

Competitive effects of the macroalgae *Caulerpa taxifolia* on key physiological processes in the scleratinian coral *Turbinaria peltata* under thermal stress

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Abstract

With the degradation of coral reefs induced by climate change and local environmental stressors, an increasing abundance of macroalgae is observed in many reefs. The sublethal damage caused by macroalgae on coral included inhibiting growth, development and reproduction. However, few studies have focused on the dynamics of the interspecific relationship between coral and macroalgae, which may change under climate change. Thus, the effects of thermal stress on the competition between the plate-like coral *Turbinaria peltata* and macroalgae *Caulerpa taxifolia* were explored in this study. The responses of corals exposed to the culture water of algae and those in direct contact with algae were also compared. The results showed that at ambient temperature (27 °C), coculture with *C. taxifolia* reduced the growth rate and protein content of *T. peltata* by 57.7~65.5% and 37.2~49.0%, respectively, and significantly increased the activities of antioxidant enzymes. Direct contact with *C. taxifolia* enhanced the activities of antioxidant enzymes further compared to coral exposed to algae. The density and chlorophyll *a* content of symbiotic zooxanthellae were not obviously influenced based on whether the coral *T. peltata* was cultured with *C. taxifolia*. When the temperature was increased by 3 °C, the growth rate of *T. peltata* decreased to the level of corals exposed to *C. taxifolia* at ambient temperature, whereas the same pattern was seen in the increase in antioxidant enzyme activity. Additionally, the density and chlorophyll *a* content of symbiotic zooxanthellae, as well as the feeding rate of coral, showed an evident decrease with increasing temperature. However, thermal stress was only shown in the feeding rate when *T. peltata* was in indirect contact with *C. taxifolia*. The interaction of macroalgae contact and thermal stress was evident in the growth rate, protein content, feeding rate and catalase activity (CAT) of coral compared to coral intact with algae under ambient temperature. These results indicated that the negative effects of the macroalgae *C. taxifolia* on the coral *T. peltata* are comparable to those of ocean warming, and the competition between corals and macroalgae may be more intense under thermal stress.

Highlights

1. Zooxanthella density and chlorophyll *a* slightly decreased when the coral *Turbinaria peltata* was in contact with the macroalgae *Caulerpa taxifolia*, but this phenomenon was alleviated under thermal stress.
2. *Caulerpa taxifolia* damaged key physiological processes and triggered a much greater oxidative stress response in *Turbinaria peltata*, which was more remarkable under thermal stress.
3. The effect of thermal stress was approximately comparable to that of indirect contact with macroalgae.

1. Introduction

In recent years, with the combined effects of climate change and anthropogenic impacts, the coral reef worldwide has been undergoing severe degradation (Leggat W et al. 2022). In 2016, > 30% of corals bleached in the Great Barrier Reef, and the coral reef ecosystem is undergoing an ecological phase

transition to succession of a large algal bed (Mumby P J et al. 2013). In healthy coral reefs, macroalgae are important functional communities that play important roles in stabilizing reef structure, generating primary productivity, maintaining nutrient cycling in reef areas, and providing food sources for herbivores (Dubinsky Z and Stambler N. 2011). Nevertheless, there is competition for habitat between macroalgae and corals that is detrimental to corals. The competitive mechanisms include occupying the original ecological niche (Manikandan B and Ravindran J 2017), triggering coral bleaching by allelopathy (Roberta et al. 2014), weakening photosynthesis performance (Rasher D B et al. 2011), causing the retraction of polyps (Jompa J and Mccook L J 2003), and increasing the number of pathogenic microorganisms (Clements C S et al. 2020; Rasher D B and Hay M E 2010). Studies have documented the negative effects of direct contact with macroalgae (Coyer J A et al. 1993; Manikandan B et al. 2021), resulting in reduced calcification of coral growth, fecundity, survival rate and settlement rate (Fong J et al. 2020; Jason E and Tanner 1995; Leong R C et al. 2018; Rasher D B and Hay M E 2010). In addition to the effect of seaweed on corals, larval recruitment is also affected by the species-specific macroalgae effect, resulting in lower fixation and survival rates (Leong R C et al. 2018).

However, the extent of the impact induced by macroalgae on corals varied between species and exposure conditions (Brown, K.T. et al. 2019; Fong J et al. 2020). Rölfer L et al. (2021) have shown that the combined effects of ocean warming, acidification and macroalgae contact could significantly reduce the light calcification rates of coral. However, the competitive ability of macroalgae, which determines the outcome of coral-algal competition, seems to have a relationship with seasonal cycles and temporal cycles, which can be related to the abundance, biomass and composition of macroalgae, as well as the seasonal dynamics of temperature, $p\text{CO}_2$, and light intensity *in situ* (Brown KT et al. 2019; 2020). Moreover, the sensitivity of various macroalgae to environmental stressors is different. For example, intermediate levels of ocean warming could enhance the growth and production of *Laurencia* and *Lobophora*, which was not the case for *Sargassum* (Gouvea et al. 2017; Fulton et al. 2014). In addition, overfishing and eutrophication have been shown to lead to an increased growth rate of some kinds of macroalgae (Lapointe B E and Bedford B J 2010), which may indirectly enhance the competitive ability of macroalgae. Therefore, to better understand the resilience of coral reef ecosystems in the future, it is necessary to determine how coral-algal interactions fluctuate under global and local stressors.

