of coral reefs. Here, we tested the effects of 26 weeks (i.e., six months) of elevated temperatures of + 2.5 °C (27.5 °C) and + 5 °C (30 °C) above a baseline of 25 °C on surface area growth, metabolic rates, energy reserves, assimilation of heterotrophically acquired food, and Symbiodiniaceae species composition in the aquaria-reared thermally tolerant coral *Stylophorapistillata* sourced from the northern Red Sea. Corals initially catabolized lipids while maintaining growth after 4 weeks of elevated baseline temperatures but acclimated after only 11 weeks. However, there was evidence of a long-term cumulative impact of chronic elevated temperatures after 26 weeks at 30 °C with corals experiencing higher metabolic demand and lower growth while maintaining biomass and energy reserves. Therefore, maintenance of tissue biomass and energy reserves appears to come at the cost of skeletal accretion but allows these corals to survive changes in baseline temperatures up to 30 °C. These physiological changes were not associated with Symbiodiniaceae species composition, which remained constant throughout the experiment. We also discovered that a return to 25 °C for four weeks allowed for recovery of metabolic demand and growth. Our data suggests that chronic exposure to high, sub-bleaching temperatures, a plausible scenario in the near future, will have some negative effects on coral growth and metabolism, but not

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https://doi.org/10.1016/j.scitotenv.2025.180234
Received 17 March 2025; Received in revised form 3 July 2025; Accepted 6 August 2025
Available online 3 September 2025

survival. Thus, while *S. pistillata* survives but does not thrive under projected shifts in baseline temperature, this study shows hope for acclimatization to temperature shifts expected in the next 50 years.

## 1. Introduction

Worldwide, coral reefs are threatened due to unprecedented increases in ocean temperatures. Since 1880, sea surface temperature (SST) has increased by approximately 1 °C, with an additional increase of 3 °C expected by 2100 under the "high emission, low mitigation" Socioeconomic Shared Pathway (SSP) 5–8.5 (Bindoff et al., 2019; Gulev et al., 2021). Warming is expected to be greater in the summer months, extending the time that marine organisms spend at stressfully high temperatures (Alexander et al., 2018; Agulles et al., 2021). Increases of this magnitude can have severe effects on many species of coral that already live near their thermal maximum. When exposed to temperatures of +1 °C above their thermal maximum for as little as 10 days, symbiotic coral lose their algal endosymbionts in a process called coral bleaching (Glynn, 1993). In response to anthropogenic climate change, bleaching events have occurred worldwide since the early 1980s, with increasing frequency, severity, and duration in recent decades (e.g., Glynn, 1993; Hughes et al., 2018; Mellin et al., 2024). Mass bleaching events lead to decreases in coral calcification and reproductive output, and increased disease outbreaks and coral mortality (Brown, 1997; Hoegh-Guldberg, 1999; McClanahan et al., 2008), leading to community-wide decreases in coral cover and biodiversity (Brown, 1997; Loya et al., 2001; Gonzalez et al., 2024). These decreases in coral cover and biodiversity are detrimental both ecologically and economically (Knowlton et al., 2021; Wernberg et al., 2024) because corals act as foundational species, providing habitat and food for a diverse array of species (Eddy et al., 2021; Wernberg et al., 2024), jobs through fishing and tourism, and storm protection for coastal communities (Spalding et al., 2017; Beck et al., 2018; Eddy et al., 2021; Reguero et al., 2021). As the ocean inches closer to many coral species' thermal maximum thresholds, the search for corals that are resistant or resilient to warming temperatures is critical as they are more likely to shape future coral reefs.

*Stylophora pistillata* from the northern Red Sea is more thermally tolerant under experimental and natural conditions than both conspecifics from the southern Red Sea and other species (e.g., Grottoli et al., 2017; Osman et al., 2018; Dobson et al., 2021; Kochman et al., 2021; Voolstra et al., 2021; Kochman-Gino and Fine, 2023). *S. pistillata* from the northern Red Sea can survive with no signs of bleaching for three weeks at +6 °C above average summer maxima, which is equivalent to 18 degree-heating weeks (DHW) (Fine et al., 2013) but shows some visual signs of bleaching and catabolizes lipid reserves after 32 DHW (Grottoli et al., 2017). However, colonies of this same species from the Indo-Pacific experience bleaching after 12 DHW and 100 % mortality after 34 DHW (Dias et al., 2019). Elevated bleaching thresholds for northern Red Sea coral appear to be the result of southern derived coral larvae being transported north and settling. Historical selection for heat tolerance in the southern Red Sea where temperatures exceed 32 °C in the summer has resulted in high heat-adapted populations of corals (Fine et al., 2013). Therefore, corals in the northern Red Sea are tolerant of temperatures above the local maximum monthly mean (MMM) temperature.

Coral tolerance of heat stress has been linked to high baseline heterotrophy, heterotrophic plasticity, high energy reserves, the presence of thermally tolerant Symbiodiniaceae algal endosymbionts, and healthy microbiomes (Berkelmans and van Oppen, 2006; Grottoli et al., 2006; Anthony et al., 2009; Houlbrèque and Ferrier-Pagès, 2009; Ferrier-Pagès et al., 2010; Voolstra et al., 2024). Compared to other species of coral, *S. pistillata* from the northern Red Sea has high energy reserves and high baseline heterotrophy when healthy (Ferrier-Pagès et al., 2003, 2010; Grottoli et al., 2017; Dobson et al., 2021; Kochman-Gino and Fine, 2023), making it potentially better suited to tolerate, survive, and persist better following heat stress than other species (Anthony et al., 2009). However, *S. pistillata* feeding rates decrease when bleached (Ferrier-Pagès et al., 2010; Tremblay et al., 2012), making this species dependent on its energy reserves to sustain itself during heat stress events (Grottoli et al., 2017). Although *S. pistillata* from the northern Red Sea shows tolerance to high temperatures in short-term and medium-term experiments, only two experiments have examined the effect of heat stress on this species for >31 days and found no visual signs of bleaching at temperatures +2 °C above the MMM (Krueger et al., 2017, 2018). However, temperatures in the northern Red Sea and elsewhere are expected to exceed experimental temperatures in Krueger et al. (2017, 2018) by the second half of this century (Agulles et al., 2021), stressing the importance of long-term experiments at projected future SSTs.

