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REPORT

Susceptibility of *Acropora tenuis* to consecutive thermal stress

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Abstract Elevated temperatures cause mass coral bleaching, leading to reef degradation. The frequency of bleaching events is increasing, and severe bleaching events have been predicted to occur annually in the next few decades. However, the ability of corals to acclimate and adapt to these unprecedented stresses remains unknown. In this study, we investigated how three years of consecutive thermal stress affect the adult fragments of the coral *Acropora tenuis*. The fragments were exposed to temperature treatments of ~ 28 °C (control) and ~ 31 °C (heat stress) until they began to bleach. We measured the survival rate, maximum quantum yield of photosystem II (*Fv*/*Fm*) of the symbiotic algae, and algal density of the fragments. The survival rate of the fragments under thermal stress decreased over the three-year period, reaching 20% by the end. Additionally, we observed a decrease in *Fv*/*Fm* and a reduction in algal density in the stressed fragments compared to those in the control fragments during all three years of the thermal stress period. These findings collectively suggested that consecutive bleaching-level thermal stress increases the susceptibility of corals to heat.

Keywords Consecutive thermal stress · Bleaching · Coral · Ocean warming · Climate change · *Acropora tenuis*

Introduction

Sea surface temperatures are rapidly and significantly increasing as a consequence of climate change (Hoegh-Guldberg and Bruno 2010; Hughes et al. 2017, 2018; IPCC 2023), posing a significant threat to ecosystems worldwide, particularly coral reefs (Berkelmans and Oliver 1999; Veron et al. 2009; Frieler et al. 2012; Hughes et al. 2018). Coral reef ecosystems are experiencing an unprecedented decline as a result of the prolonged increase in sea temperatures (Hoegh-Guldberg et al. 2007; Eakin et al. 2009; Veron et al. 2009; Hoegh-Guldberg 2011; Hughes et al. 2018). Evidence suggests that one-third of all reef-building coral species may become endangered (Carpenter et al. 2008), potentially leading to the collapse of coral reef ecosystems (Hoegh-Guldberg et al. 2007; 2017; Pratchett et al. 2021; Obura et al. 2022). The ability of coral holobionts to acclimatize or adapt plays a crucial role in the recovery of reefs following such events (Weis 2010; Logan et al. 2014; Van Oppen et al. 2015).

Dinoflagellates that form symbiotic associations with scleractinian corals can transfer up to 95% of their photosynthetic output to the coral hosts (Muscatine 1990). However, under unfavorable conditions such as high temperatures and solar irradiance, the symbiotic contribution is significantly reduced (Grottoli et al. 2004). Impairment of the symbionts' photosynthetic function is one of the initial responses to environmental perturbations (Brown 1997; Warner et al. 1999), which disrupts the symbiotic relationships between corals and their algal symbionts (Fagoonee et al. 1999). This phenomenon is commonly

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known as "coral bleaching" (Fitt et al. 2001; Muller-Parker et al. 2015; Hughes et al. 2017, 2018). Thus, coral bleaching can result in mortality if the symbiotic function is not recovered or if the coral is deprived of its primary energy source for an extended period of time (Brown 1997). Mass coral bleaching and consequent mortality events such as unprecedented bleaching in terms of stress intensity, duration, and geographical extent occurred in the Caribbean in 2023 (Goreau and Hayes 2024) and have been predicted to occur across the Indo-Pacific in 2024, likely devastating a high percentage of corals (Hoegh-Guldberg et al. 2023) and causing extensive damage to hundreds of kilometers of reefs over the period of three months of the bleaching onset, putting them at risk of extinction. However, the response of corals to environmental disturbances may vary among populations, individual colonies, and physiological traits (Schulte et al. 2011; Forsman 2015; Parkinson et al. 2015). Consequently, such disturbances have significant negative consequences for the health and survival of coral reefs worldwide (Loya et al. 2001).

While acclimatization, which involves physiological changes at the individual level, is an important process (Baird et al. 2009; Liew et al. 2020; Ziegler et al. 2014; Hackerott et al. 2021), it should be contrasted with adaptation, which includes genetic or evolutionary changes. Acclimatization can be considered a potential short-term strategy for corals to cope with changing environmental conditions (Coles and Brown 2003). Corals exhibit varying responses to bleaching stimuli depending on their resistance, resilience, and acclimatization levels. Acclimatization can contribute to improved heat tolerance (Palumbi et al. 2014). In other words, corals faced with thermal stress and subsequent bleaching show higher tolerance and resistance to bleaching in later thermal events (Maynard et al. 2008; Pratchett et al. 2013; McClanahan 2017; Singh et al. 2023), indicating their acclimatization.