Ocean warming is a major cause of coral bleaching (Leggat W et al. 2022). The successive bleaching events in 2016–2017, with the global monthly maximum sea surface temperature increasing to 30°C–31°C, devastated Australia's Great Barrier Reef and resulted in an 89% decline in larval recruitment in 2018 compared to historical levels (Hughes T P et al. 2017,2019; Lough J M et al. 2018). Ocean warming will alter the physiological and biochemical state of corals, which will affect competition between macroalgae and corals (Chadwick N E et al. 2011). To investigate the effects of macroalgae on hermatypic coral under ocean warming, the plate-like coral *Turbinaria peltata* and macroalgae *Caulerpa taxifolia*, which are common species in the Xuwen Coral Reef National Nature Reserve of China, were selected as study species. *C. taxifolia* is a multinucleate siphonous green alga and is known to have great invasive potential worldwide (Zubia M et al. 2020). Furthermore, it has been found that *C. taxifolia* can

produce potential allelochemicals, such as monoterpenes and sesquiterpenes (Guerriero A et al. 1992, 1993). Given that *C. taxifolia* usually grows on various hard substrates that contain large numbers of live coral colonies, the physical and chemical impacts cannot be underestimated. Thus, to evaluate the effect of physical and chemical effects, the indirect-contact (exposed) group was set up to investigate the chemical effects, and the direct-contact group can be used to explore the combined effects of physical and chemical processes. Through the physiological performance of coral and symbiotic algae, as well as the antioxidant enzyme activity of coral, the results can provide basic data and guidance for the development, protection, and management of coral reef resources.

2. Materials And Methods

2.1 Sample collection

T. peltata and *C. taxifolia* were collected from Xuwen Coral Reef National Nature Reserve (109° 55' E, 20° 16' N) at a depth of approximately 4 m. They were transported to the laboratory and cultured in two 200-L tanks at a temperature of 26.5°C, pH of 8.0, salinity of 33, and 200 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ with a 12: 12 h light/dark cycle. Both corals and algae were allowed to acclimate in separate holding tanks for 5 days. After acclimation, the coral colony was cut into 54 fragments of approximately 4 cm in diameter, epoxied on the ceramic bases, and placed in the holding tank for one week until the tentacles extended normally.

2.2 Experimental design

The experimental operating system is shown in Fig. 1. According to shared socioeconomic paths (SSPs) (Zhongming Z et al. 2021), ambient (27°C) and SSP2-4.5 (30°C) conditions were established in this study. After 5 days of domestication, the corals were cut into pieces of approximately 4 cm in diameter, fixed on the ceramic base with aqua rubber, and placed in a 200-L tank for one week until the corals elongated normally. Then, 54 coral nubbins were randomly placed in 18 10-L experimental tanks. 1°C per day, the temperature in each experimental group increased to the set temperature. The first three days were the temperature adjustment period. After each group reached the set temperature, the same amount of macroalgae was interacted with the coral samples in the following three ways: (1) No algae were added to the culture system, i.e., the control group (Fig. 1a). (2) Algae were cultured in external algae boxes, and there was no direct contact between the algae and the coral samples, which are referred to as corals exposed to algae (Fig. 1b). (3) In the same room, algae and corals were cultured together, and the height of the algae was set parallel to the coral samples, which is referred to as the direct contact group (Fig. 1c). Two control groups and four experimental groups were formed with three corals in each group and three parallel groups. The spoiled algae were replaced each day to ensure that the experimental group had 25 g of fresh algae. Fifty percent of the seawater was replaced every three days. The experimental samples of each group were taken 28 days later.

Table 1

Summary of values of water chemistry data for all treatments.

	Coral		Coral exposed to algae		Coral contact with algae	
	27°C	30°C	27°C	30°C	27°C	30°C
Temperature [°C]	27.1 ± 0.1	30 ± 0.2	26.9 ± 0.3	30 ± 0.2	27 ± 0.2	30 ± 0.2
PH	8.03 ± 0.04	8.03 ± 0.04	8.02 ± 0.04	8.03 ± 0.05	8.02 ± 0.04	8.03 ± 0.05
Salinity	32.1 ± 0.6	32.2 ± 0.5	32.1 ± 0.6	32.1 ± 0.7	32.2 ± 0.4	32.0 ± 0.6

2.3 Growth rate

Weights of fragments were measured on a balance (accuracy = 0.01 g) using a technique for weighing in water (Wen Huang et al. 2018). A glass beaker contained 1 L of filtered seawater (27°C, salinity 32), and the nubbins were placed on the bottom of the beaker for the growth rate measurements. Before each measurement, the surface of the coral ceramic base was lightly brushed with a toothbrush to remove algae. The growth rate (mg d^{-1}) was calculated as $\frac{M_{t_i} - M_{t_0}}{T_i}$, where M_{t_0} and M_{t_i} represent the nubbin quality of growth at the beginning and T_i of the experiment, respectively, and T_i represents the duration in days. The measurement was repeated every 7 d. Data were normalized to skeletal surface area determined by the aluminium foil technique (Marsh J A 1970).