While short-term experiments (0–7 days) may be sufficient to determine bleaching thresholds compared to medium length experiments (8–30 days, Voolstra et al., 2020, Evensen et al., 2021), baseline temperatures are increasing worldwide, subjecting coral reefs to sustained warmer temperatures year-round. Therefore, long-term experiments (>31 days) can help inform how coral reefs may look and function in the future (Grottoli et al., 2021). Under SSP5–8.5, average monthly SST in equatorial regions (roughly 30°S – 30°N) are expected to exceed MMM temperatures by 2100 for more than four months each year (Ruela et al., 2020). In some geographic regions bleaching is expected to begin as early as late-winter by 2080 (Mellin et al., 2024). The expected increases in temperature and the longer exposure of corals to high temperatures make it critical to evaluate the effects of elevated baseline temperatures on the response of currently resistant corals, since those species are most likely to persist this century. For this study, we examined the effects of chronic elevated temperatures of +2.5 °C (27.5 °C) and + 5 °C (30 °C) above a baseline of 25 °C on northern Red Sea *S. pistillata* for a total of 26 weeks (i.e., 6 months). These temperatures are below the bleaching threshold for this species (Evensen et al., 2021; Kochman-Gino and Fine, 2023). However, our experimental temperatures align with the "likely upper range" in the global mean surface temperature warming relative to pre-industrial times (IPCC, 2013, 2019). Currently, the Gulf of Aqaba experiences only eight weeks at the MMM of 27.5 °C and 0–4 weeks at 30 °C, during heatwaves (Kochman-Gino and Fine, 2023). With our experimental design, corals were exposed to 27.5 °C and 30 °C for 26 weeks, 18–26 weeks longer than in natural conditions, reflecting the end-of-century predicted increases in surface ocean warming under SSPs 4.5 (27.5 °C) and 8.5 (30 °C) (IPCC, 2013, 2019). At the end of the 6 month experiment corals were allowed to recover at 25 °C for four weeks after chronic elevated temperatures, for a total experimental duration of 30 weeks. The physiological status of the algal endosymbiont and coral holobiont was measured after 4, 11, and 26 weeks of elevated temperature treatment and again after the recovery period of four weeks at 25 °C. Here, we addressed two main questions: 1) How do elevated baseline temperatures affect *Stylophora pistillata* metabolism, physiological function, and growth, and 2) can the effects of elevated baseline temperatures be reversed with a return to baseline temperature?

## 2. Methods

### 2.1. Experimental design

We evaluated our research questions with two experiments: 1) an 11-week long experiment and 2) a 30-week long experiment. Both experiments used ramets from the same genets, making the results directly comparable. Ramets of five genets of *S. pistillata* (originally sourced from

the Gulf of Aqaba in the Red Sea) were identified at the Centre Scientifique de Monaco. To determine five distinct genets, 38 colonies were sampled and genotyped based on the coral nuclear ribosomal internal transcribed spacer 2 (ITS2). Detailed methods on coral genotyping can be found in Supplementary information. Corals had been reared for >30 years in Mediterranean flow-through seawater tanks at 25 °C on a 12:12 h day/night diurnal cycle without natural daily or seasonal fluctuations and fed brine shrimp nauplii twice a week (Table S1). Although these conditions differ from natural reef conditions, the controlled conditions these coral experienced for the last 30 years allows us to determine their genetic adaptive differences to shifting baseline temperatures. This design eliminates potential acclimatization to the last three decades of ocean warming, making them ideal candidates to test our hypotheses. Additionally, using aquaria reared coral prevents the collection of wild coral which are increasingly threatened by global and local stressors.

### 2.2. Eleven-week long experiment #1

On 16 September 2020, 54 ramets of approximately the same surface area from each of the five unique selected genets were placed in one of nine 20 L glass tanks such that at least six ramets of each genotype were in each tank. Corals recovered from fragmentation for two weeks at 25 °C in the experimental tanks. Starting on 28 September 2020, three experimental tanks were heated by 0.5 °C and three tanks were heated by 1 °C daily over five days to reach experimental temperatures of 27.5 °C (+2.5 °C above baseline) and 30 °C (+5 °C above baseline), respectively, by 3 October 2020 and sustained under those conditions until 16 December 2020 (Fig. 1; Table S1). The gradual temperature ramping minimized the chances for heat-shock and served to better mimic the rate of warming during natural bleaching events (Grottoli et al., 2021). Corals in all experimental tanks continued to be fed brine shrimp nauplii twice a week and were maintained on a 12:12 h day/night diurnal light cycle (250 ± 10 μmoL photons $m^{-2}$ $s^{-1}$). After approximately 4 and 11 weeks (27 October and 16 December 2020), two ramets from each genet and treatment were collected for measurements of several physiological variables. The first ramet (Ramet 1) was used to measure net photosynthesis, photosynthetic efficiency ($F_v/F_m$), and respiration, and then frozen and later analyzed for total chlorophyll concentration. The second ramet (Ramet 2) was frozen at −80 °C, shipped to The Ohio State University on dry ice and stored at −80 °C for

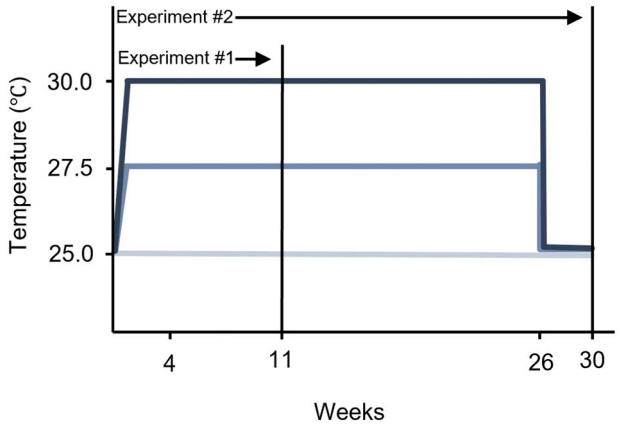



**Fig. 1.** Schematic temperature profile for each treatment: ambient control 25 °C (light blue), chronic warming of +2.5 °C (27.5 °C, medium blue), and chronic warming of +5 °C (30 °C, dark blue). The 27.5 °C treatment was ramped at 0.5 °C/day for five days and the 30 °C treatment was ramped at 1 °C/day for five days. Experiment #1 ran from 28 September–16 December 2020 with coral ramet collections on 27 October (4 weeks) and 16 December (11 weeks). Experiment #2 ran from 12 April - 16 November 2021 with all corals returned to 25 °C for four weeks on 13 October 2021. Coral ramets were collected on 13 October (26 weeks) and 16 November (30 weeks).

further physiological analyses (pigmentation intensity, biomass, lipids, cholesterol, carbohydrates, and surface area). A third ramet from each genet and treatment was collected at 11 weeks and immediately frozen at −80 °C for Symbiodiniaceae species analysis (Ramet 3).