Understanding acclimatization is crucial for predicting coral bleaching thresholds. Recurrent bleaching is becoming an increasingly severe problem worldwide (Hughes et al. 2018); however, our understanding of the effects of consecutive stress on individual coral colonies remains limited. By exposing the adults to consecutive years of thermal stress and studying their responses, we can gain insight into the resistance of coral species to extreme thermal conditions. It is essential to bridge this knowledge gap regarding the impact of climate change on the physiological conditions of adult corals, as annual severe bleaching of coral reefs is predicted to become widespread in the future (Bruno and Selig 2007; Hooidonk et al. 2013; Hughes et al. 2018).

In this study, we evaluated the impact of consecutive thermal stress on adult colonies of the coral species *Acropora tenuis*, commonly found in the Pacific region (Veron 2000; Hirose and Hidaka 2006). This species is known to be highly susceptible to bleaching in relation to other coral species (Obura 2001; Carpenter et al. 2008; van Woesik et al. 2011). The aim of this study was to determine whether *A. tenuis* could rapidly acclimatize to consecutive thermal stress over a three-year period imposed by climate change. Our findings and observations have important implications for reef regeneration and recovery from climate-related mortality events.

Materials and methods

Experiment design

In August 2018, six healthy *A. tenuis* colonies (branching morphology) were carefully collected from a depth of five to six meters in the northern region of Sesoko Island, Okinawa, Japan (26°39′N, 127°52′E). The colonies were safely transported to the Sesoko Marine Station, University of the Ryukyus. In 2016 and 2017, coral reefs around Okinawa experienced thermal anomalies (< 5.5 degree heating weeks, DHWs), and moderate bleaching was reported in some sites (Singh et al. 2019). Therefore, the colonies of the target species were collected from a site with low thermal anomalies (< 4 DHWs), no bleaching experience in 2016, and no thermal stress anomaly in 2017 (Singh et al. 2019). To prepare them for the experiment, each of the six healthy colonies was carefully divided into two fragments, one for the control condition and the other for the thermal stress condition, with a total of twelve fragments. These fragments were then placed in flow-through tanks and placed under experimental light conditions for a period of ten days to allow for proper acclimation to their new surroundings and facilitate wound healing prior to the start of the experiment. Following a ten-day acclimation period, the fragments were stored at two different temperatures: ~ 28 °C (control condition) and ~ 31 °C (thermal stress condition). Thermal stress was defined as a ~ 3 °C increase above the maximum monthly mean (MMM) temperature in the study site and ~ 2 °C increase above the coral bleaching threshold. The MMM value of the study site was 28.4 °C according to the National Oceanic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) 5-km satellite regional virtual station for the Northern Ryukyus Island (Liu et al. 2014, 2017). Three separate tanks were used for thermal stress treatment, and a heater was used to gradually increase the temperature from the ambient temperature of ~ 28 °C to the target temperature of ~ 31 °C over a three-day period, with an increase rate of 0.5 °C every 6 h. Throughout the experiment, temperature was recorded every 10 min using a temperature logger (HOBO Pro V2; Onset Computer