2.4 Feeding rate

Prior to measurement, nubbins were moved into the feeding tanks (1 L) with an *Artemia* concentration of $\sim 2 \text{ ind mL}^{-1}$, while one tank served as a control (without coral). After an incubation period of 1 h, the coral nubbins were rinsed with seawater and returned to their respective positions in the experimental tanks. The feeding rate was calculated as the decline in *Artemia* and normalized per polyp. The measurement was repeated every 7 d.

2.5 Zooxanthellae density and Chl *a* content

After culture, the nubbins were detached with a waterpick (0.45 μm filtered seawater), and the slurry was homogenized uniformly. An aliquot of the slurry was taken and centrifuged ($4000 \text{ rpm min}^{-1}$, 4°C, 10 min) to remove the supernatant. Part of the pellet was suspended in 5 mL formaldehyde to count the zooxanthellae density under the microscope with a blood counting plate. Another portion was resuspended in 8 mL methanol. The pigments were extracted at 4°C for 24 h. The extract was centrifuged ($4000 \text{ rpm min}^{-1}$, 4°C, 10 min), and Chl *a* was determined according to the method described by Ritchie R. J 2006. Data were normalized to skeletal surface (Marsh J A 1970).

2.6 SOD and CAT

Tissue was accurately weighed, and normal saline was added at a ratio of weight (g):volume (mL) = 1:9 to make a 10% tissue homogenate. The tissue was centrifuged using a freezing centrifuge (4000 rpm

min⁻¹, 10 min, 4°C), and the quantitative supernatant was collected to measure the SOD and CAT activities determined in the dilution using kits (A001-1-1, A007-1-1, Nanjing Jicheng, China) and finally a BCA kit to determine the protein concentration (A045-3-1, Nanjing Jicheng, China). The total protein content of each sample was determined, and the activity unit of the two enzymes was standardized as U mg prot⁻¹.

2.7 Data analysis

The results are presented as the means ± standard deviations. Data were tested for homogeneity of variance (visual inspection of residuals vs. fitted values), and normality of residuals was tested using the Shapiro–Wilk normality test. All response data of corals were tested using a two-factor analysis of variance (ANOVA) with “temperature” and “algae” as fixed factors, including the interaction term. Tukey’s test was used to identify significant differences between temperature treatments. A post hoc Fisher’s least significant difference (LSD) test was used to determine differences between algal treatments. The data were analysed and graphed using GraphPad Prism 8.0. P < 0.05 was considered a significant difference.

3. Results

3.1 Seawater chemistry monitoring

As shown in Table 1, temperature, pH and salinity values were averaged during the experiment and measured continuously during the experiment (30 d). The high standard deviation is due to daily variation.

Table 2

Two-way ANOVA output of different variables for *T. peltata*, with bold values indicating significant effects on the variable. *F*=*F* value; *p* =*p* value (significance <0.05).

Variable	Source of variation	F	p
Growth Rate	Algae	F(2,8) = 28.8	<0.01
	Temperature	F(1,4) = 7.8	0.049
	Interaction	F(2,8) = 28	<0.01
Feeding Rate	Algae	F(2,8) = 14.6	<0.01
	Temperature	F(1,4) = 119.8	<0.01
	Interaction	F(2,8) = 4.7	0.04
Zooxanthellae	Algae	F(2,8) = 0.75	0.5
	Temperature	F(1,4) = 21.9	0.01
	Interaction	F(2,8) = 9	0.01
Chl <i>a</i>	Algae	F(2,8) = 1.6	0.27
	Temperature	F(1,4) = 90.9	<0.01
	Interaction	F(2,8) = 7.2	0.02
Protein	Algae	F(2,8) = 31.9	<0.01
	Temperature	F(1,4) = 4.3	0.11
	Interaction	F(2,8) = 2.9	0.12
SOD	Algae	F(2,8) = 38.8	<0.01
	Temperature	F(1,4) = 16.0	0.02
	Interaction	F(2,8) = 2.4	0.16
CAT	Algae	F(2,8) = 10.0	<0.01
	Temperature	F(1,4) = 64.5	<0.01
	Interaction	F(2,8) = 5.1	0.04

3.2 Results of macroalgae on key physiological processes

Figs. 2a-b show that under different treatments, the density and pigment content of zooxanthellae exhibited similar trends. At 27 °C, the coculture of *C. taxifolia* and *T. peltata* (whether contacted or not) generated a peaceful decrease in the average zooxanthellae density and chl *a* content, but the effect was not statistically significant. Notably, there was no remarkable effect on either under thermal stress. Without seaweed, increasing temperature resulted in a 44.6% decrease in zooxanthellae density ($P<0.05$) and a 58% decrease in Chl *a* content ($P<0.01$), which disappeared when cocultured with algae.