### 2.3. Thirty-week long experiment #2

Due to space constraints and COVID restrictions at the Centre Scientifique de Monaco, a second experiment was conducted to test the effects of chronic elevated temperature over 26 weeks, followed by four weeks of reprieve at 25 °C for a total of 30 weeks in experimental tanks. Here, an additional 54 ramets of approximately the same surface area, but not necessarily the same surface area as ramets from Experiment #1, were collected on 8 March 2021 from the same genets used in experiment #1 and placed into nine tanks such that at least six ramets of each genet were in each tank. On 12 April 2021, after two weeks of recovery at 25 °C, three experimental tanks were heated by 0.5 °C and three tanks were heated by 1 °C daily over five days to reach experimental temperatures of 27.5 °C and 30 °C, respectively, by 17 April 2021. Initial collections and ramping rates were identical between experiments #1 and #2 (Table S1). Corals were kept in experimental treatments for 26 weeks until 13 October 2021 when all tanks were returned to baseline temperature of 25 °C for four weeks until 16 November 2021, for a total experimental duration of 30 weeks (Fig. 1). After 26 and 30 weeks, three ramets from each genet and treatment were collected again for physiological analyses as described above.

### 2.4. Holobiont physiology

Photosynthesis, respiration, $F_v/F_m$, and chlorophyll were all measured on Ramet 1 from both experiments. Oxygen fluxes were measured on live ramets to assess net photosynthesis ($P_{net}$) and dark respiration (R) rates according to methods described in Lange et al. (2023). P:R ratios were calculated by taking the absolute value of $P_{net}/R$. The photosynthetic efficiency ($F_v/F_m$) of photosystem II (PSII) was assessed on live ramets using a Dual PAM fluorometer (Walz, Effeltrich, Germany) according to Hoogenboom et al. (2012). Coral ramets were then frozen at −80 °C for the determination of chlorophyll content as described in Hoogenboom et al. (2010) following modified methods of Jeffrey and Humphrey (1975). Chlorophyll was standardized to skeletal surface area, which was determined using the wax dipping technique (Veal et al., 2010).

At The Ohio State University, Ramet 2 from each time point was photographed against a standard white background with a ruler for scale. Pigmentation intensity was measured within 1 cm of coral tips using established methods (McLachlan and Grottoli, 2021), where lower values indicate darker pigmentation. Surface area of each Ramet 2 was determined using the aluminum foil method (Marsh Jr., 1970). Growth was calculated between weeks 4 and 11 and weeks 26 and 30 by subtracting the average surface area at each temperature and dividing by the number of days between measurements. As individual coral were not tracked throughout the experiment, the growth measurements represent the difference in the average surface area for all genets at each time point and treatment. To account for the uncertainty of this method, error was propagated through the growth calculations. Ramet 2 from each time point was then ground into a homogenous paste using a mortar and pestle and partitioned into three 0.5 mg subsamples from the resulting homogenate. Biomass, total lipids, and total carbohydrates were measured on subsamples of each ramet following established protocols (Dubois et al., 1956; McLachlan et al., 2020b, 2020a). Both total lipids and carbohydrates were standardized to tissue biomass (g $g^{-1}$ ash-free dry weight) and converted into Joules (Gnaiger and Bitterlich, 1984). The concentration of cholesterol was measured on lipid extracts suspended in a chloroform:methanol solution (2:1 v:v) using thin-layer chromatography (TLC) according to methods modified from Solomon et al. (2020). TLC plates were loaded with standards and samples,

developed with 100 % hexane, 100 % toluene, and hexane:ethyl ether: acetic acid (70:30:1 *v*/v/v), sprayed with a solution of 3 % cupric acetate in 8 % phosphoric acid, and then dried on a 110 °C hot plate for 30 min. Once dried, TLC plates were scanned on a Xerox scanner and analyzed with ImageJ and OriginPro 2020 according to methods described in Tam et al. (2024). The error for each plate was calculated and the plate was rerun if the error exceeded 10 %. The average error for all TLC plates was 4.3 % ($n = 23$). The concentration of cholesterol was then standardized to biomass of each sample calculated during lipid extraction.

At the University of Konstanz, the tissue of each Ramet 3 collected at 11, 26, and 30 weeks was airbrushed from the coral skeleton, added to Buffer ATL (Qiagen) and frozen for Symbiodiniaceae analysis (Voolstra et al., 2020). DNA was extracted and amplified using ITS2 (Symbiodiniaceae) amplicon libraries and sequenced on the Ilumina MiSeq platform according to methods in Voolstra et al. (2020). Symbiodiniaceae ITS2 sequences were analyzed using SymPortal (Hume et al., 2019; symportal.org). ITS2 profiles were combined by majority ITS2 sequence and averaged for coral fragments according to time and temperature treatment.

### 2.5. Statistical analysis

To determine if physiological profiles (P:R, $F_v/F_m$, chlorophyll, pigmentation intensity, biomass, lipids, and cholesterol concentration) varied significantly by temperature, time, or the interaction of temperature and time, a two-way PERMANOVA analysis was conducted. Since coral ramets in experiments #1 and #2 were sourced from the same genets and all their physiological profile measurements were standardized using the same methods, we chose to combine the physiological data from both experiments to evaluate changes over time. Since there was an interaction of temperature and time, additional post hoc pairwise PERMANOVAs were run to test for significant differences among temperature treatments within each time point. Data were visualized using non-metric multidimensional scaling (NMDS) plots with vectors calculated using Pearson's correlation coefficients. Carbohydrate analyses were not possible on the smaller ramets due to insufficient material and could not be included in the multivariate analyses. Additionally, surface area was not included in the multivariate analysis because the values could not be standardized to the starting value and therefore could not be directly compared across the two experiments, though they could be qualitatively compared within each experiment for the same time points. All multivariate analyses were performed using Primer V6 software with PERMANOVA+ add-on (Clarke and Gorley, 2006).

To further explore the data, univariate two-way ANOVAs and post-hoc Tukey tests were conducted on each physiological variable where temperature and time were fixed factors and fully crossed. As above, the data from both experiments were analyzed together to assess changes over time. Surface area was analyzed for effects within but not across experiments because the values could not be standardized to the starting value. While the same five genets were represented in each treatment at each timepoint, genet was not evaluated as a random effect due to possible mis-labeling of genet identifiers between the two experiments. As a result of COVID restrictions, different teams conducted each experiment and the labeling system for the genets was not carried over. However, previous studies at the Centre Scientifique de Monaco on *S. pistillata* revealed no significant physiological differences among genets (Dobson et al., 2021) suggesting that here, genotype would not affect our statistical interpretation of the results either. Other random effects such as tank effects and colony size were not included in the statistical analyses because we did not track which tanks the individual corals were in throughout the experiment, and all corals started at roughly the same size. When assumptions of normality were not met ($p < 0.05$, Shapiro-Wilk test), data were transformed, or analyses were completed using the non-parametric Kruskal-Wallis test. Univariate statistics were run using R and statistical results were considered significant at $p \leq 0.05$.