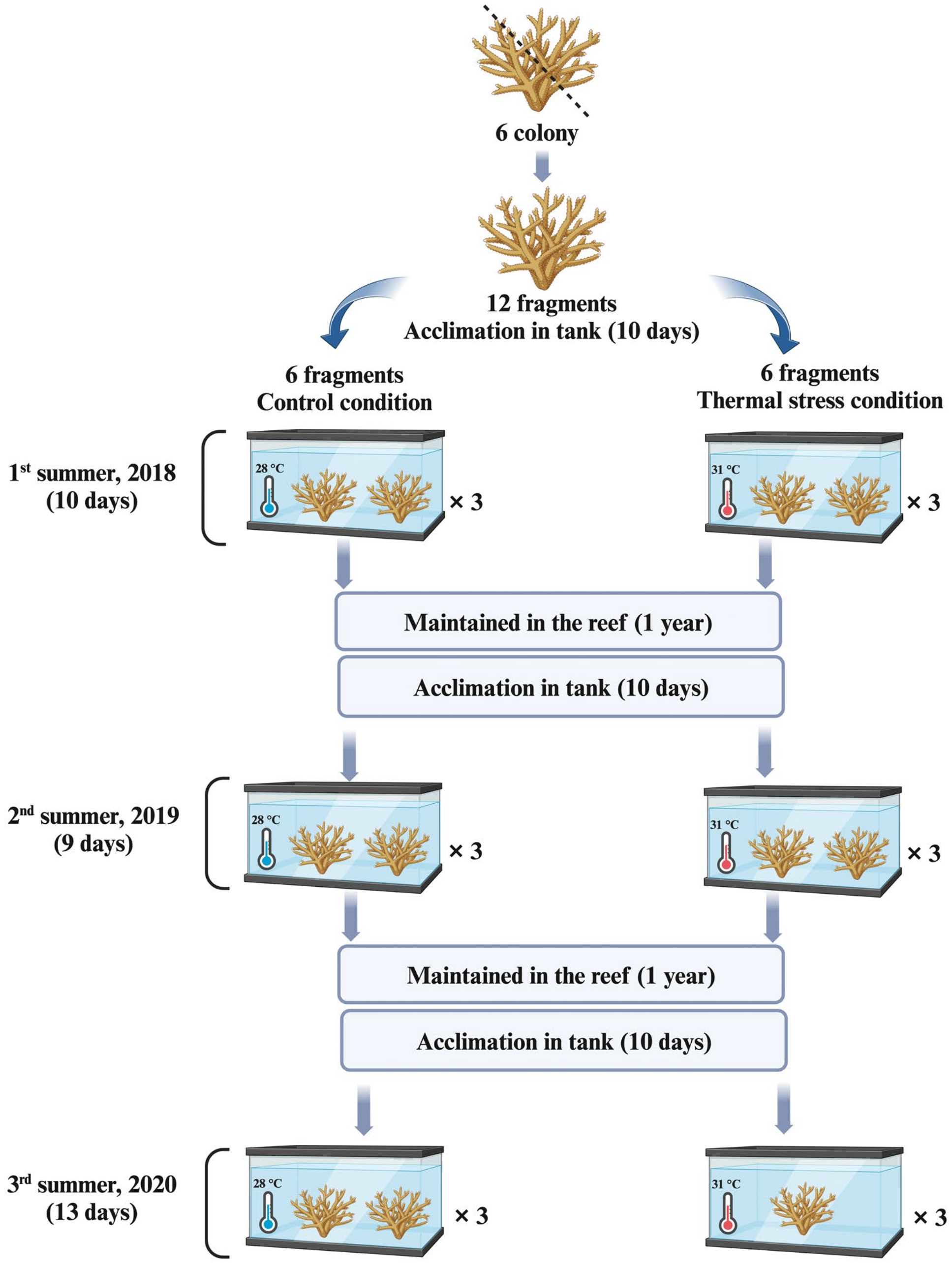


Fig. 1 Experimental design of the study examining the effects of consecutive thermal stress on *Acropora tenuis* fragments. The corals were exposed to both control conditions (~28 °C in the blue aquarium) and thermal stress conditions (~31 °C in the red aquarium) for three years. After the thermal stress period, they were maintained in the reef for one year until the next thermal stress event, and the acclimation before experiment lasted for ten days

Corporation, MA, USA). The fragments were maintained under 12 h of light (~200 µmol photons $m^{-2}S^{-1}$) and 12 h of darkness using LED lights (AI Hydra HD LED, Aqua Illumination, USA). The other three tanks were maintained at the ambient temperature of ~28 °C, serving as the control group for comparison (Fig. 1).

The thermal stress experiment was conducted over three consecutive years (in August 2018, 2019, and 2020) and can be classified as a moderate-duration heat stress experiment as defined by Grottoli et al. (2021). After the completion of the thermal stress experiment each year, all *A. tenuis* fragments were carefully transplanted back to the reef on underwater stainless-steel rectangular tables (0.5 m above the ground) and maintained until the next thermal stress (Fig. 1).

Prior to each year's thermal stress, all fragments that were kept in the reef were transferred back to the flow-through tanks and subjected to experimental light condition for a period of ten days to allow for proper acclimation. During this period, the fragments that had previously been exposed to thermal stress were once again subjected to high temperatures of ~31 °C. In the first year, signs of bleaching were observed after 10 days of exposure to thermal stress. Similarly, in the second year, the experiment lasted for

9 days, and bleaching became evident during this timeframe. In the third year, the thermal stress experiment lasted for 13 days, and signs of bleaching were observed during this period. These varying durations were designed to capture the temporal dynamics of coral response to thermal stress. Over the two years of the experiment, the fragments did not face in situ thermal anomalies before and after transplant to the sea, and sea temperatures were lower than the threshold temperature for corals (Fig. 1).

Brightness (coral color measurements)

The coral's response to heat stress was evaluated throughout the three-year experiment. During the thermal stress experiments conducted each year, all fragments in each treatment were photographed daily under identical illumination using a digital camera (Canon Powershot G10; Canon Inc., Tokyo, Japan) with constant white balance settings. A Coral Health Chart (www. coralwatch.org) was employed as the color scale to assess the degree of health, paling, or bleaching, which served as a reliable indicator of changes in symbiont density and chlorophyll a and c_2 contents. Photographs of the three parts of each fragment were analyzed using the histogram function with the RGB channel in Adobe Photoshop CC 2015.