The results of the feeding rate are displayed in Fig. 3a. The macroalgae effect did not appear at ambient temperature. Under a 3 °C increase, predation occurred most conspicuously, attaining 12.8 ± 1.1 ind polyp⁻¹ h⁻¹ when the interaction of *C. taxifolia* was in contact, which reflected the synergistic effect of thermal

stress and macroalgae ($F=4.7$, $P=0.04$). In fact, temperature had a significant effect on the feeding rate regardless of the macroalgae interaction.

As shown in Fig. 3b, the protein content was negatively impacted by macroalgae. At ambient temperature, exposure to algae caused coral to lose 37.2% protein. Although contact with algae made the mean protein content of coral even lower, the difference was not obvious. As the temperature increased, the mean protein content of coral without algae had a slight drop, which made the indirect contact effect not evident. However, the direct interaction with algae resulted in the lowest protein content of 1.2 ± 0.3 mg cm⁻². No detrimental effects on coral protein content were observed when the temperature was elevated in either algae treatment ($P=0.11$). Therefore, there was no interaction between seaweed and temperature treatment ($F=2.9$, $P=0.12$).

As indicated by the change in buoyant weight, the growth rate (Fig. 3c) of corals in the control was highest at 27 °C, with a mean value of 4.1 ± 1.4 mg cm⁻² d⁻¹. The coculture with macroalgae decreased the growth rate of coral by 57.7~65.5%, and the effect of contact was slightly more severe than that of the noncontact coculture system. Under elevated temperature pressure, the growth rates were not different in either algae treatment. Heat stress had a tremendous inhibitory effect on the growth rate in the pure coral culture system, which resulted in an 83.4% decline ($P<0.05$). The elevated temperature resulted in corals coming into contact with macroalgae growing at the lowest rate, with a value of 0.57 ± 0.45 mg cm⁻² d⁻¹, but there was no difference among the treatments. The interaction between temperature and algae was obvious ($F=28$, $P<0.01$).

As shown in Figs. 4a-b, macroalgae treatments increased the antioxidant capacity of corals in all conditions. At a surrounding temperature (27 °C), the exposure to algae increased the coral by 1.85-fold compared to SOD. Moreover, the SOD content was higher in the contact condition (288.1 ± 16.6 U mgprot⁻¹). In addition, with the temperature climbing to 30 °C, the mean SOD content increased 1.77-fold compared to the coral, while direct interaction with macroalgae resulted in the highest level of 354.3 ± 59.56 U mg prot⁻¹. However, in the coculture system, there was no prominent discrepancy caused by rising temper, indicating that both factors did not interact ($F=2.4$, $P=0.16$).

Simultaneously, the CAT content was also enhanced in the coculture system. Under ambient temperature, exposure to algae caused coral to rise CAT by 5.3-fold, which is comparable to contact. Factually, floating temper triggered the mean value of CAT content in the pure coral system to increase by approximately 7.1-fold, and in the coral-algal contact, it was more than two times higher than for the others. The combined effect of temperature and macroalgae affected the coral ($F=5.1$, $P=0.04$).

Discussion

This study explored the crucial issue of how physiology and the oxidative stress response of the hermatypic are affected by macroalgae under various temperatures. We set up different treatments of the foliaceous macroalgae *C. taxifolia* to act on the coral *T. peltata* under ambient temperatures (27 °C) and

an increase of +3 °C, including exposure and contact. Specifically, our results demonstrate that macroalgae can prominently damage the physiology of coral and trigger slight zooxanthellae escape. In addition, coral enhanced the antioxidant capacity to alleviate it. In addition, combined with rising temperature, there is a remarkable synergistic effect on the physiology of coral, in which contact with algae is much more severe than exposure. However, the zooxanthellae escape phenomenon can be modestly mitigated by macroalgae under thermal stress.