## 3. Results

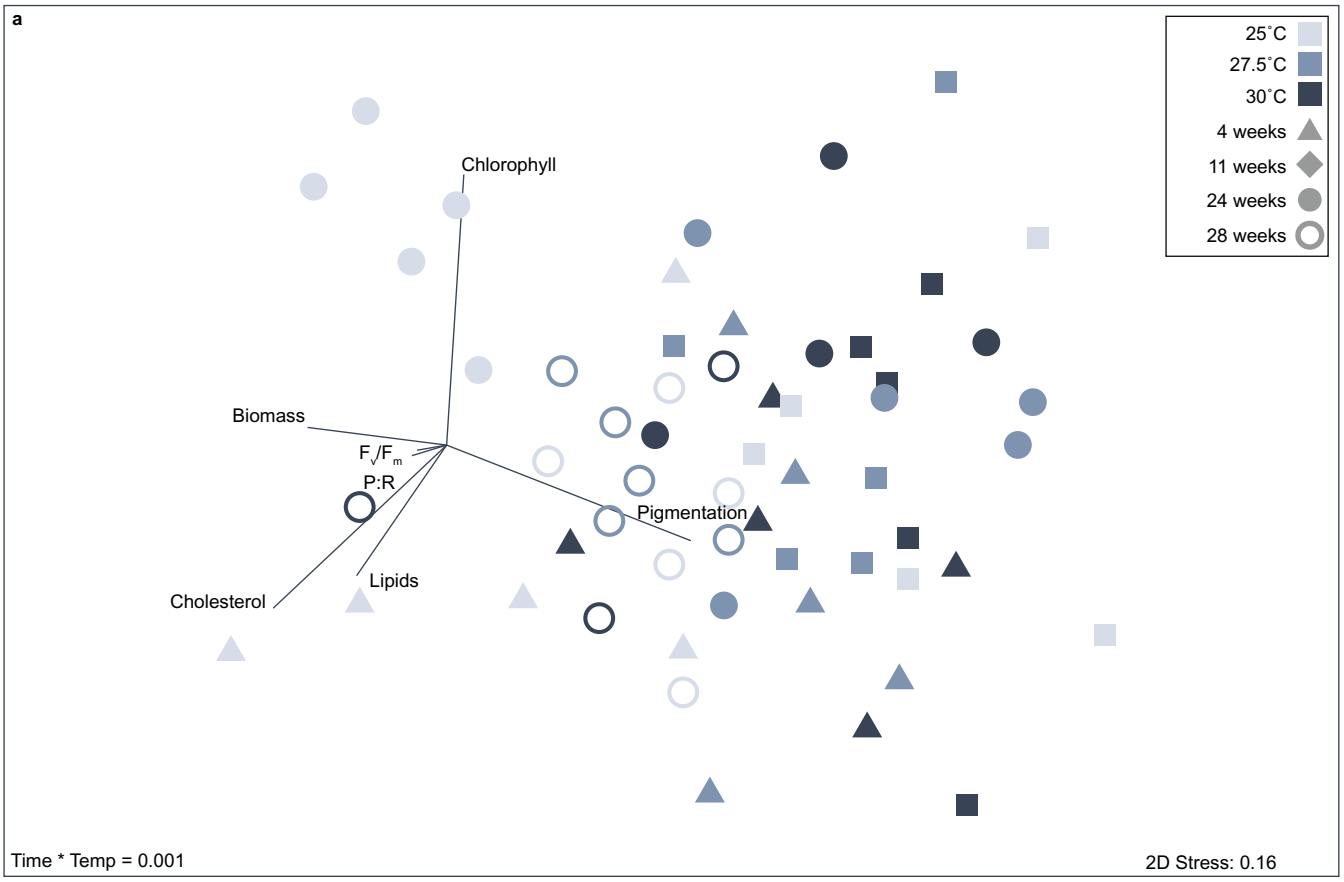
Coral ramets in all treatments survived experiment #1. During experiment #2, a power failure in the tank seawater supply pump resulted in the death of three ramets in the 30 °C treatment (one that was assigned to the 26-week time point and two that were assigned to the 30-week time point). Corals were visibly paler at 11 weeks compared to their appearance at 26- and 30-week time points, but there was no significant bleaching seen in corals at any time point or temperature (Fig. S1).

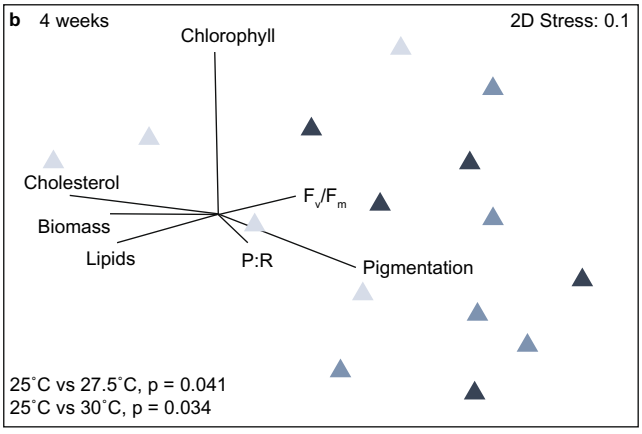
Multivariate analyses of *S. pistillata* physiological profiles resulted in an interaction effect between temperature and time, revealing that the effect of temperature on coral physiology was dependent on how long the corals experienced elevated temperatures (Fig. 2a, Table S2). After 11 and 30 weeks coral physiological profiles did not differ between 25 °C, 27.5 °C, or 30 °C treatments (Table S3). However, after 4 and 26 weeks, physiological profiles of corals in the 25 °C treatment differed from both chronically heated treatments (Fig. 2b, d; Table S3). At four weeks, this difference was driven by $F_v/F_m$, pigmentation intensity, and lipids, while at 26 weeks this difference was driven by P:R (Fig. 3).