The D hue, consisting of six distinct colored areas (D1, D2, D3, D4, D5, and D6), was utilized for the studied species. D1 (white) represented the bleached fragments, showing a value of 236, whereas D6 (brown) represented the unbleached state which color measurement per fragment, showing a value of 60. Further details regarding this parameter can be found in Siebeck et al. (2006).

Maximum quantum yield of photosystem II

Throughout the experiment, on a daily basis, the maximum quantum efficiency of photosystem II (Fv/Fm) of the symbiotic algae in each temperature treatment was measured at three specific locations: the upper third, middle, and lower third at a distance of 2−3 mm from the coral tissue of each fragment. A diving pulse amplitude-modulated (PAM) underwater fluorometer (Walz, Effeltrich, Germany) was utilized for these measurements. The fragments were measured one hour after sunset following a period of 60 min in the dark-adapted state, which is a reliable indicator of the maximum photochemical efficiency of PSII (Demmig and Björkman 1987). The measurements were repeated until signs of bleaching were detected, occurring at 10, 9, and 13 days in the first, second, and third year, respectively.

Symbiotic algal density and chlorophyll contents

Each year of the experiment, small branches were collected from each fragment before and after heat exposure to measure the density of symbiotic algae and chlorophyll contents following the protocol described by Nakamura et al. (2005). The collected fragments were then frozen at −80 °C until further analysis. To extract the coral tissue from each sample, an air-pik was used, and filtered seawater was added to a Ziploc bag, followed by homogenization. The resulting homogenate was washed three times by centrifugation (4500 × g for 20 min at 4 °C) and mixed using a vortex mixer (GeniaTM Vortex Mixer Model, Scientific Industries, Bohemia, NY, USA). The extract solutions were divided into two aliquots. The initial slurry was used to count the number of symbiotic algae cells through five replicates of hemocytometer counts under a light microscope (Olympus, Tokyo, Japan) at 400 × magnification following a standard procedure. The paraffin wax dipping technique was employed to estimate the surface area of each branch (Veal et al. 2010). The second aliquot was centrifuged at 12,000 rpm for 15 min to extract chlorophyll a and c_2. The resulting pellet was mixed with 1 mL of 90% acetone and quantified after 24 h in the dark at 4 °C until the measurement. The absorbances of the extract solutions were measured at different path lengths (630, 664, and 750 nm), as described by Jeffrey and Humphrey (1975), and standardized based on the surface area of the branch.

Survivorship of the fragments

Each year of the experiment, the fragments were transferred to the reef after the thermal stress experiment, and their health status was visually monitored monthly and photographed using an underwater digital camera.

Statistical analysis

Shapiro–Wilk and Levene's tests (Quinn and Keough 2002) were used to investigate the normality and homogeneity assumptions of the variances prior to the statistical analysis, respectively. Linear mixed effect models (LMM) followed by Tukey's honestly significant difference (HSD) post-hoc pairwise comparisons were used to assess the differences in photosynthetic efficiency and brightness between the treatments in each year's thermal stress experiment using the 'emmeans' package in R (Lenth 2019). The temperature treatments and days were considered fixed effect factors, while the colony and tank were considered random effects. Akaike information criterion (AIC) was used to compare the alternative models (Tables S1), and the model with the lowest AIC value was selected for the statistical analysis.

Table 1 The results of comparison for brightness and *Fv/Fm* of *Acropora tenuis* fragments between different treatments in three years of consecutive stress

	Years	Contrast	*n*	Estimate	SE	*df*	*t*.ratio	*p* value
Brightness	2018	Control-stress	C = 6, S = 6	− 0.32	0.09	4	− 3.248	**0.03**
	2019	Control-stress	C = 6, S = 5	− 0.41	0.12	3.7	− 3.422	**0.02**
	2020	Control-stress	C = 5, S = 3	− 0.22	0.09	3.1	− 2.438	0.08
Fv/Fm	2018	Control-stress	C = 6, S = 6	0.01	0.005	4	2.83	**0.04**
	2019	Control-stress	C = 6, S = 5	0.04	0.02	3.6	2.15	0.1
	2020	Control-stress	C = 5, S = 3	0.11	0.02	2.45	5.08	**0.02**

Significant *p* value ($p < 0.05$) indicated in bold

Symbiotic algal density and chlorophyll content ($a + c_2$) of the fragments in the treatments were determined before and after stress each year using the Wilcoxon signed-rank test. The Kaplan–Meier log-rank test was used to evaluate the differences in the survival of fragments between the treatments over the three years of the experiment. The significance level for the statistical analysis was set at $p < 0.05$. All statistical analyses were conducted using the R software.