In this study, it was found that the average density and chl a content of zooxanthellae decreased to a certain extent under the influence of *C. taxifolia*, but no obvious bleaching phenomenon occurred. Without algae, the density of zooxanthellae most distinctly decreased by 44.6% in the warming group, similar to the content of chl a decreasing by 58%, which showed that the interaction between *T. peltata* and *C. taxifolia* could slow down or even eliminate the decline of the density and pigment under heat stress. A number of studies (Smith J E et al. 2006; Rasher D B et al. 2010; Fong J et al. 2020) reported that the chlorophyll photochemical efficiency (Fv/Fm) dropped dramatically in the interaction between corals and macroalgae, indicating that benthic seaweed can affect the photosynthesis of zooxanthellae. Rölfer (2020) found that the photosynthetic to respiration rate (P/R) dramatically dropped when *Cladophora* contacted Porites. Additionally, Brown K. T et al. (2019) discovered that the photosynthetic efficiency of coral would sink in winter and float in summer when *Halimeda heteromorpha* contacted *Acropora intermedia*, which indicated that seasonal shifts might transform the coral-algae interaction.

It was remarkable that the predation of *T. peltata* was slightly affected by *C. taxifolia* at ambient temperature. However, ocean warming would whittle down predation, which resembles Chen Shen et al. (2021). Ferrier-Pagès C et al. (2010) proved that three coral species were compared in feeding rate at 31 °C, and *Pistillata* showed a vivid decrease. Moreover, our study proved that proximity to *C. taxifolia* promoted this phenomenon. In summary, thermal stress is the crucial factor in the predation of *T. peltata*, which leads to a superposition effect when contiguous with macroalgae.

The results also indicated that the impacts of seaweed can harm the protein content of corals. Damage to coral tissue by contact with seaweed has long been known. Bender D et al. (2012) asserted that coral samples lost the tissue and growth rate of bone due to allelopathy mechanisms after *Acropora* contacted *Cladophora*. In fact, macroalgae will transfer many more allelopathic substances when corals approach it, which will alter the structure of the microbial community and thus injure the physiological process of corals (Fong J et al. 2020), ultimately giving rise to protein content loss. Under stress, blocked corals with thicker tissues may overcome the effects of zooxanthellae loss through catabolism (DeCarlo TM and Harrison HB. 2019). This may be the reason why zooxanthellae are not tremendously affected by seaweed.

This issue is deemed that under the action of macroalgae, the growth rate of coral in ambient surroundings is inhibited, which is consistent with previous studies (Jason E. et al. 1995; Rölfer L et al. 2020; Rebecca V T et al. 2012; Vermeij M J et al. 2009). It is affected by a combination of macroalgae and thermal stress. Brown K T et al. (2019) also demonstrated that coral growth was reduced or even

negative at 30 °C when in contact with algae. Longo GO et al. (2015) discovered that corals that were weakened at 30 °C, and contact with *Halimeda heteromorpha* further contributed to a decreased growth rate and increased mortality rate. These results may be due to the simultaneous decline in the autotrophic and heterotrophic properties of corals under the impacts of thermal stress or benthic macroalgae, resulting in a sink of protein content and ultimately exacerbating the growth rate.

When coral under thermal stress produces reactive oxygen species (ROS) (Blanckaert A et al. 2021), which damage host mitochondria (Nii C M and Muscatine L. 1997). It may be produced by zooxanthellae mainly due to PS II dysfunction caused by damage to the D1 protein (Warner M E. 1999). Downs C A (2002) documented that when exploring the varied oxidative stress response of coral under seasonal change, the SOD content in summer was 3 times greater than that in winter. Furthermore, this study discovered that corals produced more SOD under seaweed and increasing temperature or the synergistic effect of both. In other words, it is illustrated that weakened corals are more vulnerable to competition from algae, which is the same as in Guillermo (2010). The results suggested that the level of both antioxidant enzyme activities when *C. taxifolia* indirectly contacted *T. peltata* was equal to that under thermal stress alone, which indicated that the pressure triggered by seaweed allelochemicals on coral was equivalent to that induced by increasing temperature, and the varied oxidative stress response of coral needed to resist both heat stress and macroalgae allelochemicals. Additionally, this study indicated that under indirect contact treatment, there was no significant difference in the oxidative stress response of corals between the various temperature groups. The temperature effect was more obvious in CAT under direct contact treatment, which may be related to the decrease in protein content in coral tissues caused by rising temperature under direct contact treatment. Due to the dramatic decrease in the protein content of coral tissues in the direct contact group, the amount of antioxidant enzymes produced by coral is not enough to resist the damage of ROS. Therefore, it is necessary to improve the enzyme activity of coral tissues per unit protein to alleviate the stress caused by ROS accumulation.

Declarations

CRedit authorship contribution statement

Jian Rong Fu: Investigation, Conceptualization, Methodology, Data analysis and visualization, Writing - original draft, Writing - review & editing. Jie Zhou: Investigation, Conceptualization, Methodology, Data verification and analysis, Writing - review & editing, Funding acquisition. Jia li Zhou: Investigation, Software, Methodology. Hui ting Yang: Investigation and conceptualization. Yan Ping Zhang: Investigation, Conceptualization, Methodology. Li Liu: Resources, Funding acquisition, Project administration, Supervision, Writing - review & editing.