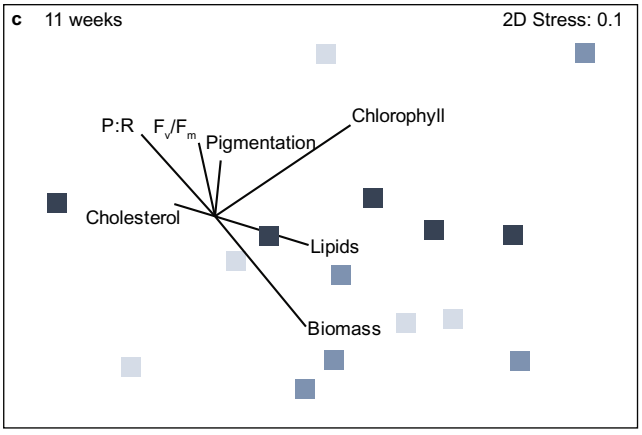
Detailed analysis of each variable showed interaction effects of temperature and time for five of nine variables, revealing that the effect of temperature depended on how long the corals were exposed to elevated temperatures for those five variables (Figs. 3–5; Table S4). Corals in 25 °C and 27.5 °C treatments had similar P:R throughout the experiment, and P:R was similar for all corals until 26 weeks of heat stress. At 26 weeks, P:R decreased in the 30 °C compared to the 25 °C treatment (Fig. 3a, Table S4), as a result of higher respiration. The P:R rate in the 30 °C treatment recovered after four weeks at 25 °C. $F_v/F_m$ for all corals was highest after 4 weeks and was lower throughout the rest of the experiment (Fig. 3b, Table S4). Additionally, at 4 weeks, corals in the 27.5 °C treatment had greater $F_v/F_m$ than the 25 °C treatment corals (Fig. 3b, Table S4). While total chlorophyll did not significantly differ for any temperature treatment throughout the experiment, there was an interaction effect for coral pigmentation intensity (Fig. 3c, d; Table S4). Control corals retained pigmentation throughout the experiment, while corals in both the 27.5 °C and 30 °C treatments were paler than the controls after 4 weeks but recovered pigmentation throughout the remainder of the heat stress period. Once returned to 25 °C for four weeks, pigmentation increased in corals from the 27.5 °C treatment (Figs. 3d, S1; Table S4).While biomass did not significantly vary throughout the study (Fig. 3e; Table S4), total lipids were higher after 4 weeks than at any other time in the study and were lower in the 30 °C treatment compared to corals in the 25 °C treatment at the 4 week time point (Fig. 3f; Table S4). Cholesterol was also highest after 4 weeks, but did not differ among temperature treatments (Fig. 3g; Table S4). Carbohydrate concentrations gradually decreased, then increased over time with no differences among temperature treatments at any time point (Fig. 4; Table S4). Surface area of the corals increased over time in both experiments (Fig. 5; Table S4). While corals grew over time, average coral surface area did not differ with temperature at 4 weeks (Fig. 5; Table S4). However, by 11 weeks, corals at 30 °C had not grown as much and were smaller than corals in the 25 °C treatment, remained smaller for the duration of the experiment, and did not catch up during the recovery phase (Figs. 5 & S2; Table S4). Lastly, corals in all treatments and time points were dominated by *Symbiodinium microadriaticum* endosymbionts (Fig. S3). Up to 3.6 % of endosymbionts were *Cladocopium* sp. (C21) at 11 weeks. But by week 26, *S. microadriaticum* represented 100 % of the endosymbionts in all corals (Fig. S3).

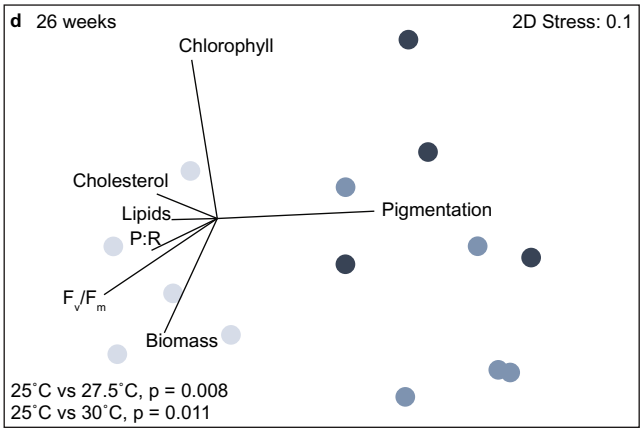
## 4. Discussion

Here we quantified the physiological responses of the thermally tolerant northern Red Sea coral *S. pistillata* to chronic shifts in baseline temperature over 26 weeks (i.e., 6 months) followed by a four week return to baseline temperatures of 25 °C. This experiment used corals



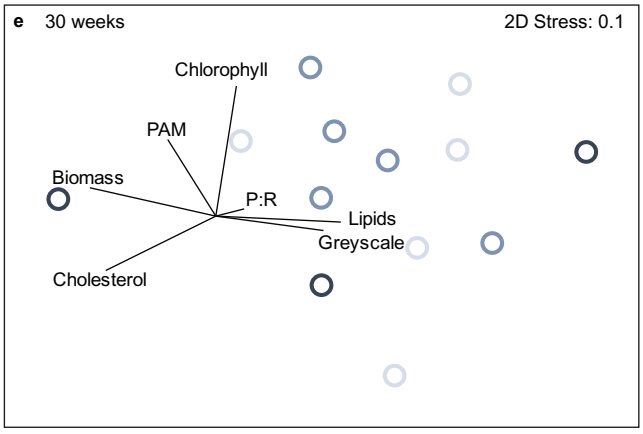




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**Fig. 2.** Non-metric multidimensional scaling plots (NMDS) of coral physiological profiles for all time points (a). NMDS within each time point highlights how coral physiological profiles changed after 4 weeks (b), 11 weeks (c), 26 weeks (d), and 30 weeks (e). Data colors correspond to temperature treatments: ambient control 25 °C (light blue), chronic warming of +2.5 °C (27.5 °C, medium blue), and chronic warming of +5 °C (30 °C, dark blue). Shapes correspond to time points: 4 weeks (triangles), 11 weeks (squares), 26 weeks (closed circles), and 30 weeks (open circles). Profiles from 4 and 11 weeks are from experiment #1, and profiles from 26 and 30 weeks are from experiment #2. All corals were at 25 °C between 26 and 30 weeks. Vectors in panel A indicate strength and direction of the relative contribution of each physiological variable to the sample distribution as determined by Pearson's correlation analysis. Significant PERMANOVA results are indicated in the bottom left corner of each panel. Statistical details can be found in Tables S2 and S3.