Results

Brightness (coral color)

Compared to the control, the fragments subjected to thermal stress exhibited significantly higher average coral color scores after 10 days in the first year, 9 days in the second year, and 13 days in the third year (Table 1) (Fig. 2a). Among these fragments, the most significant variations in whiteness hue observed in 2019, 2020, and 2018 were 166.09 ± 9.29 SE (mean ± standard error), 143.68 ± 11.62 SE, and 142.69 ± 9.07 SE, respectively, at the end of each year's thermal stress experiment (Fig. 2a, Tables 1, S2).

Maximum quantum yield of photosystem II

The maximum quantum yield of photosystem II (*Fv/Fm*) differed significantly between the control and experimental groups during the study period. In the first year, over a 10-day period, the thermal stress fragments showed a decrease in *Fv/Fm* (LMM, $p = 0.04$, $n = 6$ for each treatment, Fig. 2b, Tables 1, S2). In the second year, the control fragments consistently outperformed the thermal stress fragments throughout the 9 days of the experiment (LMM, $p = 0.1$, $n = 6$ for the control treatment and $n = 5$ for the stress treatment, Fig. 2b, Tables 1, S2). Lastly, in the third year, we observed a noticeable reduction in *Fv/Fm* starting from day four of exposure to elevated temperatures (LMM, $p = 0.02$; $n = 5$ for the control treatment and $n = 3$ for the stress treatment, Fig. 2b, Tables 1, S2).

Symbiotic algal density and chlorophyll content

We measured the symbiotic algal density and chlorophyll ($a + c_2$) content in all coral fragments over the course of three years. Exposure to the elevated temperature of ~ 31 °C resulted in a significant change in symbiotic algal density throughout the experimental period (Wilcoxon signed-rank test, $p < 0.05$; Fig. 3a, Table S3). In contrast, the effect of thermal stress on chlorophyll ($a + c_2$) concentration per cell was significantly greater than that of the control treatment (Wilcoxon signed-rank test, $p < 0.05$, Fig. 3b, Table S3) at the end of the experiment in all three years.

Effects of thermal stress on coral survival

After conducting the initial thermal stress experiment in 2018, we found that 83.33% of the stressed fragments survived the subsequent year (2019). In 2020, the survival rate of stressed fragments decreased to 50%. Meanwhile, the control fragments exhibited a 100% survival rate in 2019, which decreased to 83.33% in the 2020 thermal stress experiments. The survivorship of fragments between the two treatments showed a significant difference over the course of three consecutive years of stress (Kaplan–Meier survival estimate, $p < 0.001$; Fig. 4).

Discussion

In this study, we investigated the effects of consecutive thermal stress on the adult colonies (fragments) of *Acropora tenuis* for the first time. Our findings revealed that consecutive moderate-duration thermal stress can increase the susceptibility of adult *A. tenuis* fragments to heat stress. Previous studies conducted in various reef locations across the Indo-Pacific Ocean have indicated that branching coral species were among the first to bleach and die (Brown and Suharsono 1990; Hoegh-Guldberg and Salvat 1995; Sutthacheep et al. 2010). To date, the implications of three years of consecutive thermal stress on the predicted degradation of reefs have not been studied. The results of the present study clearly demonstrate that moderate-duration