Declaration of competing interest

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

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Figures

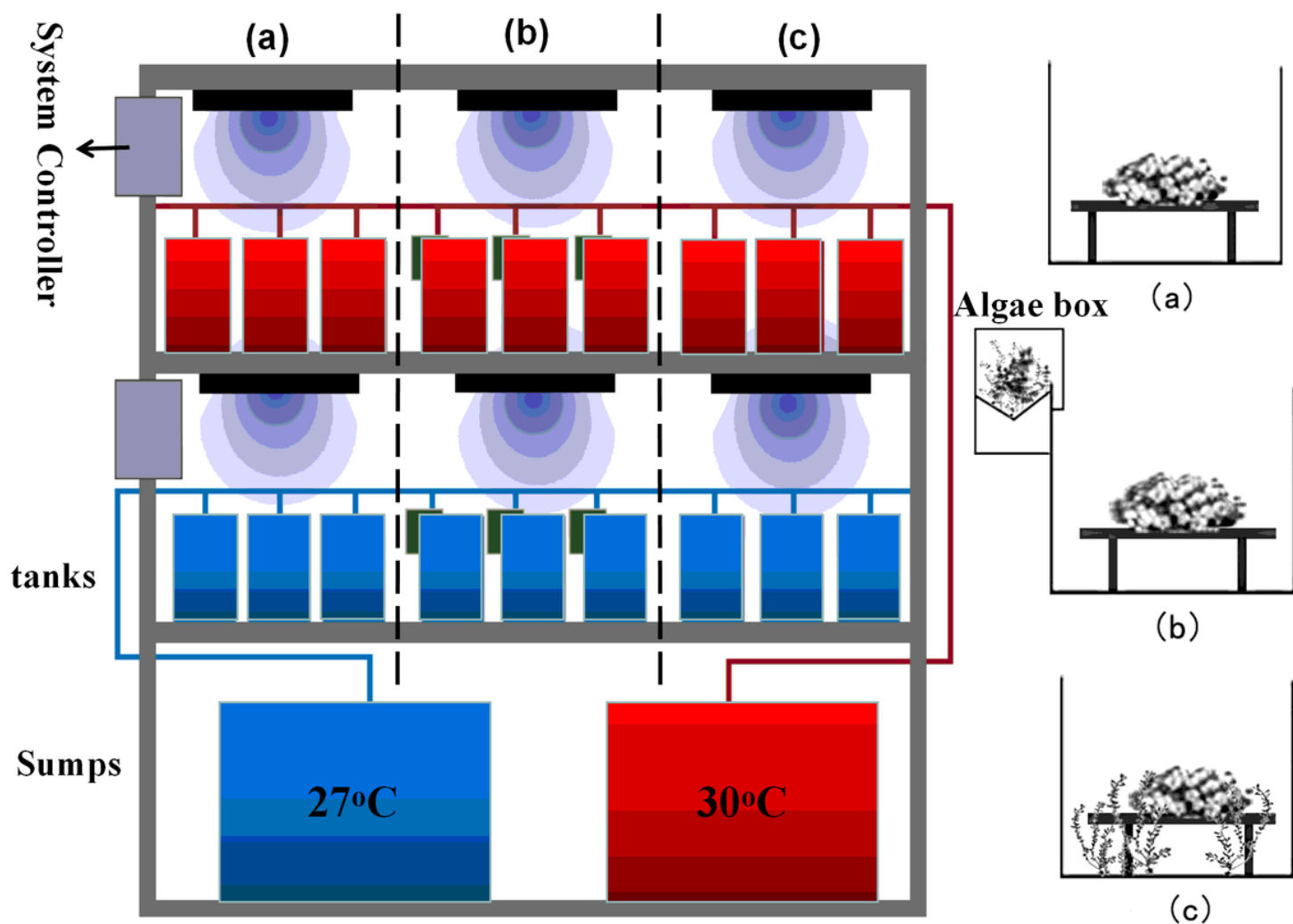


Figure 1

Experimental operating system. System control (grey) with a feedback loop to adjust the conditions. Seawater at different temperatures of 27 °C (blue) and 30 °C (red) was heated in different collection sumps and then fed into the tanks. Macroalgae treatments are applied, (a) *T. peltata* (b) *T. peltata* exposed to *C. taxifolia*, Algae box (green). (c) *T. peltata* in contact with *C. taxifolia*. Each group had three parallel tanks with three corals per tank.