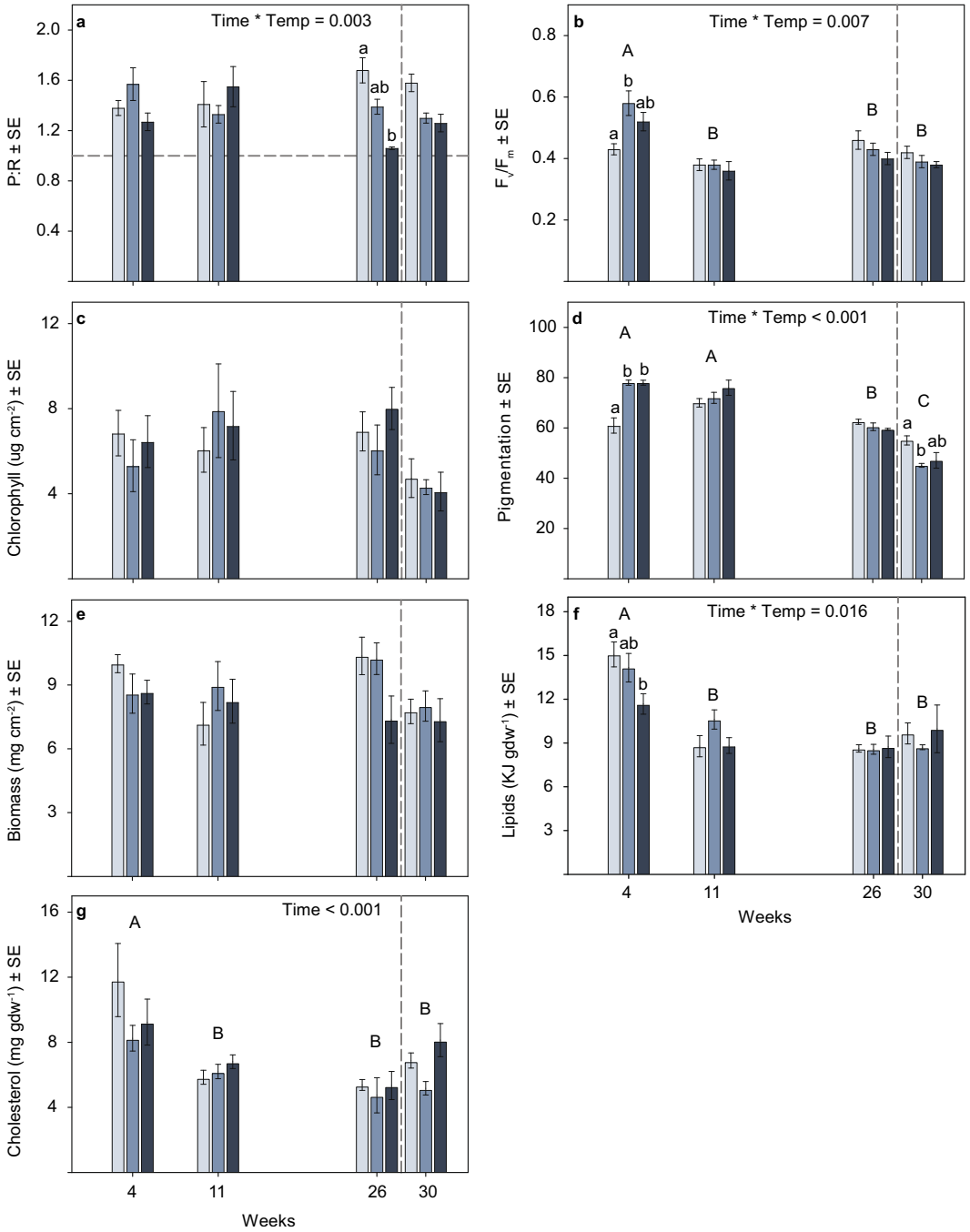


**Fig. 3.** Average (±1 SE)P:R (a), $F_v/F_m$ (b), total chlorophyll (c), pigmentation where higher numbers indicate decreased pigmentation (d), biomass (e), lipids (f), and cholesterol (g) for *Stylophora pistillata* ramets exposed to temperature treatments of ambient control 25 °C (light blue), chronic warming of +2.5 °C (27.5 °C, medium blue), and chronic warming of +5 °C (30 °C, dark blue) for 4, 11, and 26 weeks, followed by four weeks at 25 °C (30 weeks, vertical dashed line). The horizontal dashed line in panel A indicates when P:R = 1. Significant effects determined from two-way ANOVAs are indicated in the top of the panel. Uppercase letters indicate significant differences among time points, while lowercase letters indicate significant differences among temperatures within a time point. Statistical details are in Table S4.

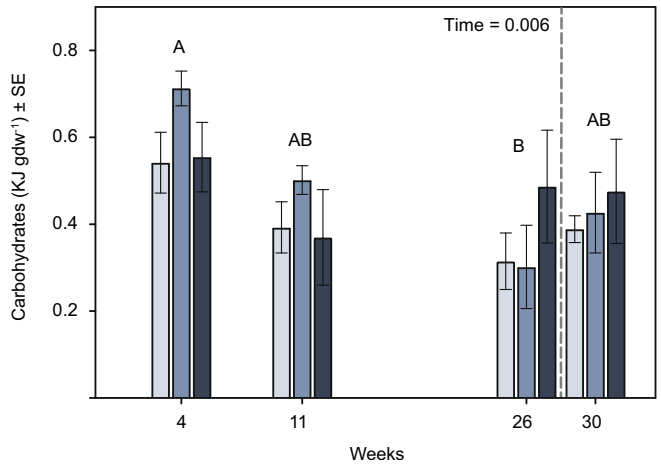


**Fig. 4.** Average carbohydrates (±1 SE) for *Stylophora pistillata* ramets exposed to 25 °C (pale blue), 27.5 °C (medium blue), and 30 °C (dark blue) for 4, 11, and 26 weeks, followed by four weeks at 25 °C (30 weeks, vertical dashed line). Significant differences determined from a two-way ANOVA are indicated in the top of the panel. Uppercase U letters indicate significant differences among time points. No significant differences were detected among temperature treatments within a time point. Statistical details are in Table S4.

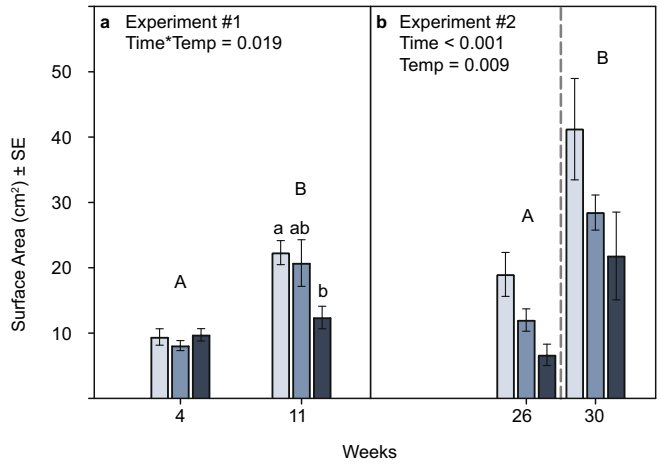


**Fig. 5.** Average surface area (±1SE) for *Stylophora pistillata* ramets exposed to temperature treatments of ambient control 25 °C (light blue), chronic warming of +2.5 °C (27.5 °C, medium blue), and chronic warming of +5 °C (30 °C, dark blue) after 4 and 11 weeks (a) and 26 weeks and 30 weeks (b). All corals were at 25 °C from 26 to 30 weeks (vertical dashed line). The solid dashed line indicates the separation between Experiment #1 and Experiment #2. Significant differences determined from a two-way ANOVA within each experiment are indicated in the top of the panel. Uppercase letters indicate significant differences between time points within each experiment. Lowercase letters indicate significant differences among temperature treatments within each time point. Statistical details are in Table S4.

that had been reared in aquaria for >30 years, allowing us to isolate the genetic effect from other confounding variables. Thus, the results here represent a robust analysis of *S. pistillata* to chronically elevated baseline temperatures. The physiological profiles of the corals chronically exposed to 27.5 °C and 30 °C changed over time, with significant temperature effects on overall physiological profiles at 4 and 26 weeks (Fig. 2b & d). While 26 weeks at 27.5 °C and 30 °C did not cause severe bleaching or mortality, and corals maintained most physiological functions, chronic elevated baseline temperature was metabolically demanding and diminished coral growth as measured by changes in surface area (Fig. 3a, f). Here we explore in-depth the responses of *S. pistillata* to elevated baseline temperature.