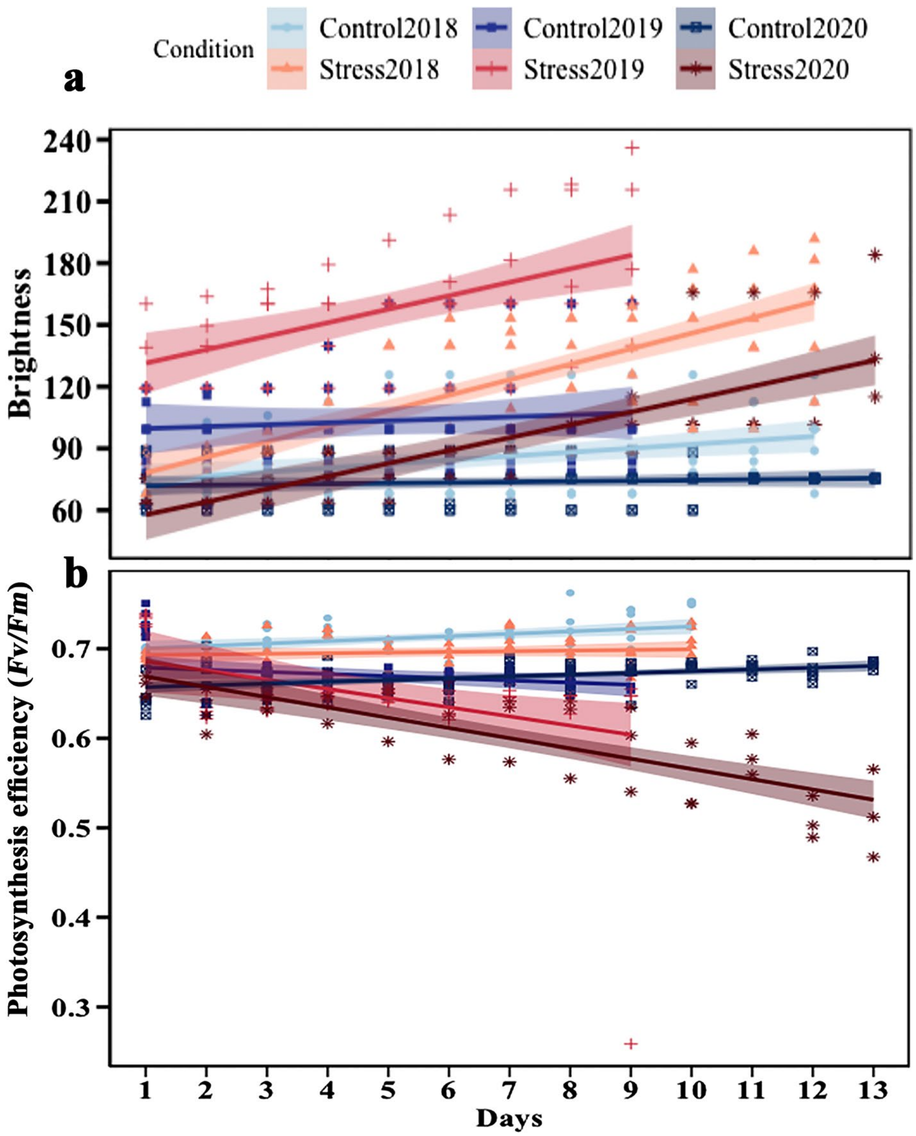


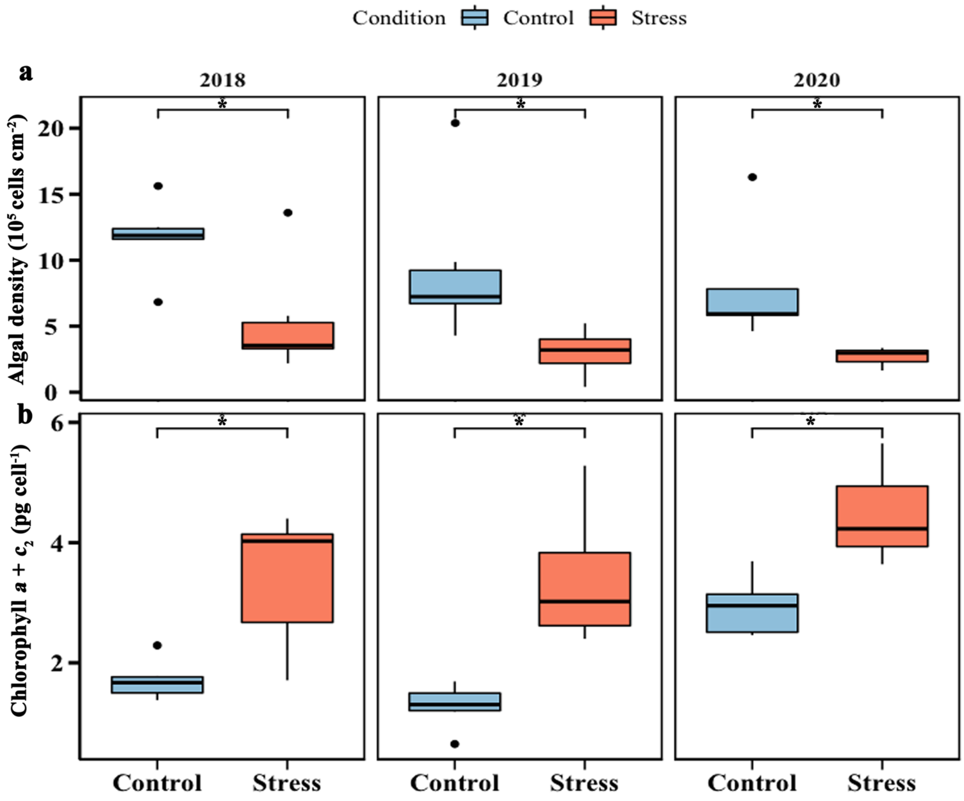
Fig. 2 Laboratory thermal stress experiment studying the fragments of *Acropora tenuis*: **a** Effect of thermal stress on the brightness of the fragments in the three-year experiment (in 2018 and 2019: LMM, $p < 0.05$; in 2020: LMM, $p = 0.08$). The scale values of 60 and 236 are equivalent to 100% health and bleach status, respectively. **b** *Fv*/*Fm*: maximum quantum yield of photosystem II for all fragments (in 2018 and 2020: LMM, $p < 0.05$; in 2019: LMM, $p = 0.1$)