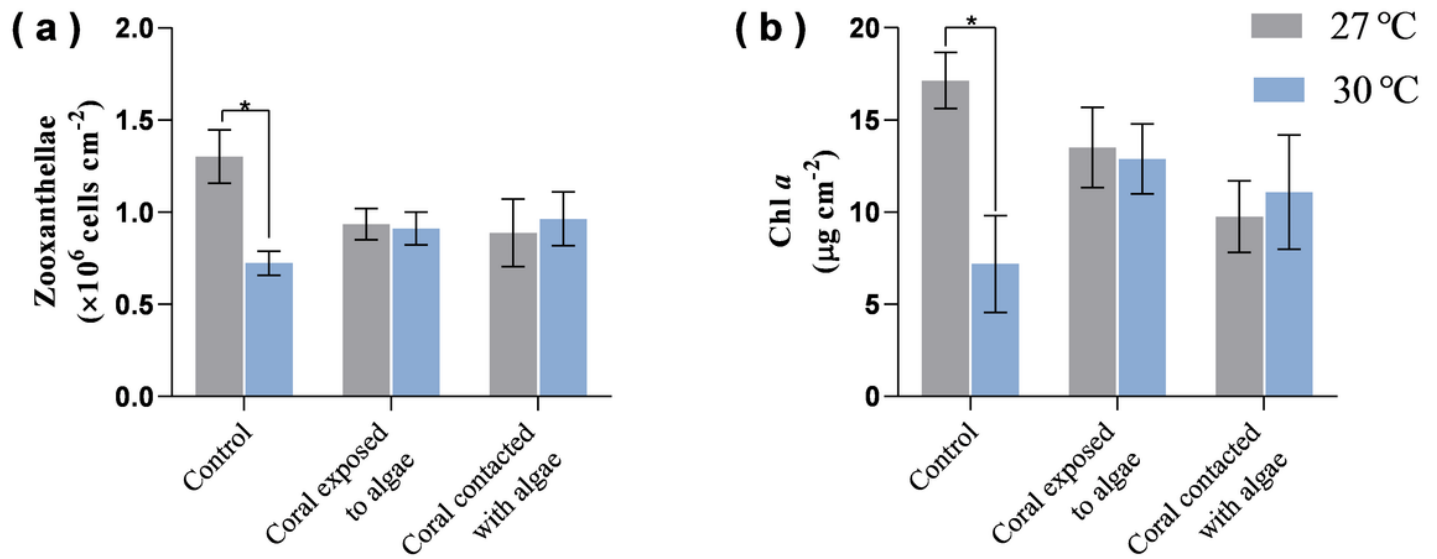


Figure 2

The effect of different temperatures of 27 °C (grey) and 30 °C (blue) on the (a) zooxanthellae and (b) Chl *a* of macroalgae-treated corals after 4 weeks of the experiment. Different letters indicate that there are significant differences between macroalgae treatments at the same temperature ($P < 0.05$), * indicates that there are significant differences between different temperatures ($P < 0.05$). Data are expressed in terms of the mean $\pm$ standard deviation, $n=3$.