### 4.1. Initial effects of elevated baseline temperature

Exposure to elevated temperatures initially caused negative changes in the overall physiological profiles of corals, which was driven by increased $F_v/F_m$ and decreased coral pigmentation and lipid concentrations (Figs. 2a, b & 3b, d, f). Thermal optimum temperatures for corals vary depending on Symbiodiniaceae species, host species, and collection location (Jurriaans and Hoogenboom, 2020; Banc-Prandi et al., 2022; Dilernia et al., 2023). Optimal temperatures for *S. pistillata* in the Red Sea range from 28.3 °C in the northern Red Sea to 30.4 °C in the southern Red Sea (Banc-Prandi et al., 2022). Increased $F_v/F_m$ at 27.5 °C is consistent with optimal photosynthetic efficiency being closer to 27.5 °C than 25 °C (Krueger et al., 2017). However, this pattern does not hold throughout the remainder of the experiment, suggesting that optimum temperatures for the endosymbiont and coral holobiont may change seasonally (Jurriaans and Hoogenboom, 2020) or decrease over time due to a cumulative negative impact of sustained elevated temperature (Grottoli et al., 2014; McRae et al., 2022). Thus, even though the corals pigmentation was a bit paler at 27.5 °C and 30 °C, and chlorophyll content did not change, their photosynthetic efficiency was optimized (Fig. 3b–d). The disconnect between both measures of coral color (chlorophyll and pigmentation intensity) is most likely an artifact of different sampling methods. Pigmentation intensity was measured within a distance of 1 cm from the apical tip to capture maximum changes in pigmentation while chlorophyll was measured on a homogenous sample of each ramet. Lastly, lipid concentrations decreased in the 30 °C treatment after 4 weeks, but surface area was the same for all treatments, suggesting that these corals initially catabolized lipids in response to elevated temperature in order to maintain P:R and growth (Figs. 3a, f & 5) (Grottoli et al., 2014; Schoepf et al., 2015). However, 30 °C may be the upper limit for this method of self-preservation as previous experiments with *S. pistillata* show declined rates of calcification in only 28 days at 31 °C (Tremblay et al., 2016).

Corals in all treatments had lower $F_v/F_m$, lipids, cholesterol, and carbohydrate concentrations at 11 weeks in experimental tanks compared to 4 weeks (Figs. 3 & 4), potentially due to differences in culture conditions of the parent genets and the experimental tanks, or differences in physiology due to coral size (i.e., parent genets vs experimental ramets). Parent colonies live in large culture tanks (300-500 L) with a variety of coral species, fish, and invertebrates to mimic a natural reef environment. Experimental coral ramets were in small experimental tanks (20 L) in monoculture. The two week acclimation period may not have been long enough for the ramets to adjust to the experimental tanks, to fully heal after fragmentation which can take up to 75 days (Counsell et al., 2019), for their microbiomes to stabilize to tank conditions (Ide et al., 2022), or some combination of these factors. Nevertheless, comparisons among temperature treatments within each time point are still robust as all coral ramets were treated the same. Therefore, these results show initial effects of elevated baseline temperatures at 27.5 °C and 30 °C.

### 4.2. Corals survive but do not thrive under chronic elevated baseline temperature

Although *S. pistillata* was initially affected by increases in baseline temperatures, temperature effects on physiological profiles, metabolic demand, algal physiology, pigmentation, or energy reserves were no longer detectable among treatments after 11 weeks (Figs. 2 & 3). However, corals in the 30 °C treatment grew the least between 4 and 11 weeks (Figs. 5, S2), resulting in corals being 50 % smaller than control corals. In contrast, other species of coral in Taiwan maintain growth for up to 12 weeks at 30 °C yet experience greater mortality than *S. pistillata* in this experiment (McRae et al., 2022). The cumulative effect of elevated temperature was apparent by 26 weeks as physiological profiles differed due to decreases in P:R at elevated temperature compared to the 25 °C treatment (Figs. 2d & 3a) and corals were 70 % smaller in

the 30 °C treatment and 30 % smaller in the 27.5 °C treatment compared to controls at 25 °C. Decreased growth is often correlated with bleaching resistance (Walker et al., 2023) and may contribute to the ability of *S. pistillata* to tolerate elevated baseline temperatures for up to six months with no bleaching or mortality. Additionally, coral growth bands in massive colonies provide evidence that coral calcification has declined in the last 30 years (De'ath et al., 2009, 2013; Tanzil et al., 2009; Carricart-Ganivet et al., 2012; Lough and Cantin, 2014; Yan et al., 2019), supporting our findings of decreased growth in response to elevated baseline temperatures. While the effect on metabolism was subtle in the 27.5 °C treatment, corals in the 30 °C treatment had compromised P:R due to increased respiration (Fig. 3a). High respiration is an indicator of increased metabolic demand that can lead to decreased energy reserve concentrations, calcification, and linear extension after long-term exposure to high temperatures (Roik et al., 2024). In this study, maintenance of tissue biomass and energy reserves at 27.5 °C and 30 °C appears to come at the cost of skeletal accretion but allows these corals to survive changes in baseline temperatures up to 30 °C. Similar trade-offs have previously been observed in long-term experiments (Grottoli et al., 2014; Schoepf et al., 2015; Levas et al., 2018; Roik et al., 2024), with decreased calcification but maintenance of lipids, proteins, and carbohydrates, suggesting shifts in resource allocation to maintain physiological function at elevated baseline temperature.