consecutive direct thermal stress leads to a decline in the survival rate of coral fragments.

Coral species display varying degrees of susceptibility to heat stress (Brandt 2009; Gintert et al. 2018; Marzonie et al. 2023; Tavakoli-Kolour et al. 2023). In the present study, fragments subjected to thermal stress treatment each year exhibited a decrease in photosynthetic efficiency and symbiotic algal density compared to those of the control fragments, and bleaching was observed in the stress treatment fragments. Additionally, in each year following heat stress exposure, mortality was observed in some fragments (Fig. 4, 5). The decline in photosynthetic efficiency and loss of algal symbionts represent the rapid responses to thermal stress exposure (Warner et al. 1999), which may increase the risk of mortality (Schoepf et al. 2015). However, the loss of algal symbionts due to heat stress is not necessarily the cause of coral mortality (Anthony et al. 2007). Instead, heat stress can reduce phototrophic carbon by destabilizing the carbon translocation process in algae (Anthony et al. 2007). Consequently, corals may face mortality even when bleaching is not visibly apparent in coral colonies due to the collapse in the nutrient cycling of symbiotic algae (Rädecker et al. 2021).

Thermal stress and consequent bleaching events can alter the ability of corals to survive other ecological disturbances, determining whether they emerge as “winners” or “losers” based on their susceptibility to increased heat stress (Loya et al. 2001; Grottoli et al. 2014). Corals can acclimate to heat stress over relatively short periods with rapid adjustments in their physiological responses (Palumbi et al. 2014). Interestingly, *A. tenuis* has been shown to use adaptation strategies in response to single bleaching events by producing heat-tolerant generations (Hazraty-Kari et al. 2022). Nevertheless, the results of this study suggested that

Fig. 3 Effect of thermal stress on the physiological response of *Acropora tenuis*. **a** The response of the physiological parameters of symbiont cell densities of *A. tenuis* to thermal stress in the three-year experiment (Wilcoxon signed-rank test, $p < 0.05$) after the thermal experiment. **b** Chlorophyll *a* and c_2 (Chl $a + c_2$) concentration measured in the three-year experiment after the thermal experiment (Wilcoxon signed-rank test, $p < 0.05$). The box plot center shows the mean of the data



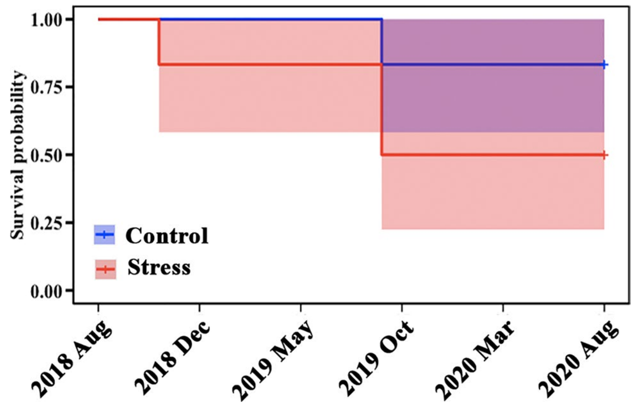


Fig. 4 Monthly survivorship of fragments of *Acropora tenuis* under thermal stress and control condition for three years in the reef (Kaplan–Meier survival estimate, $p < 0.001$)

the consequences of moderate-duration consecutive thermal stress negatively affected the survival of the adult fragments of *A. tenuis*, as previously observed in the juveniles of this species (Hazraty-Kari et al. 2023a; Hazraty-Kari et al. 2023b). Consecutive thermal stress can render certain species more vulnerable to bleaching, ultimately leading to a long-term decline in coral reefs (Grottoli et al. 2014).