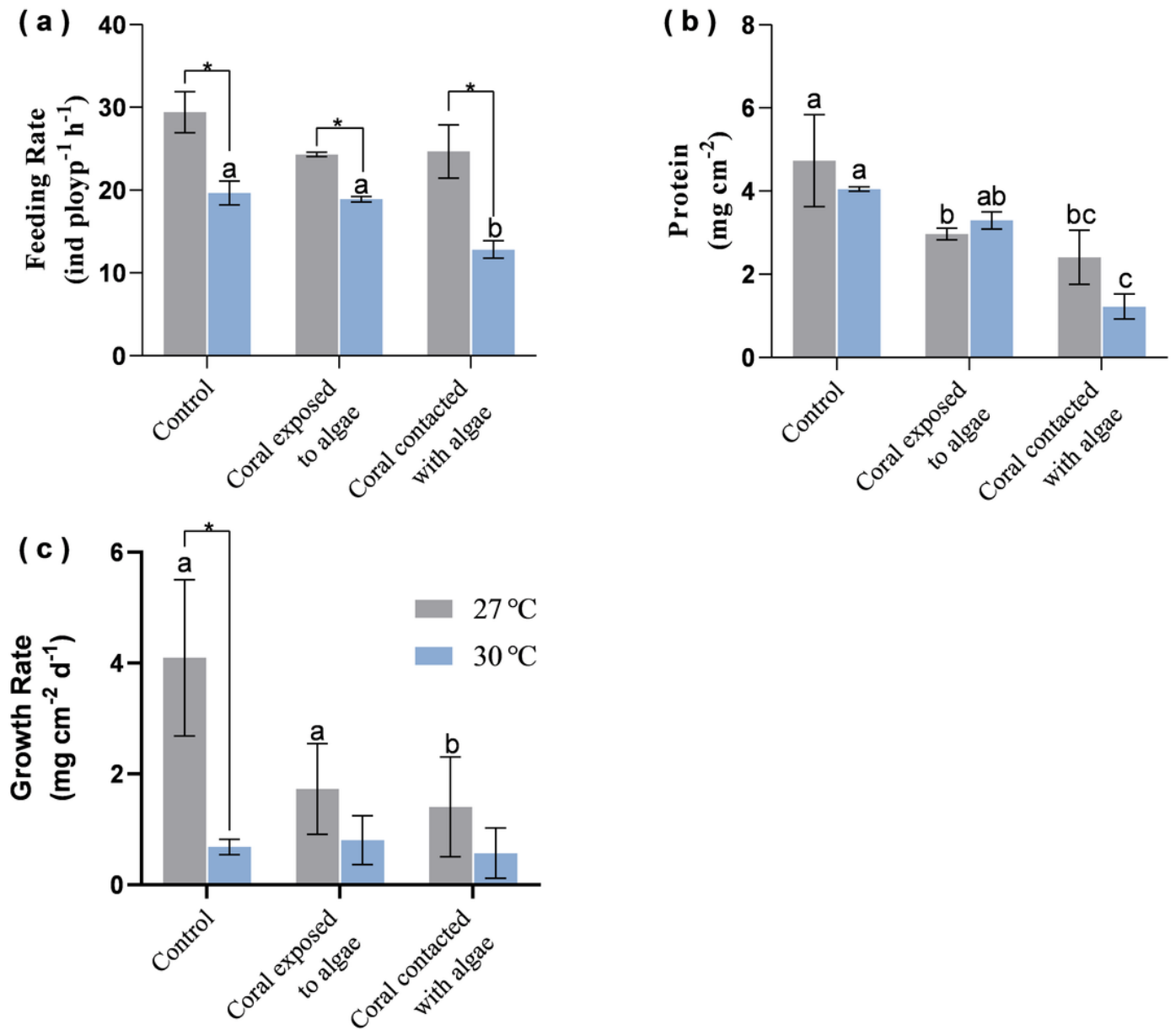


Figure 3

The effect of different temperatures of 27 °C (grey) and 30 °C (blue) on the (a) feeding rate, (b) protein and (c) growth rate of macroalgae-treated corals after 4 weeks of the experiment. Different letters indicate that there are significant differences between macroalgae treatments at the same temperature ($P < 0.05$), * indicates that there are significant differences between different temperatures ($P < 0.05$). Data are expressed in terms of the mean $\pm$ standard deviation, $n=3$.

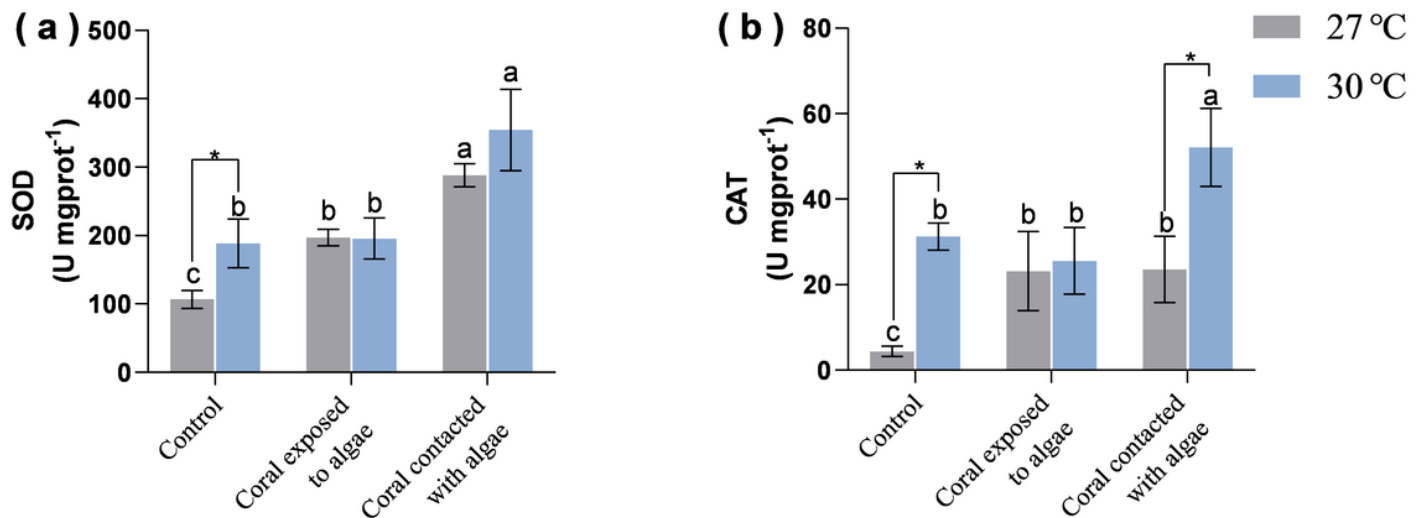


Figure 4

The effect of different temperatures of 27 °C (grey) and 30 °C (blue) on the (a) SOD, (b) CAT of macroalgae-treated corals after 4 weeks of the experiment. Different letters indicate that there are significant differences between macroalgae treatments at the same temperature ($P < 0.05$), * indicates that there are significant differences between different temperatures ($P < 0.05$). Data are expressed in terms of the mean $\pm$ standard deviation, $n=3$.

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