The contribution of algal symbiont differences to the ability of this coral to maintain important physiological function remains to be determined. From a majority ITS2 sequence perspective, symbiont shuffling of all corals at 11 and 26 weeks was not observed, as coral ramets exhibited consistent association with the A1 ITS2 sequence, indicative of *Symbiodinium microadriaticum* (Fig. S3). Besides algal assemblage, coral feeding may underly the ability of corals in this experiment to maintain physiological function. *S. pistillata* has high baseline feeding rates and relies on heterotrophy as a source of nutrients for tissue building and calcification when healthy (Ferrier-Pagès et al., 2003, 2010; Tremblay et al., 2012), but decreases feeding when bleached (Ferrier-Pagès et al., 2003, 2010; Dobson et al., 2021). However, none of the corals in this study bleached and the consistent concentration of cholesterol in all treatments throughout the experiment (Fig. 2g) indicates that heterotrophic assimilation was maintained (Grottoli et al., 2004; Rodrigues et al., 2008; Solomon et al., 2020) under chronic exposure to 27.5 °C and 30 °C. It seems that feeding alone was insufficient to fully mitigate the effects of increased temperature as corals shifted resource allocation away from growth and towards maintenance of biomass, and lipid and carbohydrate concentrations under chronic 30 °C temperatures (Figs. 3–5). Finally, the lack of bleaching or mortality at temperatures above the Gulf of Aqaba MMM (Kochman-Gino and Fine, 2023) points to a strong genetic component of thermal resistance in northern Red Sea *S. pistillata* that expresses even after >30 years in culture tanks at 25 °C (Table S1). Overall, corals survived elevated baseline temperature of 27.5 °C and 30 °C for six months but did not thrive, as evidenced by increased respiration and decreased growth.

### 4.3. Recovery after one month at 25 °C

After only four weeks of recovery at 25 °C, physiological profiles of all corals were similar. It also appears that the symbiosis between the coral host and Symbiodiniaceae did not suffer long-term effects of increased temperatures as coral ramets in both heated treatments were darker in color after four weeks of respite at 25 °C (Fig. 3d). Increases in coral pigmentation could be due to re-stabilization of nutrient cycling between the coral host and Symbiodiniaceae once temperature increases were alleviated (Rädecker et al., 2021). When healthy, coral symbionts in *S. pistillata* are the first site of nitrogen assimilation from heterotrophic feeding (Martinez et al., 2022). Since corals maintained heterotrophy in this experiment, once temperatures returned to 25 °C corals may have been able to share a larger portion of heterotrophic nitrogen with symbionts, allowing symbionts to re-gain color at the apical tip. This interpretation is consistent with the observed similarity of P:R in all treatments, indicating a return to baseline metabolic demand. Although corals continued to be smaller at 30 weeks (Fig. 4), this appears to be a legacy effect of decreased growth from the previous 15 weeks, since the change in surface area of coral was similar in all treatments after the 4 weeks at baseline temperature of 25 °C (Fig. S2). Therefore, although corals were negatively affected by 6 months of elevated baseline temperatures, they were able to fully recover after only one month at 25 °C.

## 5. Implications

*S. pistillata* from the northern Red Sea is considered to be a bleaching resistant coral because it is minimally affected by heat-stress exposures as high as 32 °C for up to six weeks (Grottoli et al., 2017; Dobson et al., 2021; Evensen et al., 2021; Kochman et al., 2021). However, we showed that sustained sub-bleaching shifts in baseline temperature for up to 26 weeks (6 months) have a cumulative negative impact and compromise this coral's metabolic function and growth. Although 27.5 °C and 30 °C are not considered temperatures that would elicit a heat-stress response in *S. pistillata* from the northern Red Sea (Evensen et al., 2021; Kochman-Gino and Fine, 2023), sustained exposure to 27.5 °C for 26 weeks begins to compromise coral growth, while 30 °C is metabolically demanding and compromises coral growth substantially. Despite physiological recovery after only four weeks at 25 °C, reduction in coral growth at sustained elevated temperatures will ultimately result in declines in overall reef accretion (Jury et al., 2024) and rugosity, decreases in the ability of *S. pistillata* to compete for space, and possibly alter coral reef ecosystem function (Perry et al., 2013; Cornwall et al., 2021). However, *S. pistillata* provides hope that resistant corals may be able to tolerate shifts in baseline temperature that are up to 26 weeks long and no more than 27.5 °C with only a small cost to growth. The number of months of respite below 27.5 °C will be critical for the long-term persistence of even the most resilient coral. *S. pistillata* further shows that resilient corals could sustain prolonged increases in baseline temperature of 30 °C, and also fully benefit with respite a cooler temperature. These results are especially interesting because the coral in this experiment were reared in aquaria for more than 30 years and had not experienced natural daily or seasonal fluctuations in temperature or the shifts in baseline temperatures that have occurred over the past three decades. Therefore, these results are a conservative estimate of the acclimation potential of *S. pistillata* to baseline shifts in ocean temperature. It is possible that *S. pistillata* in the Gulf of Aqaba today may show even greater acclimatization capacity than seen in this experiment, but additional study would be needed to confirm this hypothesis. As baseline temperatures continue to increase, corals will experience longer periods at temperatures near summer mean monthly maximum (Ruela et al., 2020). While *S. pistillata* appears to have the capacity to survive the projected shifts in baseline temperature, it may not thrive. Marine heat waves and ocean acidification stress will only exacerbate the metabolic cost and reduction in growth (Dobson et al., 2021; Klein et al., 2022; McLachlan et al., 2022) even if the corals do not die from heat stress. Our findings indicate that even thermally tolerant coral will see declines in colony size under future ocean conditions and may suffer trade-offs not explored in this study.

## CRediT authorship contribution statement

**Ann Marie Hulver:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Éric Béraud:** Writing – review & editing, Investigation, Formal analysis. **Shannon Dixon:** Writing – review & editing, Investigation. **Aurélie Moya:** Writing – review & editing, Investigation, Formal analysis. **Rachel Alderdice:** Writing – review & editing, Investigation. **Agustí Muñoz-Garcia:** Writing – review & editing, Resources. **Christian R. Voolstra:** Writing – review & editing, Supervision, Resources, Project

administration, Funding acquisition, Conceptualization. **Christine Ferrier-Pagès:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Andréa G. Grottoli:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Andrea Grottoli reports financial support was provided by National Science Foundation. Andrea Grottoli reports financial support was provided by The Ohio State University Office of International Affairs. Ann Marie Hulver reports financial support was provided by Ohio State University Friends of Orton Hall. Christian Voolstra reports financial support was provided by German Research Foundation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank J Welter, L Weaver, A Krupar, and Z Watson for help with sample analysis. This research was funded by the National Science Foundation (GR 1838667) and The Ohio State University Office of International Affairs to AGG and The Ohio State University School of Earth Sciences Friends of Orton Hall to AMH. AM was supported the German Research Foundation (DFG) project number 445529174. All corals were transferred from Centre Scientifique de Monaco (CITES code MC003) to The Ohio State University (CITES code US154) under CITES permits.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.180234.

## Data availability

Data is attached as Supplementary Material

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