The observed delay in coral colony bleaching in subsequent heat stress events may be related to the coral's acclimatization ability (Pandolfi et al. 2011; Logan et al. 2014). Observations following natural bleaching incidents in the Pacific separated by several years suggested that certain branching species more susceptible to single bleaching events may have in some cases adapted (Guest et al. 2012; Maynard et al. 2008; Pratchett et al. 2013; Lachs et al. 2023). Despite the observed delay in coral bleaching in the third year compared to those in the first and second years, our findings indicated that the fragments did not acclimate to moderate-duration thermal stress after three years. Some coral species exhibit a significantly high acclimatization capacity, leading to a delay in consecutive bleaching events (Logan et al. 2014). The duration and intensity of heat stress events can result in distinct physiological and ecological reactions in corals (Fordyce et al. 2019; Evensen et al. 2023; Tavakoli-Kolour et al. 2023). Short-term and low-intensity heat pulses may induce acclimatory responses in subsequent heat stress events (Ainsworth et al. 2016; Singh et al. 2023). However, such coral species are more vulnerable to consecutive intense thermal stress (i.e., one that triggers noticeable bleaching) and do not show an acclimatization response or beneficial stress memory. Nevertheless, additional research is required to determine the performance and acclimatization potential of other species in the face of consecutive thermal stress, which will have implications for the future of reef ecosystems.

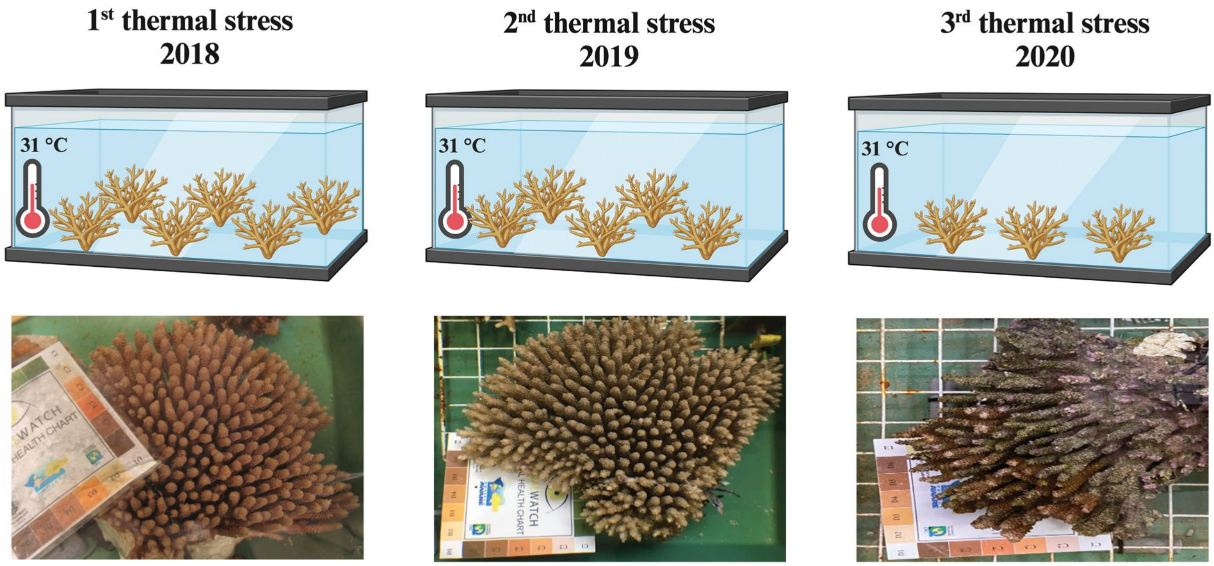


Fig. 5 Illustration of consecutive thermal stress showing that the adult fragments of *Acropora tenuis* could not acclimate over the three-year period

Conclusions and implications

Our findings unequivocally demonstrated that consecutive moderate-duration thermal stress negatively affects the adult individuals of the reef-building coral *A. tenuis*. This finding highlights the fact that three years of moderate-duration consecutive stress did not provide a beneficial stress memory in this species. However, shorter duration and small pulse of thermal stress may result in an acclimatory response in this species; therefore, further research is necessary to investigate the annual thermal stress experienced by various coral species over multiple years, with different thermal stress durations and severity. Such studies will aid in identifying which global reefs are at risk of long-term degradation on a worldwide scale. Additionally, studies should be carried out to determine the impact of thermal stress on coral physiology and resilience, as well as to determine the ability of different coral species to adapt to climate change. It is important to note that conducting such studies presents significant challenges.

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Author contributions Sanaz Hazraty-Kari conceived and designed the experiments, investigation, visualization, data analysis, and writing—original draft, review, and editing. Parviz Tavakoli-Kolour was involved in the investigation, data analysis, visualization, review, and editing. Takashi Nakamura contributed to the analytic tools, review, and editing. Masaya Morita assisted in the supervision, data analysis, and writing—review and editing.

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